Chapter 12

Emergence of complex food web structure in community evolution models

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12.1 A difficult choice between dynamics and complexity?

A food web is defined as the set of species linked by trophic interactions in a given ecological community. As such, it contains only a subset of the many possible types of ecological interactions and it is a very simplified representation of natural communities. In spite of this simplification, food webs appear to be highly complex networks, if only because any natural system contains several hundreds of species, most of them preying upon or being preyed upon by many others (e.g. Polis 1991). Many food web data sets are now available (Baird and Ulanowicz 1989; Warren 1989; Hall and Raffaelli 1991; Martinez 1991; Polis 1991; Goldwasser and Roughgarden 1993).

It is possible to divide such data sets into two broad categories. The first category will be called 'binary' data sets. Binary data sets simply list species in the food web and the trophic interactions among these species. They do not contain any information in terms of species abundances or trophic interaction strength. Food web theory that deals with binary data sets is primarily interested in:

• comparing food web networks with other types of networks such as protein, genetic, social, neuronal and communication networks (Barabasi and Albert 1999; Amaral and Ottino 2004; Milo *et al*. 2004; Grimm *et al*. 2005; Proulx *et al*. 2005)
• from this comparison, determining properties that are specific to food webs as compared with other types of networks – for example, the fact

that food webs are small worlds (Martinez *et al*. 1999; Montoya *et al*. 2006), that they are built in compartments (Pimm 1979; Krause *et al*. 2003) and that they contain many loops (Polis 1991; Neutel *et al*. 2002), a lot of omnivores (Polis 1991), etc.
• finding simple models that would be able to reproduce these features; models such as the Cascade model (Cohen *et al*. 1990; Solow and Beet 1998), the Niche model (Williams and Martinez 2000) and the Nested Hierarchy model (Cattin *et al*. 2004) have been relatively successful in reproducing some of the patterns observed in these binary data sets.

Binary approaches to food webs have been used to draw conclusions about community structure (e.g. food web stability: Pimm 1979; Krause *et al*. 2003) or conservation issues (fragility of food webs to species removal: Dunne *et al*. 2002). In spite of these results, drawing conclusions from binary data sets, or from models that are built on them, to broad ecological issues has proved to be very controversial. Binary approaches have a number of shortcomings:

• descriptors used in binary approaches are highly dependent on species lumping (Solow and Beet 1998) and on the resolution of the data set (Winemiller 1990; Martinez 1991)
• properties measured on binary data sets do not describe the ecological properties of the community satisfactorily; for example, Paine (1980) criticized the use of connectance as derived from these data sets

• binary approaches generally describe foods webs at a given time, while food webs prove to be highly variable in time (Paine 1988)

• because they do not measure species abundances and interaction strength (Cohen *et al*. 1993a; Berlow *et al*. 2004), they are unable to deal with conservation issues (mostly based on species abundance) or functional aspects of ecosystems (such as energy and nutrient fluxes).

An obvious alternative to these high-diversity, static approaches is to describe the dynamics and evolution of species in small food web modules. This approach has been recently reviewed extensively by Fussmann *et al*. (2007). Theoretical studies that follow this approach often consider coevolution of two species (e.g. Levin and Udovic 1977; Saloniemi 1993; Abrams and Matsuda 1997; Loeuille *et al*. 2002; Dercole *et al*. 2006) or evolution of food web modules that contain a restricted number of species (Vermeij 1987; Abrams 1991, 1993; Abrams and Chen 2002; Yamauchi and Yamamura 2005). These models provide interesting insights into species coexistence (Yamauchi and Yamamura 2005) the strength of bottom-up or top-down controls (Loeuille and Loreau 2004), the conditions for the maintenance of intra-guild predation or omnivory (Krivan and Eisner 2003), the conditions for the stability of food web modules (Abrams and Matsuda 1997; Loeuille *et al*. 2002; Yamauchi and Yamamura 2005; Dercole *et al*. 2006), etc. It is unclear, though, how such mechanisms derived from a small number of species may be extended to natural ecosystems that are much more speciose and complex.

Thus, theory is abundant either when dealing with large systems but without dynamics or quantitative information, or when dealing with small dynamical systems in which populations and interactions are explicitly described. The remaining challenge is to develop frameworks that are able to deal with dynamical systems that contain a large number of species and that are able to account satisfactorily for the binary and quantitative aspects of food webs. This is a long-standing issue since Polis (1991) already stressed 16 years ago that theory (Pimm 1982; Pimm and Rice 1987; Cohen *et al*. 1990) was insufficient to tackle the complexity of natural systems.

One possible solution is the use of community assembly models, in which species are drawn from a predetermined regional pool (Post and Pimm 1983; Taylor 1988; Morton and Law 1997; Steiner and Leibold 2004). This type of model has provided useful information on the conditions for the maintenance of large, stable communities. An obvious limitation of these models is that, even when the pool of species is large, it is unable to account for novelties that arise through evolution, and that are potentially infinite. This shortcoming has been addressed by the recent development of evolutionary food web models (Caldarelli *et al*. 1998; Drossel *et al*. 2001; Christensen *et al*. 2002; Anderson and Jensen 2005; Loeuille and Loreau 2005; Ito and Ikegami 2006; Rossberg *et al*. 2006).

The Webworld model (Caldarelli *et al*. 1998; Drossel *et al*. 2001), for example, is based on a large number of traits that may mutate. Traits may be present or absent; thus, species are coded by vectors of 0s and 1s of a predefined length so that the set of species is still finite. An alternative is to base evolutionary models on a few key traits (Loeuille and Loreau 2005; Ito and Ikegami 2006), among which there are trade-offs that are either known or inferred from physiological or morphological constraints. An obvious candidate in the case of trophic interactions is body size. Body size has been suggested to play an important role in the structure of food webs (Cohen *et al*. 1993b, 2003; Neubert *et al*. 2000; Jennings *et al*. 2002a, b; Woodward and Hildrew 2002; Emmerson and Raffaelli 2004; Williams *et al*. 2004, Crumrine 2005). Confirmation of this importance has come from measures showing the tight relationship between the relative difference in body size between predators and prey and the strength of their interaction (King 2002; Jennings *et al*. 2002b; Emmerson and Raffaelli 2004). Body size has also been shown to be of importance for many other life-history traits (Kleiber 1961; Peters 1983; Byström *et al*. 2004; Jetz *et al*. 2004; Savage *et al*. 2004; Reich *et al*. 2006).

In this chapter, we summarize some of the properties of a community evolution model that is entirely based on the evolution of body size. The model shows that, starting with only one morph characterized by its body size, it is possible to obtain stable, complex food webs out of repeated

adaptive radiations. The results of the model are then compared with those of other evolutionary food web models to give an overview of possible uses of community evolutionary approaches in community ecology.

12.2 Community evolution models: mechanisms, predictions and possible tests

Community evolution models let entire communities emerge from the basic evolutionary processes of mutation and selection. These models start with one or a small number of species, and new morphs emerge out of repeated mutations. When a mutant is introduced in the system, the selection process comes into play to determine whether it is able to survive or not. The mutant may not survive:

• if its fitness when rare is lower relative to the fitness of its parent
• if its fitness when rare is larger, but demographic stochasticity prevents its invasion; this second possibility is not to be neglected – as mutants are initially rare, demographic stochasticity largely constrains the potential for their invasion.

If a mutant invades the community, several scenarios can follow this invasion:

• The most likely scenario is the extinction of the parent (resident), with the better adapted mutant simply replacing its parent.
• It is also possible that the mutant and the resident coexist. This occurs because fitness may be frequency dependent, i.e. while the mutant's fitness is initially larger (since it invades), this advantage of the mutant against the resident is lost when its frequency increases in the population. When this coexistence occurs, the evolutionary process increases the total diversity of the community.
• Another species of the community goes extinct. This may occur independently of the coexistence or replacement process described in the two previous paragraphs. Because the invasion of the mutant modifies the fitness of other species of the community, it is possible that one or several extinctions follow this invasion.

Community evolution models are in some ways very close to classical community assembly models, since these also contain invasion and selection processes. The main difference between the two types of models lies in the details of the invasion process. In community assembly models, species are introduced from an existing regional species pool (e.g. Post and Pimm 1983; Taylor 1988; Morton and Law 1997; Steiner and Leibold 2004). For this reason, the introduced species do not have to be functionally similar to species already present in the community. Trade-offs between species traits are generally not considered. The timing of the invasion is not constrained, and the diversity of the local species assemblage is bounded by the total number of species present in the regional species pool. By contrast, community evolution models have harsher invasion constraints. The timing of mutation depends on the number of newborn individuals and the probability of mutation per individual. Furthermore, mutations are supposed to have a small phenotypic effect, which means that the characteristics of the mutants are strongly correlated with the phenotypic trait of one of the existing species. Finally, when phenotypic effects are explicitly identified, it is possible to link them mechanistically to physiological or ecological benefits and costs. Therefore, such community evolution models account explicitly for evolutionary trade-offs, while the traits of invading species in community assembly models are often unconstrained, leaving open the question of how such traits emerge in the first place.

12.2.1 One or many traits?

Community evolution modelling is a rapidly growing branch of evolutionary ecology (Caldarelli *et al*. 1998; Drossel *et al*. 2001; Anderson and Jensen 2005; Loeuille and Loreau 2005; Ito and Ikegami 2006; Rossberg *et al*. 2006; Ito and Dieckmann 2007; Lewis and Law 2007). An important choice that governs the characteristics of these models concerns the number of traits and their identity. Although it is obvious that the ecology of species depends on many traits, the number of traits considered is traded off against the biological realism introduced by these traits.

12.2.1.1 Models in which species are defined by many traits

The first community evolution model, named the Webworld model (Caldarelli *et al*. 1998; Drossel *et al*. 2001), had a large number of traits. In this model, each species has a given number L of features (phenotypic traits) picked out of a pool of K traits that constrain the demography of the species and its interactions with other members of the community. A $K \times K$ matrix $[m_{i,j}]$ describes the efficiency of each species' trait against other species' traits. The sum of the matrix elements over the traits possessed by two interacting species yields the strength of their trophic interaction.

A second model inspired by the Webworld model is the Matching model, conceived by Rossberg *et al*. (2006). In this model, each species is characterized by a vector that determines its attack rate and a vector that determines its vulnerability. These vectors contain n components that describe the presence or absence of the trait for the species considered. The interaction strength between two species depends on the matching between the attack traits of one and the vulnerability traits of the other.

Finally, the Tangled Nature model (Christensen *et al*. 2002; Anderson and Jensen 2005) assumes that species interactions are determined by L loci, with two alleles for each locus (noted 1 and 0). The interaction between two species then depends on the allelic composition of the two species. The coupling between two species characterized by their genome is described by a non-symmetrical matrix, whose terms are non-zero with some predefined probability, and then drawn out of a uniform distribution in a predefined interval $[-c,c]$. Contrary to the other two above-mentioned models, the Tangled Nature model is not restricted to trophic interactions *a priori* and may incorporate any kind of interaction.

Both the Webworld and the Matching models have been tested against empirical data (Caldarelli *et al*. 1998; Rossberg *et al*. 2006). They are both successful at reproducing a number of food web structural patterns. They are also particularly useful in addressing the degree of generalism of predators.

12.2.1.2 Models with a limited number of traits

Body size is a key species trait that food web theory has often considered explicitly. Empirical data show that trophic interactions are heavily constrained by body size (Jennings *et al*. 2002b; Emmerson and Raffaelli 2004). In 90% of trophic interactions, the predator is larger than the prey (Warren and Lawton 1987; Cohen 1989). Interaction strength strongly depends on the relative difference between prey and predator body sizes. One of the first models of food web structure, the Cascade model (Cohen *et al*. 1990; Solow and Beet 1998), relies on body size. Besides its effects on species interactions, body size also influences basal metabolic rate and many life-history and physiological traits (Kleiber 1961; Peters 1983; Byström *et al*. 2004; Jetz *et al*. 2004; Savage *et al*. 2004; Reich *et al*. 2006).

An example of a community evolution model based on body size is the model we built (Loeuille and Loreau 2005). In this model, body size affects a number of species traits:

• It determines demographic parameters. A species' fecundity and mortality are supposed to be directly linked to its mass-specific metabolic rate, a fact that is supported by empirical data (Kleiber 1961; Peters 1983). The model assumes that:

$$f(x) = f_0 x^{-0.25}$$
$$m(x) = m_0 x^{-0.25}$$
(12.1)

where x is the species' body size, f is its production efficiency, i.e. the percentage of the nutrient it gets that is allocated to growth and reproduction, and m is its mortality rate. Note that the model uses body mass as a proxy for body size, as is usual in allometric theory.

• Body size affects trophic interactions. A given predator whose size is y is able to consume species whose body size x is smaller because of morphological and behavioural constraints (Warren and Lawton 1987; Cohen 1989). On the other hand, the predator may disregard very small prey items, either because they are hard to detect or because they do not bring enough energy when consumed. The strength of the interaction should then be maximum for some intermediate value of x smaller than y, an assumption that is supported by empirical observations (Emmerson and Raffaelli 2004). A

possible candidate function matching all these requirements is the Gaussian:

$$\gamma(y - x) = \frac{\gamma_0}{\sigma\sqrt{2\pi}} e^{\frac{-(y-x-d)^2}{\sigma^2}} \qquad (12.2)$$

where σ^2 is the variance of the predation rate, and predators of size y forage optimally on prey of size $x = y - d$.

• Finally, differences in body size also constrain competitive interactions, particularly interference competition. Species that have similar body sizes are more likely to exploit their habitat on similar spatial scales. Habitat use being similar (Price 1978; Jetz *et al*. 2004), interference competition is more likely. A possibility is then to model interference competition between two species with body sizes x and y using a step function:

$$\alpha(|x - y|) = \begin{array}{l} \alpha_0 \;\; if\,(|x - y|) < \beta \\ 0 \;\; else \end{array} \qquad (12.3)$$

All these effects of body size are summarized in Fig. 12.1.

These allometric components (equations 12.1–12.3) are then incorporated into the dynamical model:

$$\frac{dN_i}{dt} = N_i \Big(f(x_i) \sum_{j=0}^{i-1} \gamma(x_i - x_j) N_j - m(x_i)$$

$$- \sum_{j-1}^{n} \alpha(|x_i - x_j|) N_j - \sum_{j=i+1}^{n} \gamma(x_j - x_i) N_j \Big) \;\; (12.4)$$

Variable N_i corresponds to the biomass of the species i whose body size is x_i. Species are ordered according to their body mass, so that species 1 is smallest and species n is largest. N_0 describes the amount of inorganic resource whose trait is arbitrarily set to 0 for mathematical convenience. The dynamics of this resource includes nutrient inputs noted I, diffusion of nutrients out of the system at a rate e, as well as recycling of a proportion ν of the nutrient that is not assimilated during the consumption process or that is released as a result of
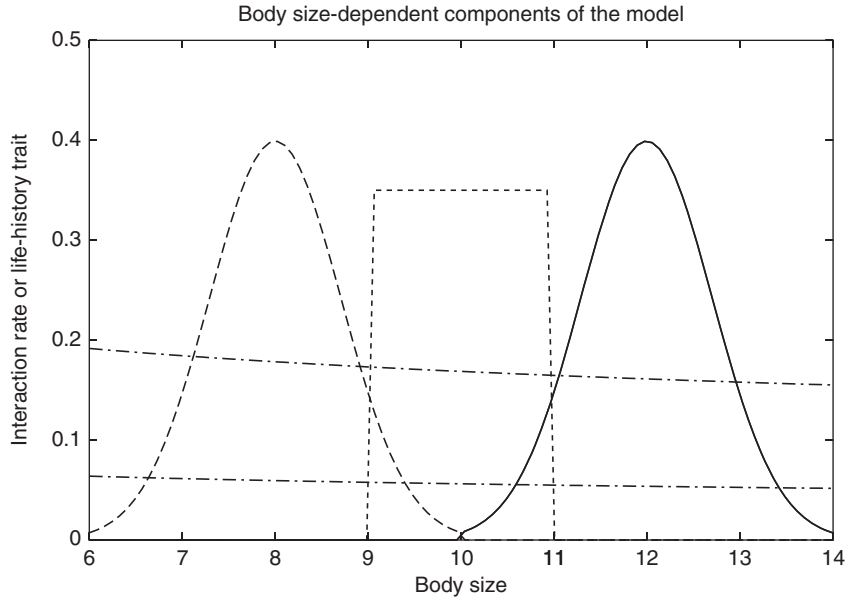
Figure 12.1 Influence of body size on the components of the model. The two dashed-dotted lines show the production rate and mortality rates (equations 12.1). The three other curves detail how interaction rates of a species whose body size is 10 depend on the body size of other species of the community. The solid curve shows the interaction rate with any predators whose body size is included in the interval [10, 14] while the dashed curve shows potential predation rates with a species smaller than itself (equation 12.2). Finally, the dotted step function shows the interference competition rate of the species with species of similar sizes (equation 12.3). Parameters: $m_0 = 0.1$, $f_0 = 0.3$, $\alpha_0 = 0.35$, $\beta = 1$, $\gamma_0 = 1$, $\sigma^2 = 1$.

mortality and excretion. The equation that describes nutrient dynamics is then:

$$\frac{dN_0}{dt} = I - eN_0 - \sum_{i=1}^{n} \gamma(x_i) \ N_i N_0 + \nu N_i \left(\sum_{i=1}^{n} m(x_i) \right.$$

$$+ \sum_{i=1}^{n} \sum_{j=1}^{n} \alpha(|x_i - x_j|) N_j$$

$$+ \sum_{i=1}^{n} \sum_{j=0}^{i-1} \left(1 - f(x_i) \right) \ \gamma(x_i - x_j) N_j \right) \qquad (12.5)$$

Each simulation starts with a single species N_1, which consumes the inorganic nutrient N_0. At each time step, mutation may occur with a probability μN_i for each species (but the inorganic nutrient does not mutate), where μ is the mutation rate per unit biomass. If a mutation occurs, a mutant is introduced, whose trait is drawn at random in a uniform interval centred on the trait of the parent. When a mutant is introduced, its biomass is set equal to the threshold biomass below which a

species goes extinct and is removed from the system.

There are other models based on few species traits. For instance, Ito and Ikegami (2006) used a continuous version of the Webworld model to include two traits for each species, one that describes the species as a prey, and the other that describes it as a predator. We focus below on our own model because it provides an intuitive illustration of how evolutionary dynamics may influence food web structure via one clearly defined trait.

12.2.2 Evolutionary emergence of body-size structured food webs

While the model presented in section 12.2.1.2 starts with a single species, the mutation-selection process adds new morphs to the system, so that total
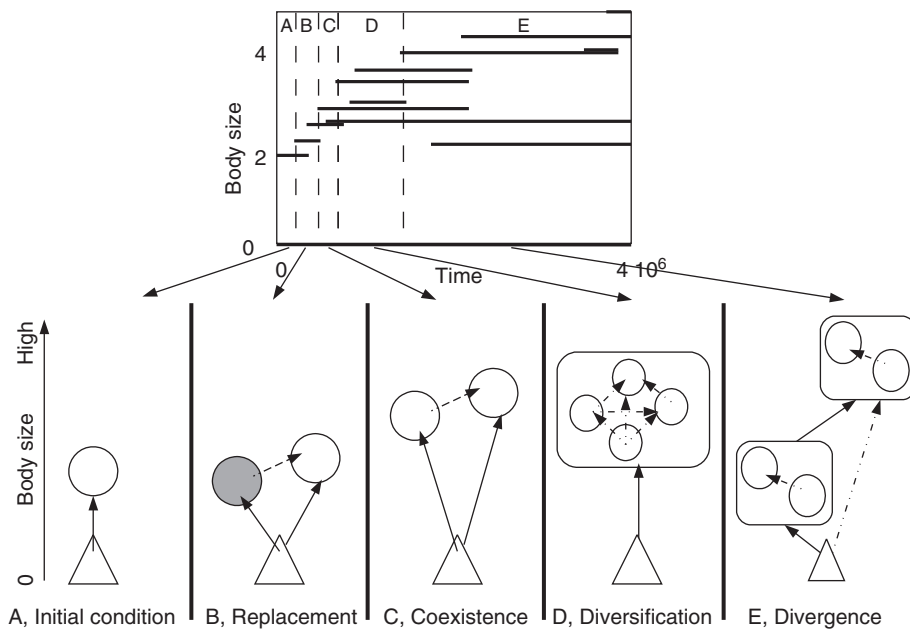

Figure 12.2 First steps of the emergence of a size-structured food web. The main panel shows the trait composition of the community through time, while the lower panel details the different steps of the emergence. The simulation starts with one species that is consuming inorganic nutrient (A). Once in a while, mutants appear (here larger than the resident) and replace their parent (B, in which the grey morph goes to extinction). After several replacements, an evolutionary branching happens, as the mutant and the resident are able to coexist (C). A rapid diversification then occurs in which several morphs are able to coexist (D) but then are selected in differentiated trophic levels (E).

diversity increases through time. This increase in diversity is very fast at the beginning, as the evolutionary process fills (and builds) a niche space that is quite empty at the beginning of the simulation. When mutants invade the system, extinction of the parent species or of other morphs of the community may occur, and after a while total diversity reaches a plateau and compositional turnover becomes small (Fig. 12.2). This plateau is the evolutionary quasi-equilibrium.

The final structure of the food web depends on the parameters of the model. The dimensionality of the food web (total number of morphs and length of the food chain) is mainly limited by energetic parameters such as the nutrient input I and the basal production efficiency f_0. Other characteristics of the food web are sensitive to two parameters:

• The interference competition rate α_0. If there is no interference competition, diversity within a trophic level is reduced and the food web tends to become a food chain. In such cases, the demographic dynamics may become unstable. A small amount of competition (e.g. $\alpha_0 = 0.005$), however, is enough to generate very diverse food webs. At the other end of the spectrum, if the competition rate is very high, individual fitness is mostly determined by competition while selective pressures due to trophic interactions become less important. Under these conditions, having a size that differs at least β from other sizes in the community is the most important condition for a morph to be favoured. As a result, species body sizes become evenly spaced and trophic structure is lost (Fig. 12.3).

• The niche width $nw = \frac{s^2}{d}$, which describes the degree of generalism of predators. The wider a species' niche, the less it is specialized on a given range of body size. Note also that, because the function that describes the niche (equation 12.2) is normalized, when the niche is wider, the maximum consumption rate is smaller. To understand the role of the niche width in the emergence of food web structure, consider the beginning of a simulation in which niches are very narrow. As the inorganic resource has a size 0 and niches are very narrow, morphs whose size is d are strongly favoured because they are the only ones that are capable of taking advantage of the resource efficiently. As a
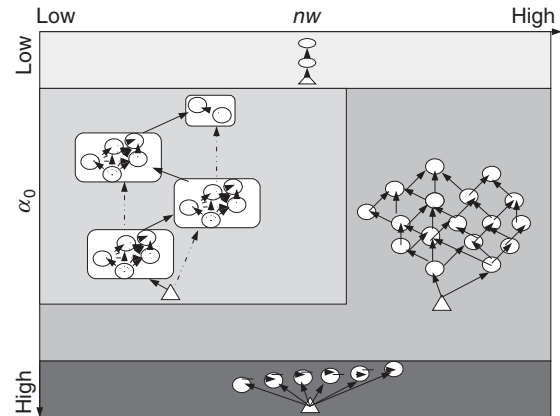
Figure 12.3 Diversity of possible trophic structures emerging from the body-size-based evolutionary model described in section 12.2.1.2. If the interference competition rate α_0 is zero, then a food chain emerges out of the co-evolutionary process. When it is very high, the fitness of the individuals in the community mainly depends on competition, and the trophic structure is organized on one trophic level. In between these two extremes, a wide diversity of outcomes is possible and their structure depends on the niche width parameter nw. If niches are narrow, food webs that emerge are structured by an assemblage of distinct trophic levels, but if niches are wide, the trophic structure is blurred as competition and omnivory are ubiquitous in the simulated community.

result, evolution will select for body sizes that are close to d. These morphs in turn will provide available energy for morphs whose body size is $2d$. Consequently, evolution generates well-defined body size classes, which also correspond to differentiated trophic levels. By contrast, when niches are wide, the consumption function described by equation 12.2 becomes flatter, so that the consumption advantages described above may be offset by other effects of body size or other components of the model. In these cases, the trophic structure is blurred.

These effects of niche width and competition strength are illustrated in Fig. 12.3. The interplay of these two parameters is able to produce a complete continuum of trophic structures. Communities that reach an evolutionary quasi-equilibrium may then be used to generate a snapshot describing

the shape of the food web. To do this snapshot, all morphs are considered, and the trophic links between them are retained if the interaction strength γ is larger than a threshold value (here, 0.15). The result is a binary food web that describes species and trophic links but ignores quantitative information on biomasses and nutrient fluxes. These simulated food webs can then be compared with empirical data from natural communities (e.g. Warren 1989; Winemiller 1990; Hall and Raffaelli 1991; Martinez 1991; Polis 1991; Havens 1992; Memmott *et al*. 2000). This comparison was done in the following way:

• Food webs were generated for 36 pairs of parameters $\begin{cases} a_0 = \{0, 0.1, 0.2, 0.3, 0.4, 0.5\} \\ nw = \{0.5, 1, 2, 3, 4, 5\} \end{cases}$ and their properties were examined.
• For each property, a surface was drawn in parameter space by interpolating the results of the 36 simulations.
• A least squares fit determined which pair of parameters yielded the community closest to empirical data.

For each empirical data set, it is possible to find parameters that generate a food web whose properties are very similar. For all simulated communities, the properties used for the least squares fit are compared with those of the empirical data in Table 12.1. While the match between the communities produced by the model and the empirical data sets is far from being perfect, it is as good as the match obtained using the best binary food web models, at least for the descriptors listed in Table 12.1 (Loeuille and Loreau 2005). The model introduced here also produces the connectance and total diversity of the community, while these quantities were used as parameters (and therefore left unexplained) in the Niche model as well as in other binary food web models.

12.2.3 Advantages of simple community evolution models

In discussing the advantages of the above model or other simple community evolution models, our aim is not to show that simple models based on one or a few traits are better than more complex ones, but rather to identify their specific contribution to understanding food webs.

12.2.3.1 Comparison with other community evolution models
The main advantages of community evolution models based on a restricted and clearly identified set of traits are a better understanding of the role of evolutionary constraints (trade-offs) and a greater ability to test their predictions.

Models that use a large number of traits do not identify these traits explicitly. The influence of these traits on species interactions and demography is usually determined using a matrix whose elements are drawn at random (see section 12.1). Therefore, traits are not linked mechanistically to the biology of the species. No benefits or costs of the phenotypic traits are explicit. In community evolution models, community properties emerge spontaneously from the evolutionary dynamics, so that a complete understanding of these evolutionary dynamics is required to discuss thoroughly the possible mechanisms producing these properties. In the examples detailed in section 12.2.1.2, an explicit link is made between body size and the biology of species. Of course, such knowledge involves additional hypotheses on trade-offs producing the selective pressures acting on the phenotypic trait. But in the case of body size, these trade-offs are well known because body size has been the focus of a lot of work in ecology and physiology (Kleiber 1961; Peters 1983; Brown 2004). It is then possible to use our model as a tool to understand which allometric components of the model are responsible for the observed community structure. For instance, it is possible to turn off the effects of body size on the life-history parameters f and m and examine the consequences of the allometric components of competitive and trophic interactions, independently of the effects of body size on life-history parameters.

12.2.3.2 Comparison with binary qualitative models
A large part of food web theory concerns food web topology in tight connection with empirical data. These models use binary data, i.e. species and links are either present or absent but are not quantified.

Table 12.1 Comparison between the characteristics of empirical data sets and those of communities emerging from the model described in Section 12.2.1.2 that are the closest when the interference competition rate α_0 varies from 0 to 0.5 and the niche width nw varies from 0.5 to 5

Value	Error	SMI	CD	YE	CB	BBL	LRL	SP
Connectance	99	0.26 (0.12)	0.26 (0.31)	0.23 (0.061)	0.24 (0.072)	0.2 (0.17)	0.15 (0.12)	0.27 (0.32)
Chain length	26	4.15 (4.2)	6.2 (7.18)	3.79 (4.89)	4 (2.77)	4.14 (2.55)	4.6 (N.A.)	5.44 (4.81)
Omnivore	19	54 (60)	76 (79)	42 (53)	46 (38)	48 (36)	47 (N.A.)	74 (60)
Top	22	17 (17)	5 (0)	24 (38)	21 (28)	4 (0)	4 (0)	5 (4)
Intermediate	7	63 (69)	80 (90)	55 (53)	60 (62)	68 (68)	82 (87)	79 (92)
Bottom	75	20 (14)	15 (10)	21 (9)	19 (10)	28 (32)	14 (13)	16 (4)

SMI, St Martin Island; CD, Coachella Dessert; YE, Y than Estuary; CB, Chesapeake Bay; BBL, Bridge Brook Lake; LRL, Little Rock Lake; SP, Skipwidth Pond. In each instance, the characteristics of the simulated community are given, while the empirical data is given in parentheses. Matching of the two is comparable to the ones obtained using the Niche model. Other parameters are fixed: I, 10; e, 0.1; v, 0.5; μ_0, 1; d, 2; f_0, 0.3; m_0, 0.1; β=0.25.

Models of this kind use community properties (usually the total diversity of the system as well as its connectance) to determine other community properties. Species and links are distributed among species using rules that are different among models. The Cascade model (Cohen *et al*. 1990; Solow and Beet 1998), the Niche model (Williams and Martinez 2000) and the Nested Hierarchy model (Cattin *et al*. 2004) are examples of such models. All of them are able to match a number of topological descriptors of the empirical data sets satisfactorily.

Compared with these binary models, community evolution models have the advantage that they can provide quantitative information such as interaction strength and species abundances (Loeuille and Loreau 2006). Moreover, since they let community structure emerge from the evolutionary process, they provide the whole dynamics that leads to this structure, not just a snapshot of it (Caldarelli *et al*. 1998; Drossel *et al*. 2001; Loeuille and Loreau 2005; Ito and Ikegami 2006; Rossberg *et al*. 2006). In the case of models that are based on one or a few traits (such as the body-size model presented above), parameters are also measured at the individual level, so that all the community topologies emerge out of processes defined at a lower level. For this reason, these models are able to assess quite accurately how the dynamics really lead to the observed structure. In contrast, binary models are parametrized using community properties (species diversity and connectance). Consequently, they simply use large-scale patterns to infer other large-scale patterns, but whether the internal dynamics of the system can lead to these patterns or not is left unknown.

12.2.3.3 Testing predictions

One of the major caveats of food web theory is the proper test of models. Although the study of topological features such as those listed in Table 12.1 may lead to rejection of a model if the latter fails to reproduce them, the ability of a model to reproduce these topological features is insufficient to accept it. For instance, the Cascade model (Cohen 1989; Solow and Beet 1998), the Niche model (Martinez *et al*. 1999), the Nested Hierarchy model (Cattin *et al*. 2004), the model presented here (Loeuille and

Loreau 2005 2006) and the Matching model (Rossberg *et al*. 2006) all provide a good fit to these data, although their assumptions and mechanisms are quite different. Community evolution models, however, provide dynamical features, which may be used for additional tests of model predictions (provided that empirical data on the dynamics of food webs is also available).

Community evolution models also produce additional quantitative predictions that can be tested. For instance, at any given time of the evolutionary process, it is possible to get the distributions of species abundances and interaction strengths in the system. Nutrient and energy flows can also be quantified in the simulated communities. These quantitative predictions can be compared with corresponding empirical data or with existing theories that deal with energy constraints in natural ecosystems (e.g. Quince *et al*. 2005; Loeuille and Loreau 2006; Rossberg *et al*. 2008).

When models are based on clearly identified traits, it is also possible to use empirical information on these traits to assess the quality of the model. For instance, using the model presented in section 12.2.1.2, it is possible to get the density and body size of each species. It is then possible to use these additional pieces of information to test the model. The food web data for Tuesday Lake incorporate these pieces of information (Cohen *et al*. 2003).

An obvious limit to quantitative tests is the quantity and reliability of empirical data (Winemiller 1990; Hall and Raffaelli 1991; Martinez 1991; Havens 1992; Krause *et al*. 2003). Topological measures already depend quite strongly on the sampling effort and on the aggregation of species in functional groups (or tropho-species). Quantitative data are hard to get and require new standards to make them comparable across different ecosystems (Berlow *et al*. 2004). Another problem is the short-term variability of quantitative descriptors (Baird and Ulanowicz 1989; Winemiller 1990; Polis 1991). Measures of energy fluxes or biomasses are highly variable depending on the season, while long-term averages require a large sampling effort and long-term funding. Under the assumption that food webs are at equilibrium, it is possible to infer some quantities using only partial information (Christian and Luczkovich 1999; Trites *et al*. 1999;

Neira *et al.* 2004; Neira and Arancibia 2004; Sànchez and Olaso 2004). The applicability of such an equilibrium hypothesis, however, is debatable, as evidence of short-term variability and long-term changes accumulates. For all these reasons, although quantitative tests of community evolution models are desirable and theoretically possible, they have not been performed so far.

12.3 Community evolution models and community ecology

In addition to predictions on food web structure, community evolution models can provide interesting insights into many other topics of interest to community ecology. A few of these insights are discussed below, but the possibilities of such extensions depend greatly on the particular assumptions of the models.

12.3.1 Community evolution models and the diversity–stability debate

As seen in Section 12.2.2, community evolution models allow the emergence of diverse communities. The model detailed in section 12.2.1.2 gives rise to food webs that can maintain several hundreds of morphs (Loeuille and Loreau 2005). Similar diversity may be obtained using the Webworld model (Caldarelli *et al.* 1998; Drossel *et al.* 2001) or the Matching model (Rossberg *et al.* 2006, 2008). Remarkably enough, our model as well as the Webworld model generate communities in which population dynamics are quite stable in spite of the large diversity that emerges.

This is an important contribution of these models, since the relationship between diversity and stability has puzzled ecologists for decades. Since May (1973) demonstrated that increased diversity means an increased likelihood that the system may be unstable, ecologists have been looking for mechanisms that could explain the stable assemblages of species that constitute ecosystems. While functional complementarity between species may provide a basis for the ability of ecosystems to maintain a stable overall functioning and resist disturbances (the insurance hypothesis: Yachi and Loreau 1999; Loreau *et al.* 2003), the mechanisms behind the sta-

bility of population dynamics in systems that contain a large number of species are still very much an open question. Compared with community evolution models, community assembly models often show more unstable dynamics (e.g. large extinction cascades or cyclic trajectories; Steiner and Leibold 2004). Results of community evolution models suggest that the stability of the food webs that emerge during the evolutionary process is linked to the evolutionary process itself. Adaptation may be one of the bases for the reconciliation of diversity and stability.

In food web models that deal with a restricted number of species, it is noteworthy that the functional response of consumers plays an important role in the stability of population dynamics. Strong instabilities can be produced as non-linearities, such as Holling type II functional responses, are included (Gross *et al.* 2004). In our abovementioned evolutionary model, it is noteworthy that even the incorporation of type II functional responses did not lead to unstable dynamics, or that such dynamics were only transient (results not shown). As in ours, the initial version of the Webworld model used type I functional responses (Caldarelli *et al.* 1998). An updated version of the model uses a functional response determined by optimal foraging of predators (Drossel *et al.* 2001). Both models generate stable species assemblages. Although these results are still limited in scope and other functional responses should be tested before definitive conclusions can be made, these results suggest that stable communities can be obtained when adaptation takes place, regardless of the functional response used.

One of the possible reasons for the stability of complex systems is low interaction strength. If a community contains only species that interact strongly with one another, it is unstable. But stability may be obtained if a large proportion of the interactions are weak (Kokkoris *et al.* 1999, 2002; McCann 2000; Neutel *et al.* 2002). Interestingly, the model presented here possesses a large number of weak interactions (Loeuille and Loreau 2005; see also Emmerson and Raffaelli 2004). Thus, the evolutionary process may favour the maintenance of weak interactions, thereby enabling stable population and community dynamics. The same

phenomenon seems to be responsible for the stability of the food webs produced by the Webworld model (Quince *et al*. 2005).

12.3.2 Effects of perturbations on natural communities

Understanding the effects of sustained press perturbations on natural communities is increasingly important as the rapid growth of human populations disrupts natural ecosystems. Unfortunately, tools to assess the effects of such perturbations are few, especially on a long timescale.

Yodzis (2000) found that the uncertainty of the effects of changes in one population on the rest of the food web was high in the Benguela ecosystem because of a large number of indirect demographic effects. In addition to these difficulties, recent studies have shown that evolution of species may occur on a short timescale (Reznick *et al*. 1997; Hendry *et al*. 2000; Huey *et al*. 2000; Heath *et al*. 2003; Reale *et al*. 2003; Hairston *et al*. 2005). Thus, changes in life history and species interaction traits because of evolutionary changes may not be negligible in perturbed ecosystems.

Although our model as well as the other community evolution models discussed here are too simplified to provide detailed realistic predictions, they may provide interesting and testable insights into the evolutionary and population dynamical effects of perturbations. Understanding the influence of evolution on species extinctions would be particularly valuable because this issue has hardly been explored. We can decompose the evolutionary effects on species extinctions due to anthropogenic perturbations in three categories:

• Evolution of species following a perturbation. This evolution may help them to respond to the perturbation. For instance, evolution or phenotypic plasticity has helped some species to track global changes (Wing *et al*. 2005; Balanya *et al*. 2006; Franks *et al*. 2007; Sherry *et al*. 2007).
• The extinction probability of species that interact with the species experiencing the perturbation most strongly is modified because of the latter's evolution (evolutionary murder: Dercole *et al*. 2006).

• The extinction probability of species that interact with the species experiencing the perturbation most strongly is modified because of its evolution in response to changes in the latter's density or trait.

On all these issues, community evolution models are able to provide first answers.

To illustrate this, consider a model based on a trait influenced by the perturbation. For instance, the model introduced in section 12.2.1.2 is based on body size. One of the most common perturbations experienced by animal populations is harvesting by humans, which very often depends on body size. For instance, trophy hunting is preferentially directed towards individuals with a large body size, and has already been shown to have evolutionary effects on bighorn rams (Coltman *et al*. 2003). It may also be linked to the size of ornaments (as in the case of rams), but even then it has a selective effect on body size because the latter is correlated with the size of ornaments (Kodric-Brown *et al*. 2006). In fisheries, harvesting is also heavier on large-sized fish (Pauly *et al*. 1998).

In size-structured food webs, the effects of harvesting on large-sized organisms can be assessed directly. These effects include (1) demographic effects, since population dynamics in the model presented in section 12.2.1.2 depend explicitly on body size (equation 12.4), and (2) evolutionary effects, through correlated modifications of the fitness landscapes of the species composing the community. Selective harvesting of large body sizes means that top predators are more likely to be the target of harvesting, a situation that is well documented in fisheries (Pauly *et al*. 1998). Harvesting predators can disturb the food web through top-down effects. These demographic effects include:

• primary extinctions, as the target species may disappear from the system
• secondary extinctions, if the extinction or decline in population size of the harvested species produces extinctions of other, non-targeted species in the web. In the instance of harvesting predators, this may happen when the disappearance or decrease of the predator population generates negative effects on its prey populations (keystone predator *sensu* Paine 1966).

When top predators are harvested in the model of section 12.2.1.2 a surviving predator's mutant whose body size is smaller may be favoured because it has a lower probability of being harvested. This, in turn, modifies the size refuges of its prey (equation 12.2), so that prey that were protected from strong trophic pressures may now decline or go extinct. Such evolutionary extinctions are theoretically possible and observed in community evolution models, but very little is known about their implications in terms of conservation.

Finally, evolution may rescue some species. Evolution of a harvested species may allow it to adapt fast enough to escape extinction. Even if this is not the case, indirect evolutionary effects of harvesting as described above may provide the necessary conditions for the appearance of new morphs. As evolution possibly creates new extinctions but also new species, the net effect of evolution on the total diversity of the system is not obvious. An analysis of these issues with the model presented in section 12.2.1.2 is currently under way.

12.3.3 Models with identified traits: other possible applications

Part of community ecology relies on traits whose importance has been established in many empirical or experimental studies. The same traits could be used in evolutionary food web models. It would then be possible to make an explicit link between evolutionary dynamics in food webs and other areas of community ecology that are usually discussed without any evolutionary considerations.

Empirical and experimental observations show that the stoichiometry of consumer and resource species influences their interaction (Loladze and Kuang 2000; Grover 2003). For instance, stoichiometric effects are one of the possible explanations for the prevalence of omnivory in nature (Matsumura *et al.* 2004). Stoichiometry also influences the whole structure of food webs (Turner *et al.* 1998; Schade *et al.* 2003). Much is known about elemental ratios, from both a physiological and an ecological point of view, so that trade-offs driving the evolution of elemental ratios can be derived from this knowledge. Therefore elemental ratios could be incorporated in evolutionary food web models.

Some work along these lines is already under way. Hopefully, it will then be possible to predict community patterns related to ecological stoichiometry, such as the differences between elemental ratios at different trophic levels, differences in their variance, the prevalence of the Redfield ratio in ecosystems.

Evolution of dispersal and habitat preference also largely determines community organization. Integration of spatial effects in the structure of communities is a rapidly expanding theme of community ecology. A particularly useful framework that has been developed recently is the metacommunity concept, which describes a set of local communities connected by dispersal of individuals among patches (Leibold *et al.* 2004). Studies of the interaction between evolution and dispersal in these metacommunities has already begun (Urban 2006, Rossberg *et al.* 2008; Loeuille and Leibold 2008). However, the integration of spatial components in community evolution is not properly done yet (but see Rossberg *et al.* 2008). Incorporating the evolution of dispersal or habitat choice (Gyllenberg and Metz 2001; Metz and Gyllenberg 2001; Kisdi 2002) would allow evolutionary food web models to link to metacommunity theory, but such an extension is very costly in terms of complexity and few insights are yet available.

The strongest link currently available between evolutionary food web models and other areas of community ecology is with the allometric theory of ecology (reviewed in Brown 2004). This theory uses the relationship between body size and various physiological or life-history traits (metabolism, production rate, etc.) to make various predictions on species biomass and nutrient fluxes in ecosystems. Allometric theory is often successful in describing macro-scale patterns of community structure and ecosystem functioning. However, it usually deals with snapshot pictures of communities. It does not account for the dynamical processes that generate the structure itself, although it often invokes coevolution of species as a mechanism (Damuth 1981; Maiorana and Van Valen 1990; Marquet *et al.* 1995; Brown 2004). As a result, community evolution models relying on body size are complementary to allometric theory. First, models based on body size such as the one detailed in section 12.2.1.2 rely on

some similar assumptions. For instance, our model contains the influence of body mass on individual production and mortality rates (equations 12.1), two components of allometric theory. Second, community evolution models account explicitly for the coevolutionary dynamical process that is supposed to underlie the patterns revealed by allometric theory.

Consider one of the main results of allometric theory, i.e. the distribution of species abundances as a function of body size. Damuth (1981) showed with empirical data that the density D of a given species is related to its mean body mass, noted x by the relationship $D = kx^{-0.75}$. Since the mean metabolic rate M of an individual is linked to its body size by the relationship $M = k'x^{0.75}$ (Kleiber 1961), the total amount of resources E consumed by a given species in the system should be $E = MD = kk'x^0$, i.e. the energy consumed by a species is independent of its body mass. This prediction is called the energetic equivalence rule (Damuth 1981; Nee *et al*. 1991). Although the mechanism that is supposed to lead to this equal partitioning of resources among species is somewhat vague, coevolution of species that share a same set of resources has been invoked (Damuth 1981; Maiorana and Van Valen 1990). This influential rule has been tested using empirical data with both successes (Damuth 1981, 1991, 1993; Marquet *et al*. 1990; Nee *et al*. 1991; Long and Morin 2005) and failures (Brown and Maurer 1986; Greenwood *et al*. 1996; Cyr 2000; Cohen *et al*. 2003; Russo *et al*. 2003) Although it was initially derived for species within a single trophic level, it was later extended by others to systems that contain multiple trophic levels. Allometric theory then predicts that the exponent that links density and body size is -1, so that $D = kx^{-1}$ (Brown and Gillooly 2003).

Interestingly, the model presented in section 12.2.1.2 contains some components that are similar to the ingredients used in Damuth's energetic equivalence rule. The allometric relationships used for production and mortality rates are inferred from individual metabolism, and the model simulates species coevolution on shared resources, the mechanism that was proposed for the emergence of the perfect sharing of resources between community members. Therefore, it is possible to test this mechanism (keeping in mind, of course, the limits of the model's assumptions) and to see for which parameters, if any, the predicted links between population density or energy use and body size are observed. The results show that population density is a decreasing function of body mass, but the exponent of the relationship depends on the strength of competitive interactions and on the niche width of consumers, so that coevolution does not lead to an equal partitioning of energy among species (Loeuille and Loreau 2006). This example illustrates how community evolution models may give additional insights to the allometric theory of ecology. Such models can include allometric components when they consider body size as an evolving trait. Because they consider dynamical components of populations instead of focusing on the equilibrium communities, they may also be used to test mechanisms assumed to explain allometric patterns.

12.4 Conclusions, and possible extensions of community evolution models

Community evolution models make three major contributions to community and ecosystem ecology. First, they extend classical pairwise coevolutionary models to large, complex ecosystems, with new results. Take the example of how evolution, or coevolution, affects population dynamics. In small communities, some studies show that evolution or coevolution may have stabilizing effects (Pimentel 1961; Saloniemi 1993; van Baalen and Sabelis 1993) while others suggest the contrary (Abrams and Matsuda 1997; Yoshida *et al*. 2003). As we have pointed out in section 12.3.1, the results seem to be less ambiguous in more complex community evolution models, in which evolution tends to produce large assemblages of species that are stable on a demographic timescale.

Second, they provide, for the first time, insights into the evolutionary emergence of entire food webs or ecosystems. Classical evolutionary models have mostly considered evolution or coevolution of pre-existing species. In community evolution models, species themselves emerge spontaneously from the evolutionary dynamics of the system.

Third, they provide new perspectives on food web and community properties, and potentially a more complete understanding of the mechanisms that generate them. We provided several examples of such applications in sections 12.2.2 and 12.2.3. Community evolution models are capable of giving as good a match to binary data sets as classical food web models such as the Cascade and Niche models. But, additionally, they provide the dynamics of food web structuring whereas other models are only able to reproduce empirical data at a given time. Finally, community evolution models describe species interactions based on individual-level traits, so that community properties are emergent properties of processes that take place at a smaller scale. As a consequence, the mechanisms underlying emerging structures are much clearer than in the case of the Niche or Cascade models, which use large-scale patterns, such as species diversity and connectance, to predict other large-scale patterns, but cannot account for species diversity and connectance in the first place.

12.4.1 Possible extensions of community evolution models

As discussed in section 12.3.3 community evolution models can include other traits than body size. Whatever other traits are chosen, however, body size seems a natural candidate for a primary trait. Body size has well-documented effects on many life-history traits and trophic interactions in all taxonomic groups, on both plants and animals. It has been suggested as a good proxy for a species' trophic level, and has been used abundantly in both static food web models and the new community evolution models.

Although the importance of body size is undisputed, species interactions are the product of several traits. Therefore, a straightforward extension of these models would be to include one or several other traits to better account for species interactions. Some of the good candidates, such as elemental ratios, habitat choice and dispersal rates, are discussed in section 12.3.3. In addition to these, another important trait is niche width, which encapsulates a species' ability to consume a more or less large array of prey species. In the model presented in section

12.2.1.2, we made the simplifying assumption that niche width is constant among species and does not evolve. We are currently working to add evolution of niche width in this model.

Another possible extension of the model is the incorporation of other types of interactions. Current community evolution models account for trophic interactions, and sometimes interference competition. There is increasing evidence that other types of interactions, such as mutualism and parasitism, play an important role in the structure and dynamics of natural communities (e.g. Callaway *et al*. 2002; Lafferty *et al*. 2006; Michalet *et al*. 2006). Networks of mutualistic interactions are now documented, and some recent studies suggest a possible role of evolution in constraining their structure (Jordano *et al*. 2003; Vázquez and Aizen 2004; Bascompte *et al*. 2006). The biomass of parasites is sometimes comparable to the biomass of predators, so that nutrient flows involved in parasitic interactions may no longer be neglected (Lafferty *et al*. 2006). The main problem with the inclusion of such interactions in community evolution models is to find traits that can be linked to them unambiguously in the same way as body size is for trophic interactions. Goudard and Loreau (2007) recently proposed a first community assembly model that includes all types of species interactions. Their model could be extended to include evolutionary dynamics.

12.4.2 Empirical and experimental implications of community evolution models

When community evolution models are based on well-defined traits, it is possible to include physiological or genetic information on these traits. The benefits and costs of these traits are then assessed from empirical or experimental knowledge, and the evolutionary trade-offs that constrain them are built as assumptions into the models. This is both a blessing and a curse. The advantage is the possibility to play with the various fitness components to determine how each trait influences emerging patterns. On the other hand, evolutionary trade-offs are notoriously difficult to obtain, and their shape strongly influences the results of the evolutionary

dynamics (de Mazancourt and Dieckmann 2004; Loeuille and Loreau 2004).

In the case of body size, many observations exist, so that costs and benefits can be determined relatively safely. Things are less obvious for the other traits that were proposed as possible extensions to existing community evolution models (section 12.4.1). Elemental ratios are typically linked to the growth rate of individuals (Justic *et al.* 1995; Kooijman 1998; Makino *et al.* 2003; Klausmeier *et al.* 2004; Frost *et al.* 2006). Similarly, predators modulate their attack rates between their different prey depending on prey stoichiometry (Loladze and Kuang 2000; Grover 2003). Thus, life-history and species interactions are dependent upon elemental ratios, but the exact shape of this dependence is not well known.

Habitat choice and dispersal probably affect interaction strength too. For instance, habitat choice by a predator may be driven by prey palatability, so that interaction strength is increased. By a symmetric argument, it may be assumed that dispersal or habitat choice by prey can reduce interaction strength. Habitat choice involves costs linked to the uncertainty of finding a suitable place and increased mortality while moving, in addition to the energy spent.

Finally, evolution of niche traits implies a trade-off between the maximum consumption rate and niche width. Note that this trade-off is already included in equation 12.2. When niche width increases, for example because σ^2 is increased, then the maximum interaction rate is decreased because the function γ is normalized (i.e. its integral is constant and equal to γ_0). But niche width might also influence other traits that determine the species' life-history or their trophic interactions. These indirect costs and benefits are less documented.

Thus, including other traits hinges on the empirical knowledge we have of their associated trade-offs. To determine these trade-offs, controlled experiments in common garden are promising tools. Such experiments have already yielded interesting results on the costs of anti-herbivore defences in plants (Mauricio 1998; Strauss *et al.* 2002). Such studies are required for other traits so that their effects on life-history and ecological interactions are better represented in models.

Other empirical needs include the development of quantitative data. Quantitative data sets exist (Baird and Ulanowicz 1989; Winemiller 1990; de Ruiter *et al.* 1995; Christian and Luczkovich 1999; Trites *et al.* 1999; Yodzis 2000; Neira and Arancibia 2004; Neira *et al.* 2004; Sànchez and Olaso 2004; Williams *et al.* 2004; Tewfik *et al.* 2005), but several problems remain:

- There is a need for new standards for these quantitative data (Cohen *et al.* 1993a; Berlow *et al.* 2004). Some studies use density to describe species abundances while others use biomass. Some use energy flows for measuring interaction strength, others use the frequency of the interaction, still others use the effect of predator removal, etc. Because of this lack of standards, quantitative data sets are very heterogeneous, making it difficult to test some predictions of community evolution.

- There is a need for longer term studies. Quantitative data typically show a high variability in species abundances and interaction strength, for instance through seasonal variations. Long-term trends, however, might show less variability. This means that the quantification of food web properties should be performed over several years. Projects that describe food webs should be funded on a long-term basis, as requested by Cohen *et al.* (1993a).

- There is a need for better assessment of some critical hypotheses underlying quantitative food web data. Because *in situ* measurements are very costly, both in money and in time, many indirect methods have been used, such as an extensive use of bibliographical or gut content data and reliance on equilibrium assumptions to infer some of the data set using partial information (e.g. using the ECOPATH software). Errors involved in these methods should be carefully quantified and error bars included in food web quantification, as should possible errors of direct observations.

The ideal data sets to test evolutionary food web models contains species abundances, interaction strengths and detailed knowledge of the traits described in the model under standardized conditions. Of course, getting such data is very difficult, perhaps sometimes even impossible. But linking model predictions and empirical data will be an indispensable step to fully assess the scope and potential of recent theoretical advances.