FLEXIBLE FORAGERS IN FOOD WEBS

Consequences of adaptive foraging in diverse communities

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Summary

1. Selective pressures acting on foraging activities constrain the strength of interaction, hence the stability and energetic availability in food webs.
2. Because such selective pressures are usually measured at the individual level and because most experimental and theoretical works focus on simple settings, linking adaptive foraging with community scale patterns is still a far stretch.
3. Some recent models incorporate foraging adaptation in diverse communities. The models vary in the way they incorporate adaptation, via evolutionary or behavioural changes, and define individual fitness in various ways.
4. In spite of these differences, some general results linking adaptation to community structure and functioning emerge. In the present article, I introduce these different models and highlight their common results.
5. Adaptive foraging provides stability to large food web models and predicts successfully interaction patterns within food webs as well as other topological features such as food chain length.
6. The relationships between adaptive foraging and other structuring factors particularly depend on how well connected the local community is with surrounding communities (metacommunity aspect).

Key-words: adaptive foraging, complex adaptive systems, diffuse co-evolution, food web structure, metacommunity, optimal foraging

Introduction

Incorporating adaptive foraging—or any influence of adaptation on species interaction—in a community context is not a simple matter. Communities are defined as a collection of species selected by local abiotic and biotic conditions, but niches are most often expressed using abiotic components. Interactions with other species of the community are usually simplified. Adaptation to the physical environment is most often studied while species adaptation in response to interactions and co-evolution are usually separated from community structure.

As an illustrative example of the focus on abiotic conditions, consider the recent development of climate change effects on natural communities. Most predictions are based on climate-envelope models (e.g. Pearson et al. 2002; Peterson et al. 2002; Pyke & Fischer 2005), in which it is assumed that species react as independent entities and according to their own climate tolerances and dispersal abilities exclusively. The role of species interactions and their plasticity has only just begun to be incorporated in such models (Sutherst, Maywald & Bourne 2007) though their relevance to climate change has been shown in many instances (Davis et al. 1998; Suttle, Thomsen & Power 2007, Tylianakis et al. 2008). Similarly, models used to reproduce food web structures have long focused on equilibria situations and did not incorporate any dynamical or adaptive components (Cohen 1989; Williams & Martinez 2000; Cattin et al. 2004).

That adaptation takes a secondary place in food web ecology seems paradoxical given the multiple ways in which we know it affects trophic interactions. Adaptive foraging behaviour is known to be common and it is supported by many empirical observations. From a behavioural point of view, choices of prey species depend on the energy they bring and how the prey might constrain the predator diet breadth (McArthur & Pianka 1966; Charnov 1976; Charnov 1976; Parker & Stuart 1976). Switching from one prey species to another or their handling is also dependent on the predator behaviour. Handling and switching are commonly included in functional responses (Holling 1959; Beddington 1975; Oaten & Murdoch 1975). Their effects on stability and equilibrium densities are well-known in small models. From the prey point of...
view, predator avoidance is an important behavioural trait with large consequences for community structure (Wootton 2002; Werner & Peacor 2003; Schmitz, Krivan & Ovadia 2004, Trussell, Ewanchuck & Matassa 2006, Hammond, Luttbeg & Sih 2007).


The accumulated empirical evidence that adaptive foraging commonly happens, has led to it being included in many simple models (summarized in Abrams 2009). Because of their relative simplicity, such models provide robust results showing the effects of adaptive foraging on population dynamics and species co-existence, results that can then be tested in empirical settings. It is comparatively less common to include adaptive foraging in web models that contain many species. Most often, models that tackle food web structures (characterized by topological descriptors such as chain length, connectance, generality of predators, vulnerability of prey, etc) do not include any dynamical aspects, interaction strengths or even population densities (e.g. Cohen 1989; Williams & Martinez 2000; Cattin et al. 2004). These models are usually parametrized using community scale characteristics such as species diversity and connectance to match other community scale descriptors, so that making a link with individual scale processes such as adaptive foraging or even population dynamics is far from straightforward.

Fortunately, a few recent models account for adaptive foraging in diverse communities. They explicitly link interaction between individuals and structures on larger scales (populations, communities or ecosystems). They complement nicely the predictions made by smaller and more tractable models (see Abrams 2009) by testing how such predictions scale up in more complex settings. This article summarizes the progress made by such models to distinguish how adaptive foraging structures food webs and affect their functioning.

The first part of the article reviews the results of several food web models regarding the effects of adaptive foraging on community structure, particularly how changes in foraging behaviour produce similar patterns of connectance as the ones observed in nature and how it can stabilize complex communities. It then details evolutionary components of adaptive foraging. Diffuse co-evolution between predators and preys leads to contrasting trophic structures or functional aspects that can be compared with relevant empirical data sets. These evolutionary models suggest that adaptive foraging may well produce stable structures, whose properties are comparable to those observed in nature. They also yield interesting insights regarding the distribution of interaction strengths and the transmission of energy through the web.

The second part of the article discusses the place of the adaptive foraging process in other processes that structure communities. It especially focuses on the effects of various characteristics of the community, such as its connectivity to other communities (metacommunity aspects), temporal variations of the abiotic environment and local species diversity.

Structural and functional consequences of adaptive foraging

A necessary requisite to this article is to define clearly what I mean by adaptive foraging. Adaptive foraging corresponds to changes in resource or patch exploitation by consumers that give the consumer a higher fitness compared with conspecifics that exhibit alternative strategies. The fitness definition usually includes many components, such as the energy acquired and spent while foraging, predation risk, interference competition due to foraging activities, etc.

In this section, I want to illustrate a few processes by which adaptive foraging can affect community structure. I identify the key mechanisms, explain how they operate and, where possible, compare their effects to the ones observed in smaller communities. I divide these consequences in two broad categories: adaptive foraging as a behavioural or evolutionary effect.

Changes in behaviour: a focus on the consequences of optimal foraging

One of the simplest and most successful kinds of adaptive foraging theory is the one of optimal foraging. Optimal foraging is distinct from adaptive foraging in two ways. First, definition of fitness is restricted to the energetic balance of the foraging activity. Second, this energetic balance is supposed to be maximized (McArthur & Pianka 1966), so that optimal foraging can be considered as the ultimate situation, while adaptive foraging need not be considered as an equilibrium situation. Under optimal foraging, a predator consumes a nearby prey $k$ that brings an amount of energy $E_k$ but takes an amount of time $H_k$ to kill, consume and digest, if its profitability is higher than the mean profitability it can expect from more distant prey:

$$\frac{E_k}{H_k} > \frac{\bar{E}}{H + \bar{s}}$$

where $\bar{s}$ is the average search time it needs to find another prey, $\bar{E}$ is the average energy brought by prey already in the vicinity.
Theoretical works on optimal foraging often suggest that it is attributable to predator behaviour, happening on a short time-scale. Recent models show that optimal foraging can play an important role in the structure and functioning of food webs in at least two ways: as a factor of increased stability and as a key constraint for connectance.

**Effects of optimal foraging on stability and co-existence**

Adaptation can play a major role in population dynamics stability. Such effects have been predicted by several models (Pimentel 1961; van Baalen & Sabelis 1993; Yoshida et al. 2003; reviewed in Abrams 2009; Fussmann, Loreau & Abrams 2007), observed in experiments (Yoshida et al. 2003) and in empirical data sets (Seldal 1994). Given the increasing number of results that suggest that adaptation and evolution can happen on similar time-scales as demographic changes (Grant & Grant 1995; Reznick et al. 1997; Hendry et al. 2000; Huey et al. 2000; Hairston et al. 2005), its stabilizing or destabilizing effects are particularly relevant to understand how natural communities react to disturbances.

Consider an example in which a predator has prey that becomes rare. When prey populations become low, the average search time increases, so that the right hand side of equation 1 is low. Under such conditions, the incorporation of a new encountered prey species in the predator diet is facilitated. Optimal foraging can therefore dilute predation pressure, creating a negative feedback for prey abundances. The rarer species eventually undergoes less predation so that its population grows. Such frequency dependence can enhance stability and promote species co-existence (Fig. 1, panel a). This positive effect of adaptive foraging on diversity is suggested by theoretical works (Krivan 2003; Krivan & Eisner 2003) and observed in data from several experiments (reviewed in Bolker et al. 2003). As diversity partly determines the degree of complexity of the community, this establishes a clear link between adaptive foraging and food web size.

The stabilizing mechanism described above can be extended to diverse communities as illustrated by the work of Kondoh 2003a, see also (Brose, Williams & Martinez 2003 and Kondoh 2003b). Kondoh’s model builds on the work of May (1973) which suggested that increased diversity can lead to unstable communities. However, Kondoh simulated food webs in which a fraction F of the consumers are adaptive foragers. Their foraging efforts increase on prey species that bring more energy than average (for instance, because they are very abundant) at the expense of foraging efforts on other preys. In this instance, foraging is determined out of the energetic balance, so that the distribution of consumption rates follow optimal foraging theory. Kondoh shows that provided that the fraction F is sufficiently large and that adaptation occurs fast enough, diversity increases stability. The interpretation of these stabilizing effects relates to how optimal foraging affects the distribution of interaction strengths. Many weak links are created by the redistribution of foraging efforts, and theoretical work suggests that the

![Fig. 1. Three ways by which adaptive foraging has been shown to change community structure in complex models. (a) Adaptive foraging redistributes interaction strengths depending on prey populations and quality, predation risk and possible additional factors. This creates both weak links and strong links (Kondoh 2003a; Loeuille & Loreau 2005), a mix that could lead to stable food webs (McCann, Hastings & Huxel 1998). (b) It is possible to assess the parameters of the marginal value theorem (equation 1) from food web data sets, to successfully reproduce the overall connectance (Beckerman, Petchey & Warren 2006) or even to predict the existence of interactions based on species body size (Petchey et al. 2008). (c) Adaptive foraging modifies fluxes of energy between adjacent trophic levels. When energy constrains food chain lengths, adaptive foraging then increases the height of the overall food web (Loeuille & Loreau 2005).](image-url)
association of many weak links with few strong ones is known to promote stability (McCann, Hastings & Huxel 1998).

**Predicting connectance using optimal foraging**

Redistribution of trophic interaction strengths described in the previous section leads in extreme cases to the exclusion of some of the prey species from the predator diet (Fig. 1, panel b). Thereby, optimal foraging constrains the very existence of trophic links.

This idea has been successfully explored by Beckerman, Petchey & Warren (2006). In this work, the authors build a model in which prey species are included in the predator diet if their energetic content is high enough (equation 1). This constrains the predator diet breadth, that is to say the number of prey species it consumes. The authors then note that connectance is the ratio between the average diet breadth and the total number of species. Thereby they make an explicit link between an individual behaviour and a structural aspect of the whole community (connectance).

Connectance observed in 13 real food webs is very similar to the one found using this optimal foraging argument. The model reproduces the negative relationship between connectance and species diversity, as commonly observed in empirical data sets (Montoya & Solé 2003). In a companion article (Petchey et al. 2008), the same authors include the dependence of energetic parameters (prey energetic contents and handling energy spent by predators) on body sizes of the prey species $i$ and of the predator $j$. This allows them to use body size distributions to predict a large proportion of the interactions within many different empirical food webs.

That optimal foraging constrains the number of prey species a predator consumes, hence the connectance of a food web, may seem a simple consequence of equation 1. Such a line of reasoning implicitly acknowledges that conclusions made from a few species will be applicable to more complex settings. It also implicitly assumes that optimal foraging is the main force driving community structure. None of these two statements are obvious, which makes the link between the theoretical model and the empirical data quite striking.

**DIFFUSE CO-EVOLUTION WITHIN FOOD WEBS**

Recently, several models have investigated the incorporation of components other than energetic constraints in foraging adaptation. These models are based on diffuse co-evolution, in the sense that all species evolve not only in response to the direct interaction with another species, but also due to all indirect effects within the community. Fitness may be based on many components, not only available energy. For instance, in Loueille & Loreau (2005), evolution of the size of a consumer depends on its advantage in terms of prey consumption, but also on how it modifies vulnerability to predators, interference competition, as well as reproductive and death rates.

Optimal foraging is purely based on energetic arguments, it produces simple predictions (such as equation 1) that can be tested experimentally or compared with empirical observations (Mori & Boyd 2004; Mayntz et al. 2005; Hammond, Luttbeg & Shi 2007). For this reason, optimal foraging is widely used and provides important insights concerning the determinism of trophic interactions. However, energetic components are only part of the selective pressures acting on foraging activities. Looking back at equation 1, a new prey $k$ is going to be included in the predator diet if it brings enough energy or if it is not hard to kill. This does not account for the fact that incorporating the new prey can increase the vulnerability of the consumer to other predators (for feeding habits are changed) or increase interference competition. Ecology of fear (Brown, Laundre & Gurung 1999) has been shown to be potentially important in explaining community patterns (Trussell, Ewanchuck & Matassa 2006) and it is not included in optimal foraging arguments. Adaptive foraging is more flexible, because it is not restricted to energetic components of fitness. It can include other components, such as the ones mentioned above, that influence foraging behaviours. Such evolutions of foraging have been implemented recently in various models, that can be divided in two groups based on the number and the nature of traits considered.

1. Evolutionary models based on a large number of traits. Examples include the webworld model (Caldarelli, Higgs & McKane 1998, Drossel, Higgs & McKane 2001, McKane 2004) or the matching model (Rossberg et al. 2006). In such models, trophic interactions depend on a set containing many traits. For instance, the webworld model relies on a set of $L$ traits. All species are characterized by a subset of $K$ traits. Interaction strength is determined by the sum of elements taken out of a $L \times L$ matrix that describes the effect of each trait against the others. This matrix is drawn at random. When a mutation occurs, the mutant has $K - 1$ of the $K$ traits of its parent, and one additional trait taken among the $L$ traits. In such settings, traits are discrete as the organisms either possess them or not, with no in-between.

2. Evolutionary models based on a restricted number of traits (e.g. Loueille & Loreau 2005; Ito & Ikegami 2006). Usually one or two traits determine trophic interactions as well as basic demographic rates. When a mutation occurs, the mutant is introduced as being slightly different from its parent for one of the incorporated traits. In this kind of model, traits are explicitly identified and they take continuous values.

The two types of model have different strengths and limits. While the large-trait approach is appealing in the sense that trophic interactions are probably determined by many traits in nature (but see Stouffer, Camacho & Nunes Amaral 2006), they do not constrain the traits on biological grounds (the interaction matrix being drawn at random). It is impossible to make any clear link between the dynamics it proposes and knowledge of relevant trade-offs. It is also not possible to make any quantified test of the trait changes through time or
of their distribution at equilibrium, since the traits are not explicitly identified.

The restricted trait approach usually incorporates biological arguments and trade-offs based on the knowledge of the traits. Loeuille & Loreau (2005) is based on body size, whose implications for trophic interactions and biological rates are well-known (Peters 1983; Brown 2004; Emmerson & Raffaelli 2004). Quantitative tests on the trait distributions are then possible, as well as discussions of their biological interpretations (Loeuille & Loreau 2006). As body size is usually one of the traits involved, results also provide mechanistic insights to the metabolic theory of ecology, largely based on allometric arguments (Brown 2004). On the other hand, such models cannot describe fully interspecific interactions, only the part of the interaction that can be attributed to the incorporated trait(s).

Both kinds of models define fitness on ecological grounds, using the rate of variation of the population of a given phenotype in the community, when rare. Fitness then includes many components in addition to the energetic aspects tackled in optimal foraging theory. The drawback to this flexibility is that the rules of adaptation are entirely dependent on the definition of fitness used by the model, so that generalities are harder to get. In spite of these differences, intriguing similarities concerning the consequences of adaptive foraging emerge when comparing these co-evolution models, either with one another or with these based solely on behaviour. I will now focus on these generalities.

Adaptive foraging and food web structure in diffuse co-evolutionary models

Simulated networks obtained in diffuse co-evolution models produce communities whose characteristics are analogous to empirical observations. For instance, Loeuille & Loreau (2005) showed that adaptive foraging constrained by body size could produce a large diversity of trophic structures. Provided that some other important components such as interference competition are included, some of these structures are analogous to the ones observed in the best documented food webs. The webworld model is also able to produce a large diversity of trophic structures (Caldarelli, Higgs & McKane 1998; Drossel, Higgs & McKane 2001; McKane 2004) and the matching model has a high power of reproduction of food web characteristics (Rossberg et al. 2006). In none of these cases is the fit linked to the use of a large number of parameters. Reproduction of empirical patterns in Loeuille & Loreau (2005) involves variations in just two parameters that balance competitive and trophic interactions, while the matching model uses eight parameters (Rossberg et al. 2006). As the parameters are in fact the relative weights of different fitness components, these models propose a link between individual-based evolution and community scale structures.

So far, simulations have been compared with topological properties of empirical food webs. To determine such characteristics, food webs are represented as nodes (species present) and edges (actual interactions), whose distributions are described. Examples of such characteristics are the mean vulnerability of preys (average number of outgoing edges per node), mean generality of predators (average number of incoming edges per node), connectance, link density, total number of nodes (diversity) etc. Although models based on co-evolution match some of these patterns, simpler models do too (Cohen 1989; Williams & Martinez 2000; Cattin et al. 2004). But, there are crucial differences between evolutionary food web models and these simpler models:

- The simpler models use some graph theory characteristics to get the others. Connectance and total diversity of the food web are the parameters of these models. Such models therefore do not aim (and cannot) at explaining how these two features are constrained. They play the role of null models to which empirical data sets are compared. On the other hand, diffuse co-evolution models get the structure of the community, including diversity and connectance, based on key ingredients at the interaction level such as competition strength or allometric constraints of predation. Interaction between the individuals of the community produce the larger scale patterns.

- Diffuse co-evolution models are dynamic, not static. In principle, it is possible to evaluate the building phase of the community, by comparing variations in the food web structures through time with succession stages in ecosystems.

- When the model is based on identified traits, such as body size, diffuse co-evolution models provide quantitative information in addition to the graph theoretical aspects. It is for instance possible to discuss the relationship between density and body size (Loeuille & Loreau 2006) or to produce patterns regarding the abundance of species or interaction strengths (Quince, Higgs & McKane 2005, Loeuille & Loreau 2006; Rossberg et al. 2008).

The two last points suggest possible new tests for the role of adaptive foraging, to extend the understanding of structural aspects beyond graph theory and tackle functional and quantitative aspects of food webs.

Adaptive foraging and stability in diffuse co-evolutionary models

In addition to reproducing food web structures, diffuse co-evolution models also seem to produce stable communities. This is not to be expected, as adaptive foraging in low-diversity models tends to stabilize or destabilize the system, depending on the details of the model (Fussmann, Loreau & Abrams 2007). Interestingly, the relationship between community stability and evolution seems to be simpler in more complex systems. This stabilizing effect happens even when possibly destabilizing processes are incorporated in the model. For instance, Holling type II functional responses are known to produce population cycles, as illustrated by the paradox of enrichment (Rosenzweig 1971). Even when trophic interactions are described by such functions, adaptive
Adaptive foraging seems to produce stable communities in diverse systems (Drossel, Higgs & McKane 2001; Loeuille & Loreau 2005).

As stated above, adaptive foraging models based on diffuse co-evolution produce distributions of interaction strengths (Quince, Higgs & McKane 2005; Loeuille & Loreau 2006). Adaptive foraging, redistributing interactions strengths, produces many weak links and a few strong ones (Fig. 1, panel a). Such a pattern stabilizes communities (McCann, Hastings & Huxel 1998; Neutel, Heesterbeek & de Ruiter 2002). The same process is at hand in the case of Kondoh’s work (Kondoh 2003a) detailed earlier.

Transmission of energy within diffuse co-evolutionary food webs

Adaptive foraging links consumption and fitness for a predator individual. If one restricts the many possible components of adaptive foraging to the energetic balance of foraging activities (optimal foraging), energy intake is then maximized. Optimal foraging therefore increases energy availability for upper trophic levels. As other components (predator avoidance for instance) are incorporated, adaptive foraging no longer maximizes energy transfer, but balances this transfer with additional costs (e.g. vulnerability, competition). In an adaptive foraging model containing many components, energetic supply for the upper level should be larger when the weight of energetic ingredients in the fitness definition is increased.

In Loeuille & Loreau (2005), body size is selected based on energetic acquisition, but also based on its effects on life history, vulnerability to predators and interference competition. How differences in body size constrain energetic transmission is dependent on the degree of specialization of the species of the community. When the niche width is chosen to be large, body size evolves rather independently from energy brought by foraging, because relative differences in body size between predators and prey have little effect on consumption. Conversely, when niches are narrow, evolution of body size is mainly constrained by foraging activities, and it favours a small range of body sizes. The narrower the niche, the more prevalent energetic consumption is in the fitness definition.

Such conditions produce communities that have:

- well-distinguished trophic levels.
- a larger number of trophic levels.

The first characteristic is a direct consequence of the weight of foraging in the selective pressures. As predators focus on a narrow set of body sizes, there is a strong directional selection toward body sizes that optimize consumption. Little omnivory happens and trophic levels are well separated.

The second characteristic is a direct consequence of the greater transmission of energy through the web. Foraging is now the major component of individual fitness so that evolution increases the transfer of energy from prey to predators. Energy is one of the main factor limiting food chain lengths and the number of trophic levels in food webs (Lindeman 1942; see also Oksanen et al. 1981; Abrams 1993). The second observation is consistent with these theoretical results.

Adaptive foraging has many structural and functional consequences. It imposes energetic constraints that affect the connectance of the web and allows the predictions of interactions based on species body size (Beckerman, Petchey & Warren 2006, Petchey et al. 2008). It lets systems emerge whose characteristics are close to the ones observed in nature, including important structural components such as mean food chain length or amount of omnivory within a web (Loeuille & Loreau 2005). It may also be a key ingredient to explain the stability of complex communities. Most of these interesting results are not only predictions of models, but also of the comparison of these predictions with topological patterns observed in empirical data sets. The following part aims at discussing the interaction of this role with other constraints commonly thought to be involved in community structures.

Adaptive foraging in a changing world: environmental and metacommunity aspects

For adaptive foraging to have a structuring impact on community structure, it is necessary that it happens faster than demographic changes of prey or than evolutionary or plastic changes in the prey affecting energetic content or consumption time (e.g. toxins or digestibility reducing compounds in plants, defensive strategies in general) (Pyke, Pulliam & Charnov 1977, Pyke 1984). Two major components accelerate changes in prey populations: variations in abiotic environment and dispersal from and to neighbour communities. Conditions under which a community is structured by adaptation has been addressed under broader assumptions (Loeuille & Leibold 2008; Urban et al. 2008). Adaptation structures the community when it is fast relative to environmental changes or when dispersal from one community to another is very unlikely. If it is very fast, it may structure the community both at the local and at the regional scale. I revisit these predictions while accounting for the specifics of adaptive foraging. I particularly focus on how adaptive foraging happens, the characteristics of the consumer and of the community.

I distinguish two ways by which adaptive foraging may happen: behavioural plasticity and evolution of new traits. For each of these two, I now discuss how consumer type and community settings interact with adaptation and when adaptive foraging is likely to play an important structuring role.

Adaptive foraging through behavioural plasticity

At a given point in time, the consumer species possess a set of morphological and physiological traits that allows some plasticity in its behaviour. Although the study of behavioural plasticity and its link with foraging is beyond the scope of this article, different types of consumers strongly differ in this amount of plasticity (see Kondoh 2009). This plasticity allows a fast response of the organism to changes in prey popula-
Adaptive foraging through the evolution of new traits

It may seem that evolution of new traits or behaviours has to take a much longer time than the plastic changes described in the previous subsection. It does not have to be the case. Consider a long term environmental change such as global warming. It is indeed very fast for long lived species (elephants for instance), but would be very slow for species that have a short generation time (e.g. bacteria). Therefore, characteristics of the consumer species are very important to determine if foraging adaptation may happen through evolution before environmental change affects its prey. Most critical are the characteristics that directly influence the amount of genetic variation present in the consumer population, as this genetic variation increases the potential for fast evolution. Two obvious characteristics are population size and generation time. Population size may be positively correlated with the amount of genetic variability present in natural populations (Soule 1976; Frankham 1996; Leimu et al. 2006). During a given period, new genetic variation is created through mutations and this additional variability increases when generation time is small and population size high (Wilke 2004). In Fig. 2, I picture two different kinds of consumer. The potential for fast evolution is depicted by the total grey area. It is high for panel 1, because the consumer either has a large population, a short generation time, or both. On the contrary, Panel 2 shows a consumer species whose potential for foraging adaptation via the evolution of new trait is smaller.

In addition to the characteristics of the consumer, the characteristics of the community are also likely to affect evolution of new traits. It is particularly the case for connectivity, measured as a probability of passive dispersal to and from surrounding communities. Evolutionary changes are largely constrained by gene flows, so that the potential for adaptive foraging strongly depends on the dispersers coming in the local food web from surrounding communities. At very low connectivity, gene flow is negligible so that all the genetic novelties on which natural selection acts come from mutations. Evolution of foraging is then quite slow and hardly able to structure the local food web. If connectivity is very high, genetic variability is also low, as genetic variability is reduced at the regional scale due to global competition (Olden et al. 2004; Loeuille & Leibold 2008; Urban et al. 2008). For lack of genetic variability, evolutionary processes will then again be too slow to matter in face of other structuring processes. In between these two extremes, genetic variability is fueled by dispersal, speeding up evolution. In such intermediate scenarios, adaptive foraging process can play an important role in the community structure, hence the hump shape of the grey area in Fig. 2. For more details on the relationship between dispersal and evolutionary adaptation, see Urban et al. 2008.

Integrating foraging adaptation, consumer characteristics and community connectivity

Figure 2 aims at integrating the components presented in the two previous subsections. Panels 1 and 2 correspond to...
different types of consumers, potential for foraging adaptation to happen sufficiently fast is pictured based on plasticity (hatching) or evolution (grey).

Population characteristics that determine the potential for evolution are not independent of behavioural plasticity. Species that have short generation time and high densities are small species (Peters 1983; Damuth 1991; Brown 2004), that usually have limited power in terms of foraging information acquisition and treatment. They are pictured in Fig. 2, panel 1. When adaptive foraging matters for such species it is more likely due to evolution than to behavioural plasticity (but see Dukas & Bernays 2000; Egas & Sabelis 2001). On the contrary, large species have generation times that are long compared with the time-scale on which other structuring effects happen, but their analytical abilities are better, making fast behavioural adaptation more likely (see Kamil & Roitblat 1985 for review, see also Kondoh 2009).

In figure, different food webs are distinguished using letters. When they end up in a white area (B, C and E”) for instance), adaptive foraging is unlikely to play a role, because large changes in the environment or mass effects due to connectivity have much stronger impacts on community structure. If environmental change is very slow, such as for A and D, adaptive foraging can play a key role in the structure of the food web. Note that in the case of D, such adaptive foraging will happen because of behavioural plasticity rather than by evolution. Finally, the Es communities show food webs with intermediate rates of environmental change and intermediate connectivity, likely representing most relevant situations. Adaptive foraging can affect the food web through evolutionary dynamics or behavioural plasticity (E). When environmental change becomes faster (E’), only the most efficient of the two processes will be involved, evolution in the case of the organism displayed in panel 1 and behavioural plasticity in the case of organism displayed in panel 2.

This figure is a simplified version of a complex issue. It pictures only one axis for environmental changes, while abiotic factors involved in ecological niches are many. It is also presented for one consumer. When all predators of the food web are accumulated, each with their specific adaptive capacities, the probability that adaptive foraging of some of them affects food web structure increases. While it is easy to imagine some particular communities, with large or frequent environmental disturbances or extremely open, adaptive foraging could still affect most communities.

**Conclusion**

If and how adaptive foraging affects the structure of complex communities is far from resolved. Communities submitted to very high rates of environmental change or very open to invasion from surrounding communities are probably structured by other processes. So should be communities in which predators have limited behavioural or evolutionary adaptability. Populations of their prey vary too rapidly to allow their adaptation to be meaningful. When conditions under which adaptive foraging matters are met, it is not obvious how its effects, well-known in low-diversity settings, can be scaled up to more diverse food webs. In such webs, adaptive foraging produces additional indirect demographic and adaptive effects that both increase structuring effects and decrease their predictability. In this context, it is reassuring that first theoretical works suggest that the effect of adaptive foraging on food web structures can be often be understood in quite simple terms. The redistribution of interaction strengths among prey species by predators stabilize large food webs. Adaptive foraging also constrains the existence of trophic links thereby determining the connectance of food webs. Finally, adaptive foraging plays a role in the height of the web by affecting the energetic supply from one trophic level to the next. Further theoretical work is needed to understand other effects of adaptive foraging at the community level. Most models presented here use empirical data sets to test their predictions. Such correlations between empirical patterns and theoretical results are important, but they should be complemented by community scale experiments to assess the reality of adaptive foraging as a major driving process. Only such experiments as well as new empirical methods tackling the effects of adaptive processes at population and community scales would allow a full test of the theoretical results summarized here.

**Acknowledgements**

I would like to thank Andrew Beckerman and Owen Petchey for their useful comments, as well as the CNRS and the University Paris VI for support. I thank Ulrich Brose, Frank Messina as well as an anonymous referee for their constructive reviews.

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