CHAPTER TWENTY-ONE

Integrating trait-mediated effects and non-trophic interactions in the study of biodiversity and ecosystem functioning

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The need to consider trait-mediated effects and non-trophic interactions in the study of biodiversity and ecosystem functioning

The relationship between biodiversity and ecosystem functioning has emerged as a central issue in ecology during the past two decades because of increasing concerns about the potential ecological and societal consequences of current biodiversity loss (Loreau *et al.* 2001; Naeem *et al.* 2009; Loreau 2010). Biological invasions are one of the main drivers of this biodiversity loss as human activities contribute to accelerate introductions of exotic species in many of the world's ecosystems, with considerable economic impacts (Williamson 1996; Mooney and Hobbs 2000). Although the effects of biodiversity loss on ecosystem functioning have now been studied in a wide range of organisms and ecosystems (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006; Naeem *et al.* 2009), most experimental and theoretical studies have considered either competitive communities at a single trophic level or relatively simple food webs (Duffy *et al.* 2007). The only direct species interactions considered in these studies are trophic interactions, and the only indirect species interactions considered are density-mediated interactions (for instance, exploitation competition). Similarly, the impacts of biological invasions on native ecosystems and the relationship between biodiversity and invasion resistance have been mainly studied in experimental plant communities (e.g., Kennedy *et al.* 2002) and models that consider a single type of species interactions, either competition (e.g., Case 1990; Byers and Noonburg 2003) or trophic interactions (e.g., Law and Morton 1996).

Although there is growing recognition of the significance of non-trophic and trait-mediated interactions in communities and ecosystems (Bolker *et al.* 2003; Bruno *et al.* 2003), these interactions are still poorly studied theoretically, and we still know little about general patterns and mechanisms. Ecosystems are much more than mere food webs; they are complex systems that involve multiple

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forms of interactions and multiple ecological networks (Ings *et al.* 2009; Olff *et al.* 2009). Recent experiments have showed that non-trophic interactions, such as facilitation and habitat modification (Mulder *et al.* 2001; Cardinale *et al.* 2002; Rixen and Mulder 2005), play an important role in ecosystem functioning, and that different kinds of species interactions typically co-occur in natural ecosystems (Callaway and Walker 1997). Very few theoretical studies have explored the role of non-trophic interactions in ecosystems, and most of these studies consider only one kind of species interaction, in particular mutualism. But simple models of mutualism do not respect the physical principle of mass conservation, and hence often lead to unrealistic explosive systems (Ringel *et al.* 1996). Therefore, an important current challenge is to develop theories and models to provide generalizations on the role of non-trophic and trait-mediated interactions in the maintenance of biodiversity, in ecosystem functioning, and in the relationship between biodiversity and ecosystem functioning.

Here we present an interaction web model that includes all types of direct species interactions, both trophic and non-trophic (interference competition, mutualism, exploitation, commensalism, amensalism), as well as all types of indirect effects, be they density-, trait- or habitat-mediated. Our model also satisfies mass balance constraints, which allows study of aggregate ecosystem properties in a consistent manner. Non-trophic interactions are added to a food web through trophic interaction modifications, a form of trait-mediated effects. We analyse this model numerically, and mimic a community assembly process of successive species introductions, following Loreau *et al.*'s (2001) recommendation to study the relationship between biodiversity and ecosystem functioning with a dynamical approach. We then study the relationships that emerge from community assembly between species diversity, the strength and prevalence of non-trophic effects, and a range of ecosystem properties, including the biomass and production of the various trophic levels, invasion resistance, and robustness to resident species extinctions due to invasions. We compare the results obtained for full interaction webs with those obtained for simple food webs without non-trophic interactions, and we further compare our theoretical predictions with some empirical data from competitive plant communities and food webs. The description of the model and the results on the effects of non-trophic interactions on ecosystem functioning and its relationship with biodiversity are summarized from Goudard and Loreau (2008); all the other sections present entirely new material.

Different kinds of indirect effects in ecosystems

Density-mediated indirect effects versus trait-mediated indirect effects

Indirect effects are usually classified into two types (Abrams, 1995): (1) density-mediated indirect effects, which act through changes in species

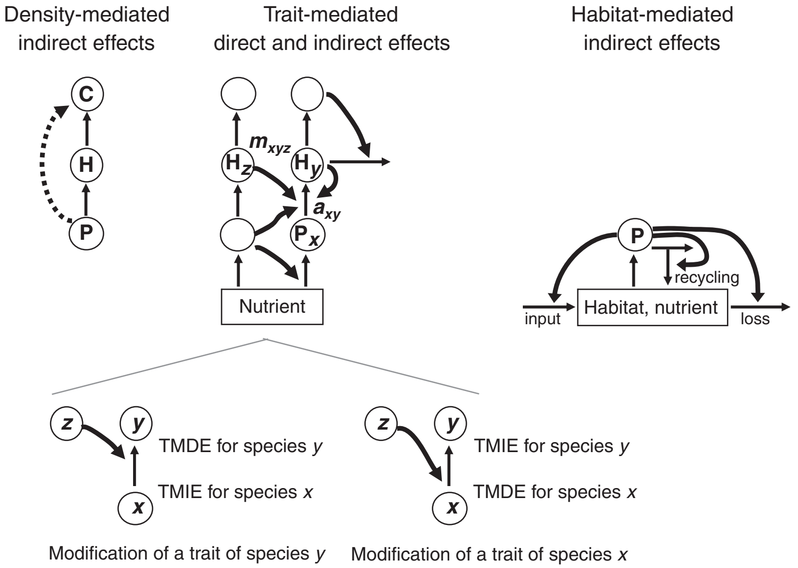

Figure 21.1 A classification of indirect effects. Examples of density-mediated indirect effects, trait-mediated direct (TMDE) and indirect (TMIE) effects, and habitat-mediated indirect effects. The latter two types of effects show the importance of interaction modifications and ecosystem engineering.

densities and propagate along a chain of direct interactions (e.g., indirect competition by exploitation of a shared resource); (2) trait-mediated indirect effects (TMIEs), which are caused by changes in species traits and may affect several species simultaneously (Fig. 21.1). TMIEs can take a variety of forms, such as non-lethal effects of a predator on its prey. A number of recent contributions have discussed methodological approaches to detect and quantify these effects and some of their potential pitfalls (Werner and Peacor 2003; Schmitz *et al.* 2004; Okuyama and Bolker 2007; Abrams 2007).[1]

Interaction modifications

Interaction modifications (Wootton 1994; Arditi *et al.* 2005) are modifications of an interaction by a species. We can consider two types of interaction modifications (Figs 21.1, 21.2): (1) the modification of an interaction between two species by a third species (for instance, a non-trophic modification of a trophic interaction) through some behavioural (e.g., interference) or chemical (e.g., allelopathy) effect; (2) the modification of an interaction between a species and an abiotic factor. Both types generate trait-mediated effects. Although interaction modifications were regarded by Wootton (1994) as a class of indirect effects, they may be viewed as either direct or indirect trait-mediated effects (Abrams 1995). If species *z* changes a

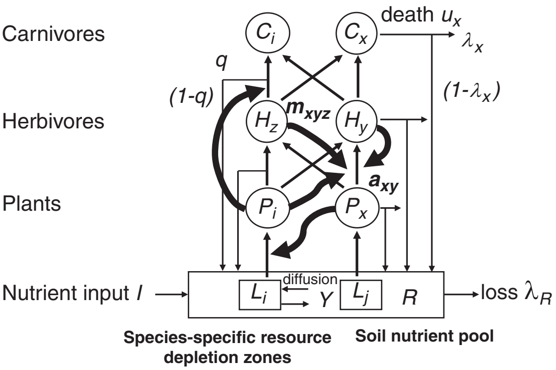

Figure 21.2 The interaction web model. Solid thin arrows represent nutrient flows. For clarity of the figure, flows of non-assimilated nutrient returned to the soil nutrient pool during consumption by carnivores and herbivores are represented only on the left trophic chain, while flows of nutrient either recycled or lost from the ecosystem following death are represented only on the right trophic chain. Thick lines represent interaction modifications, a form of trait-mediated effect. Only five examples of interaction modifications are represented here for the sake of clarity. For instance, herbivore species H_z modifies the trophic interaction between herbivore species H_y and plant species P_x with a magnitude of interaction modification m_{xyz}. The modification of the nutrient flow between plant species P_i and its species-specific resource depletion zone L_i corresponds to intraspecific competition or facilitation.

trait of species x, for instance the resistance of a plant x to predation by a herbivore y, then species z has an indirect effect on species y and an direct effect on species x (Fig. 21.1). If species z changes traits of both species x and y simultaneously, however, then species z has direct effects on both species x and y. Habitat modification always generates indirect effects; for instance, a dense habitat may allow prey to hide and avoid predators or, conversely, predators to hide and better hunt prey. Thus, a trait-mediated effect is a modification of a biotic parameter of a species, and may be either direct or indirect, whereas a habitat modification is a modification of an abiotic factor that has an indirect effect on all the species that are affected by this factor.

Density-, trait- and habitat-mediated indirect effects

Therefore it may be useful to extend Abrams's (1995) definitions to include three types of indirect effects in ecosystems (Fig. 21.1): (1) *density-mediated biotic indirect effects*, i.e., indirect effects that occur through changes in the density of a transmitter species; (2) *trait-mediated biotic indirect effects*, i.e., indirect effects that occur through changes in the traits of a transmitter species; and (3) *habitat-mediated indirect effects* i.e., indirect effects that occur through modification of the physical and chemical habitat. TMIEs are also associated with *trait-mediated direct effects*.

This extension of Abrams's definitions allows us to include *ecosystem engineers* (Jones *et al.* 1994) as vehicles of trait- and habitat-mediated indirect effects. By modifying their physical environment, ecosystem engineers directly or indirectly modify the availability of resources for other species, and thus create many non-trophic species interactions. Autogenic engineers change the environment by modifying their own structure, i.e., their living or dead tissues (e.g., cyanobacteria biofilms, wood structure of forest trees). Allogenic engineers change the environment by transforming living and non-living materials from one physical state to another (e.g., earthworms, bioturbation).

Species that modify trophic interactions can be regarded as ecosystem engineers because they modify a trophic resource flux, either directly through their own materials or indirectly by transforming materials. For instance, the plant cover of the invasive species *Eichhornia crassipes* creates refuges for mosquito larvae, thereby decreasing the strength of their trophic interaction with their predators. Species that modify an abiotic parameter (e.g., light intensity, recycling rate, water fluxes such as infiltration, evaporation and runoff) are also ecosystem engineers because they modify an abiotic resource flux or the control of a resource by an abiotic factor.

An interaction web model that includes non-trophic interactions and trait-mediated indirect effects

Building the model

Our interaction web model (Fig. 21.2) extends the food web model developed by Thébault and Loreau (2003) for a nutrient-limited ecosystem with three trophic levels by adding non-trophic modifications of trophic interactions. The model respects the principle of mass conservation, and allows a wide range of non-trophic interactions to occur. A complete description can be found in Goudard and Loreau (2008).

The key feature of the model is the potential for each species z to modify the trophic interaction between any two species x and y (including itself), and thereby to increase or decrease their per capita population growth rate or fitness. These interaction modifications are non-trophic modifications of trophic interactions, and are thus trait-mediated biotic effects (Fig. 21.2). The non-trophic effect of a species z on the interaction between species x and y depends on both its biomass X_z and a magnitude of interaction modification m_{xyz}. μ_{xy} is the non-trophic coefficient: it is the total non-trophic effect of all the $3S$ species in the ecosystem (S species per trophic level) on the trophic interaction between species x and y. Thus, the realized consumption rate of species y by species x, $a_{xy}\mu_{xy}$, is the product of the potential consumption rate

a_{xy}, i.e., the intensity of the trophic interaction between predator species x and prey species y ($a_{xy} \geq 0$ and $a_{xy} = -a_{yx}$), and the non-trophic coefficient μ_{xy} :

$$c_{xy} = a_{xy}\mu_{xy}$$

$$\text{where } \mu_{xy} = \exp\left(\sum_{z=1}^{3S} m_{xyz} \log\left(1 + b_z X_z\right)\right) = \prod_{z=1}^{3S} \left(1 + b_z X_z\right)^{m_{xyz}} \tag{21.1}$$

The function that describes non-trophic effects in this equation was chosen such that it satisfies several conditions. First, it is a strictly increasing function of both the magnitude of interaction modification m_{xyz} and biomass X_z. Second, the non-trophic coefficient μ_{xy} is unchanged if either $m_{xyz} = 0$ or $X_z = 0$. Third, the magnitude of interaction modification is symmetrical ($m_{xyz} = m_{yxz}$) to maintain mass balance. Fourth, the non-trophic coefficient must be strictly positive whatever the sign of the interaction modification, so that the sign of the realized consumption rate does not change, and thus the nutrient flow between species x and species y is not reversed. Fifth, the non-trophic coefficient must be larger than 1 if the interaction modification is positive, and smaller than 1 if the interaction modification is negative. Thus, each species z can affect any two species x and y by increasing ($\mu_{xy} > 1$) or decreasing ($\mu_{xy} < 1$) the realized consumption rate of species y by species x. The coefficient b_z converts biomass X_z into a dimensionless number; we used $b_z = 1$ for simplicity in our simulations.

In the absence of trait-mediated effects, the only direct species interaction is predation, and our interaction web reduces to a food web. When interaction modifications are added, all types of species interactions are present (competition, mutualism, exploitation, commensalism, amensalism), including negative or positive intraspecific effects ($m_{xzz} \neq 0$ for species z). Our model, however, respects the principle of mass conservation since interaction modifications affect the material flow between a resource and a consumer in the same way for both species. The model also includes nutrient cycling and a volume allocation rule in the soil, allowing functional complementarity between plant species (Loreau 1998).

We constrained the model as little as possible to explore its general properties. Accordingly, we randomly assigned the various biological parameters (potential consumption rates, intensities of interaction modifications, death rates, non-recycled proportions of nutrient) to a regional pool of species from a uniform distribution within appropriate intervals, and let the local ecosystem assemble spontaneously. Each simulated ecosystem resulted from an assembly process involving successive introductions of species picked at random from the regional species pool and species eliminations as a result of local interactions. Despite constant species turnover, aggregate ecosystem properties turned out to stabilize relatively quickly in a quasi-stationary regime.

Assessing ecosystem properties and species interactions

We analysed the effects of species richness and non-trophic interactions in the regional species pool on a wide range of community and ecosystem properties in the local ecosystems resulting from the assembly process, in particular total local species richness, local species richness of each trophic level, proportions of the various types of net species effects and interactions, interaction web connectance, total biomass, biomass of each trophic level, production of each trophic level, invasion resistance, and robustness to resident extinctions. Non-trophic interactions were manipulated by varying the connectance and maximal magnitude of interaction modifications in the regional species pool. The *non-trophic connectance* of the regional species pool, defined as the probability that a species modifies the trophic interaction between any two species, measures the connectance of trait-mediated effects. Food web connectance was kept constant in our simulations. The magnitude of interaction modification, m_{xyz}, was randomly taken between a maximum value called *maximal non-trophic magnitude* and a symmetrical minimum (minus maximal non-trophic magnitude). This maximal non-trophic magnitude represents the maximal value of trait-mediated effects.

Since all species can affect other species in a large number of different ways, we defined *net species effects* (facilitation, inhibition, or no effect) and *net species interactions* (mutualism, competition, exploitation, commensalism, amensalism or neutral interaction) phenomenologically. The net species effect (sum of trophic and non-trophic effects) of species g on species i, E_{ig}, was measured by the partial derivative of the growth rate of species i with respect to the biomass of species g:

$$E_{ig} = \frac{\partial\left(\frac{dX_i}{dt}\right)}{\partial X_g} \tag{21.2}$$

This measure includes trophic and non-trophic direct effects, as well as, potentially, TMIEs. If $E_{ig} > 0$, the effect of species g on species i is facilitative. If $E_{ig} > 0$ and $E_{gi} > 0$, the interaction between species i and g is mutualistic. Local *interaction web connectance* was measured as the proportion of non-neutral species interactions among all possible species interactions. We called *mean value of facilitation* (*inhibition*) the mean value of positive (negative) net species effects. We considered only interspecific species effects and interactions, without taking into account the effect of a species on itself (E_{ii}).

We also measured invasion resistance and robustness to resident extinctions following species introductions in the assembled local ecosystems. An invasion attempt was considered successful if the introduced species was able to increase when rare (Kokkoris *et al.* 1999). Invasion failure probability was computed as the ratio between the cumulated number of failed invasion attempts and the number of introductions from the beginning of the simulation. *Invasion resistance* was then measured by the short-term failure probability of an introduced species, obtained by recording the presence or absence of the introduced species 100 time steps after the introduction event. *Robustness to resident extinctions* following species introductions was measured by recording the number of resident species extinctions caused by an introduced species during the 100 time steps that followed its introduction. The smaller the number of resident extinctions, the higher the ecosystem's robustness to resident extinctions.

The interdependence between species richness and species interactions

Effect of species richness on the prevalence of species interactions

Although the relationship between trophic connectance and species richness has been well studied in food webs (Martinez 1992; Montoya and Solé 2003), we lack knowledge about the connectance of ecosystems considered as full interaction webs. Recent experimental studies suggest that the prevalence of species interactions such as facilitation may increase with species richness (e.g., Cardinale *et al.* 2002). Our model predicts that interaction web connectance increases with species richness and that the proportions of the various types of species effects and species interactions depend on species richness (Fig. 21.3a, b). A higher species richness increases the number of trophic links of a given species (as long as consumers are not strict specialists), which increases the probability for this species to have at least one trophic link modified by any other species in the web, and thus the probability for each species to interact with any other species. The fact that interaction web connectance tends to 100% here (Fig. 21.3a), however, is due to the assumption that consumers are generalists in our model. Other food web configurations may lead to smaller upper limits.

Effect of species richness on the strength of species interactions

The analysis of natural food webs (Neutel *et al.* 2002) suggests that natural ecosystems are characterized by a large number of weak interactions and a small number of strong interactions. Our model predicts that the strength of species effects (interspecific facilitation and inhibition) decreases with species

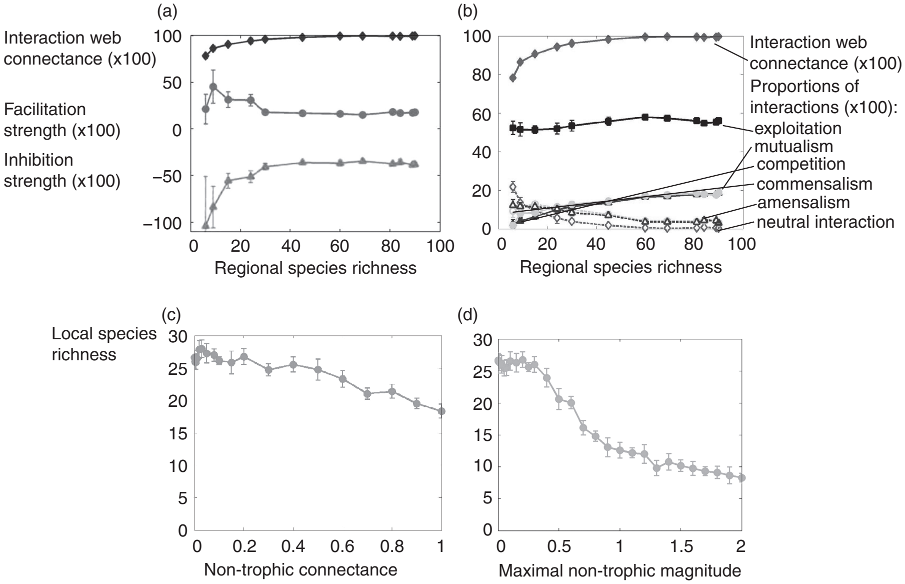

Figure 21.3 Reciprocal effects between species richness and species interactions: results from the interaction web model. Strength of species effects (a), interaction web connectance and proportions of species interactions (b) in the community as a whole in the quasi-stationary regime as functions of regional species richness (non-trophic connectance = 0.2, maximal non-trophic magnitude = 0.2) in interaction webs. Panel (a) shows means and standard deviations of facilitation strength, inhibition strength, and interaction web connectance. Panel (b) shows the means and standard deviations of interaction web connectance and the proportions of mutualism, competition, exploitation, commensalism, amensalism, neutral interactions. Total local species richness in the quasi-stationary regime as a function of non-trophic connectance (c, regional species richness = 45, maximal non-trophic magnitude = 0.2) and maximal non-trophic magnitude (d, regional species richness = 45, non-trophic connectance = 0.2).

richness (Fig. 21.3a), in agreement with competition models (Kokkoris *et al.* 1999, 2002). Thus, species-rich interaction webs are more connected but have weaker species interactions on average. Their lower interaction strength is probably what allows them to maintain a high diversity and connectance, in agreement with previous theory (May 1972; Kokkoris *et al.* 1999, 2002).

Effect of interaction modifications on the prevalence and strength of species effects

Our model shows that both non-trophic connectance and maximal non-trophic magnitude affect the prevalence, strength and variability of species effects. In particular, non-trophic connectance increases interaction web connectance and the proportions of non-trophic species interactions such as mutualism and competition (Goudard and Loreau 2008).

Effect of interaction modifications on local species richness

Our model also predicts that high levels of non-trophic connectance and maximal non-trophic magnitude have negative effects on local species richness (Fig. 21.3c, d), in particular at the plant trophic level. Interaction modifications are likely to generate strong constraints on species coexistence. The species selected during the assembly process have higher realized consumption rates on average, which makes them more efficient but also more competitive (Goudard and Loreau 2008).

These results emphasize the mutual interdependence between species richness and species interactions. Species richness affects the prevalence and strength of species interactions, just as the latter affects species richness. This interdependence makes the relationships between ecosystem structure (species richness and species interactions) and ecosystem functioning more complex (see below).

Effects of non-trophic interactions on ecosystem functioning and its relationship with biodiversity

Effects of non-trophic interactions on biomass and production

Our model predicts that biomass and production at all trophic levels tend to decrease as either non-trophic connectance or maximal non-trophic magnitude increases (Fig. 21.4a, b). Two factors explain this counterintuitive result (Goudard and Loreau 2008). First, non-trophic connectance increases the mean realized consumption rates of the various species, which eventually contributes to decrease biomass and production. Second, it also increases the proportions of inhibition and competition more than those of facilitation and mutualism in plants.

In contrast, Arditi *et al.* (2005) found an increasing proportion of 'super-efficient' systems as the magnitude of interaction modifications increases in another interaction web model. These contrasting predictions are likely explained by two key differences between the two models. The first difference is the level of trophic connectance among species, which was relatively low in their model and high in ours. We allowed all species to be more or less generalist consumers, and this increases the potential for resource overexploitation. The second difference concerns the way interaction modifications are represented in the two models: interaction modifications combined additively in their model, and multiplicatively in our model (Equation (21.1)). Non-trophic effects can increase resource consumption more strongly in our model, again enhancing the potential for resource overexploitation. The two models

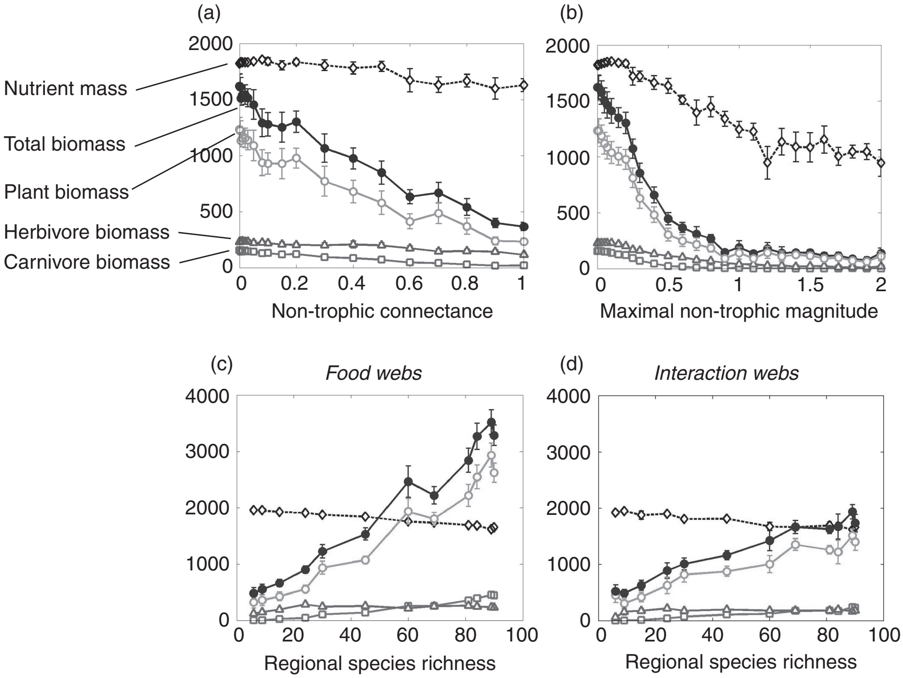

Figure 21.4 Effects of non-trophic interactions on biomass and the biodiversity–biomass relationship in food webs and interaction webs: results from the interaction web model. Biomass in the quasi-stationary regime as a function of non-trophic connectance (a, regional species richness = 45, maximal non-trophic magnitude = 0.2) and maximal non-trophic magnitude (b, regional species richness = 45, non-trophic connectance = 0.2) in interaction webs. Biomass in the quasi-stationary regime as a function of regional species richness in food webs (c, non-trophic connectance = 0, maximal non-trophic magnitude = 0) and in interaction webs (d, non-trophic connectance = 0.2, maximal non-trophic magnitude = 0.2). The various curves show the means and standard deviations of total biomass, nutrient mass, plant biomass, herbivore biomass and carnivore biomass.

highlight different potential outcomes that might occur in natural ecosystems. Experimental tests of these contrasting predictions are now needed to move forward on this topic. We still have very limited knowledge of the mechanisms and consequences of non-trophic interactions, trait-mediated effects and habitat-mediated effects in ecology. In particular, their effects on ecosystem properties such as biomass and production deserve much more attention.

Relationship between biodiversity and ecosystem functioning

Our model predicts that total biomass and biomass at each trophic level increase with regional species richness both in the absence and presence of non-trophic interactions (Fig. 21.4c and d), with a bottom-up control of plants on carnivores, a top-down control of carnivores on herbivores and a better exploitation of the limiting nutrient by plants. Production at all trophic levels increases with regional species richness (Goudard and Loreau 2008). Biomass and production, however, increase less rapidly with species richness in interaction webs with non-trophic interactions than in food webs without non-trophic interactions. This is explained again by the fact that non-trophic interactions tend to increase the average realized consumption rate, and that this effect becomes stronger as species richness increases. Thus, species become more efficient at exploiting resources, but also more competitive, and this increases the probability of observing resource overexploitation. Our model predicts positive biodiversity–ecosystem functioning relationships in both food webs and interaction webs, due to the same mechanisms, but with a strong impact of non-trophic interactions on the shape of the diversity–biomass relationship (Goudard and Loreau 2008).

Thus, our interaction web model allows a generalization of the positive biodiversity–ecosystem functioning relationship typically found in simple single-trophic-level ecosystems to complex interaction webs resulting from a long assembly process. Interestingly, we did not observe the unimodal relationships predicted under some conditions by existing theory on multitrophic ecosystems (Thébault and Loreau 2003; Ives *et al.* 2005; Loreau 2010). This highlights the difference between potential ecosystem configurations and those actually realized at the outcome of an assembly process.

Effects of non-trophic interactions on ecosystem responses to biological invasions

Effects of biodiversity on invasion resistance and robustness to resident extinctions

Our model predicts that species introductions induce extinctions of resident species, and that the number of these extinctions increases, while biomass and production decrease, as the frequency of species introductions increases. Thus it confirms empirical evidence for the ecological impacts of species introductions, which are widely regarded as one of the main drivers of species extinctions, and hence of loss of ecosystem services.

In turn, biodiversity affects the ability of ecosystems to resist invasions. Experimental studies conducted at local scales and controlling for abiotic extrinsic factors show that species richness increases invasion resistance in plant communities (e.g., Kennedy *et al.* 2002), in contrast to empirical studies at regional scales, which often show positive or negative relationships between species richness and invasion resistance (e.g., Stohlgren *et al.*

1999) because of covarying extrinsic factors. Models of competitive communities and food webs have usually showed positive relationships between biodiversity and invasion resistance, at least at small scales in the absence of covarying extrinsic factors (e.g., Case 1990; Law and Morton 1996; Byers and Noonburg 2003), but no theoretical or empirical study is available on the effects of other non-trophic interactions on the relationship between biodiversity and invasion resistance.

Our model also predicts that regional species richness increases invasion resistance (Fig. 21.5a), thus extending previous findings to complex interaction webs. This result is probably explained by an increased resource-use complementarity in species-rich ecosystems, which decreases the amount of resources available to invaders, and by an increased probability of including natural enemies of invaders or species with traits similar to invaders.

Few experimental (Pfisterer *et al.* 2004) or theoretical (Case 1990) studies have investigated the effect of species richness on ecosystem robustness to resident extinctions. Our model predicts that species richness increases robustness to resident extinctions in species-rich ecosystems (Fig. 21.5a). The decrease in the number of resident extinctions at a high regional species richness was mostly due to a decrease in the number of consumer extinctions (figure not shown).

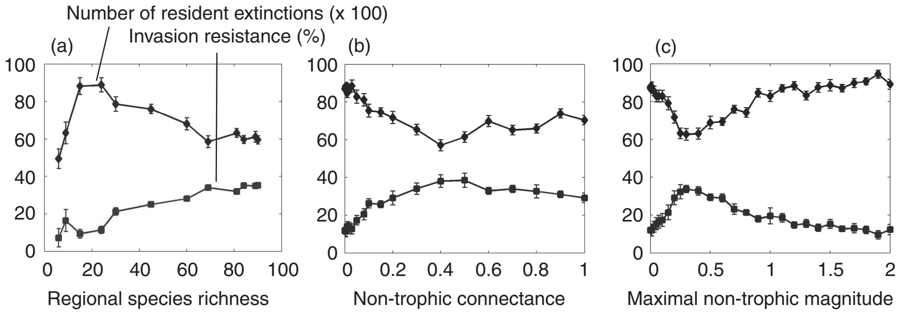

Figure 21.5 Species richness, non-trophic effects and biological invasions: results from the interaction web model. Invasion resistance and robustness to resident extinctions as functions of regional species richness (a, non-trophic connectance = 0.2, maximal non-trophic magnitude = 0.2), non-trophic connectance (b, regional species richness $3S = 45$, maximal non-trophic magnitude = 0.2) and maximal non-trophic magnitude (c, regional species richness $3S = 45$, non-trophic connectance = 0.2). Lower curves show the mean and standard deviation of invasion resistance (short-term failure probability × 100); upper curves show the mean and standard deviation of the number of resident extinctions during an interval of 100 time steps (× 100) in interaction webs.

Effects of non-trophic interactions on invasion resistance and robustness to resident extinctions

Few studies have explicitly explored the effects of species interactions on invasion resistance (Case 1990; Kokkoris *et al.* 1999) and robustness to resident extinctions. Experiments and theory suggest that trophic connectance strongly affects robustness to cascading extinctions due to primary species loss in food webs (Law and Blackford 1992; Thébault *et al.* 2007). Our interaction web model predicts that both resistance to invasions and robustness to extinctions due to invasions depend strongly on species interactions. Interestingly, intermediate values of non-trophic connectance and magnitude of interaction modifications maximize invasion resistance and robustness to resident extinctions (Fig. 21.5b and c).

The reciprocal interaction between ecosystem properties and biological invasions

Our model shows that biological invasions alter the structure and functioning of ecosystems, by inducing loss of species, biomass and production, especially when species introductions are frequent. Since ecosystem functioning depends on its structure and diversity (species richness, species interactions), invasive species can alter ecosystem functioning both directly and indirectly. But ecosystem structure – species richness and the prevalence and strength of species interactions – also conditions the probability of success of introduced species and their impacts. For instance, Mitchell *et al.* (2006) studied introduced plant species that modify interactions between native species (exploitation, competition, mutualism), and these changes in ecosystem structural properties had a feedback effect on the success of the introduced species. Thus, structural and functional ecosystem properties and biological invasions are strongly interdependent.

Our model shows that the positive relationships between biodiversity and invasion resistance and between biodiversity and robustness to resident extinctions are partly explained by the diversity-dependence of species interactions and the impacts of species interactions on invasion resistance and robustness to resident extinctions. These results suggest that species interactions, and especially non-trophic effects, trait-mediated effects and habitat-mediated effects, should receive more attention in the study of the relationship between ecosystems and biological invasions. Understanding how species interactions affect the success of biological invasions and the damage they cause is likely to improve our ability to avoid undesirable invasions and their associated costs.

The complex relationship between ecosystem structure and functioning

The structure of an ecosystem describes the elements it contains and the relationships between these elements. 'Ecosystem structure', thus, is a generic term that includes species diversity, species interactions and abiotic factors. In contrast, the term 'ecosystem functioning' denotes the various processes and properties that make the ecosystem operate as an entity; these processes and properties include biomass, production, nutrient cycling, ecosystem stability and invasion resistance.

Our results show consistently that ecosystem structure and ecosystem functioning are strongly interdependent (Fig. 21.6). They further predict strong relationships between various structural ecosystem properties as well as between various functional ecosystem properties. In particular, species diversity affects the nature and prevalence of species interactions, and, reciprocally, species interactions affect species diversity, creating a complex web of relationships between ecosystem structure and ecosystem functioning (Fig. 21.6). Biodiversity has not only direct effects on ecosystem processes, but also indirect effects through its effects on the strength and

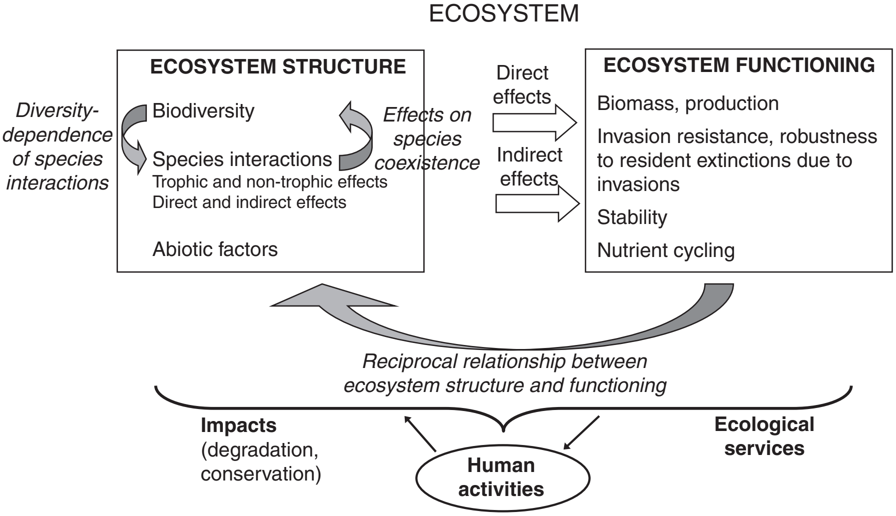

Figure 21.6 Importance of non-trophic interactions and trait-mediated effects in the relationship between ecosystem structure and functioning. White arrows show the importance of non-trophic interactions and trait-mediated effects for ecosystem functioning. Grey arrows show the complexity of the ecosystem structure–functioning relationship due to the interdependence between biodiversity and species interactions and the reciprocal effect of ecosystem functioning on ecosystem structure.

prevalence of species interactions. Similarly, species interactions have direct effects on ecosystem functioning, but also indirect effects through their effects on species coexistence. Therefore, biodiversity–ecosystem functioning relationships are much richer and more complex in complex interaction webs than in relatively simple plant communities or even in food webs, not only because they take into account non-trophic effects and trait-mediated or habitat-mediated indirect effects, but also because of the additional interdependence that these effects generate between species richness and species interactions. It would be interesting to explore further the relationships between abiotic factors, ecosystem structure and ecosystem functioning.

Incorporating non-trophic interactions, trait-mediated effects and habitat-mediated effects in theoretical ecology

Our theoretical work, together with recent empirical evidence, strongly suggests that non-trophic interactions, trait-mediated effects and habitat-mediated effects play an important role in ecosystems and should be taken into account in experimental and theoretical ecology. It also suggests specific hypotheses that would deserve to be tested experimentally. In particular, it would be interesting to test the effects of species richness predicted by our model on the strength and prevalence of species interactions in experimental ecosystems. It would also be useful to study experimentally the impacts of species interactions, and especially non-trophic, trait-mediated and habitat-mediated effects, on ecosystem processes and properties, such as biomass and production at various trophic levels, invasion resistance and robustness to resident extinctions due to biological invasions. In order to study the impacts of non-trophic effects, it would likely be easier to manipulate the number of species interactions in microcosms that have the same species richness, than the strength of these interactions.

Because our interaction web model incorporates non-trophic interactions in the form of interaction modifications, it could easily be applied or extended to the study of ecosystem engineering, either using specific forms of non-trophic modifications of trophic interactions or through modifications of abiotic parameters such as those that govern the input, recycling and loss of nutrients. Ecosystem engineers can modify ecosystem structural properties, such as species richness, composition and interactions, as well as ecosystem functional processes such as primary production (Badano *et al.* 2006; Zhu *et al.* 2006). Our model could also be applied straightforwardly to ecological studies of manipulative parasites. Manipulative parasites are perfect examples of interaction modifiers: by altering their host's behaviour, they affect the strength of the trophic links involved in their transmission as well as other trophic interactions (Lefèvre *et al.* 2009). Thus, the approach we have presented here has great potential in addressing a wide range of trait-mediated and habitat-mediated effects in theoretical ecology.

Conclusion

Our chapter highlights the importance of species interactions, in particular non-trophic interactions, in the structural and functional properties of ecosystems and in the relationships between biodiversity and ecosystem functioning. Species richness affects the nature, prevalence and strength of species interactions, and these in turn affect species richness, thus making the mechanisms of the biodiversity–ecosystem functioning relationships more complex in interaction webs than in classical food webs or competitive communities. Non-trophic interactions, trait-mediated effects and habitat-mediated effects should be given more attention in studying the relationships between ecosystem structural properties (such as species richness, species interactions and abiotic factors) and ecosystem functional properties (such as biomass, production, nutrient cycling, ecosystem stability and invasion resistance) to understand better the ecological consequences of biodiversity loss and predict the impacts of environmental changes, including biological invasions, on ecosystem services.

Note

1. Abrams (2007) also notes a gradual terminological shift from ‘indirect effect’ to ‘indirect interaction’ in the recent literature. We keep here the initial distinction between ‘indirect effect’ as a directional pathway of effects from one species to another and ‘indirect interaction’ as reciprocal action between two species through some transmitter.

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