REVIEW AND SYNTHESIS

Consequences of adaptive behaviour for the structure and dynamics of food webs

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Abstract

Species coexistence within ecosystems and the stability of patterns of temporal changes in population sizes are central topics in ecological theory. In the last decade, adaptive behaviour has been proposed as a mechanism of population stabilization. In particular, widely distributed adaptive trophic behaviour (ATB), the fitness-enhancing changes in individuals' feeding-related traits due to variation in their trophic environment, may play a key role in modulating the dynamics of feeding relationships within natural communities. In this article, we review and synthesize models and results from theoretical research dealing with the consequences of ATB on the structure and dynamics of complex food webs. We discuss current approaches, point out limitations, and consider questions ripe for future research. In spite of some differences in the modelling and analytic approaches, there are points of convergence: (1) ATB promotes the complex structure of ecological networks, (2) ATB increases the stability of their dynamics, (3) ATB reverses May's negative complexity–stability relationship, and (4) ATB provides resilience and resistance of networks against perturbations. Current knowledge supports ATB as an essential ingredient for models of community dynamics, and future research that incorporates ATB will be well positioned to address questions important for basic ecological research and its applications.

Keywords

Adaptive dynamics, adaptive foraging, anti-predator responses, community stability, community structure, ecological networks, population dynamics, resilience, robustness, stability–complexity debate.

Ecology Letters (2010) **13**: 1546–1559

INTRODUCTION

The coexistence of species in natural ecosystems and the stability of patterns of temporal changes in population sizes are central topics in contemporary ecological theory (McCann 2000). Since the transformative work of May (1972), the earlier conventional wisdom that more diverse communities are more stable than simple communities (McArthur 1955; Hutchinson 1959) lost its hegemony. May (1972), using a mathematical approach to modelling dynamical systems and local stability as the stability criterion, demonstrated that the greater the number of interacting populations in a community, the more unstable the population dynamics tend to be. However, this result rests on simplifying assumptions that there are no constraints on the architecture of species interactions or in the

magnitude of the interaction strengths (May 1972), whereas most natural populations appear to display dampened dynamics (Kendall *et al.* 1998), despite being embedded in complex communities (Pascual & Dunne 2006a). May (1972) encouraged scientists to find the biological mechanisms, the 'devious strategies', that promote the stability of real multispecies systems, which, regarded simply as randomly interacting physical entities, would exhibit unstable dynamics. Since then, various stability concepts have been used in relation to food-web organization and dynamics, including local stability of population densities, persistence of species in the community, and robustness of food webs to species loss (McCann 2000; Pascual & Dunne 2006b). Recently proposed mechanisms that appear to promote various aspects of stability of interacting species in complex systems include high incidence of omnivory (Fagan

1997), particular predator–prey body size ratios (Brose *et al.* 2006), and Type III functional responses of predators (Williams 2008).

One mechanism of population stabilization that has received considerable attention among ecologists and evolutionary biologists is adaptive behaviour exhibited by the individuals that compose populations (Abrams 2000; Bolker *et al.* 2003). For example, early predator–prey models for plankton systems included adaptive prey switching, which tends to stabilize dynamics (e.g. Fasham *et al.* 1990). Among the different types of adaptive traits suggested to have important implications for the dynamics and stability of populations are the adaptive behaviour of prey in response to predation risk (Abrams 2000), the choice of optimal time for ontogenetic niche transition (Takimoto 2003), decisions related to microhabitat occupation (Ramos-Jiliberto & González-Olivares 2000), and optimal diet choice (Krivan & Sikder 1999). A few recent modelling studies of food-web dynamics have begun to explore the implications of adaptive behaviours for the stability of complex ecological networks (e.g. Drossel *et al.* 2001; Kondoh 2003a; but see Matsuda & Namba 1989; for an earlier study). This area of theoretical research has developed quickly through work by a diverse group of researchers from different academic backgrounds using a variety of techniques, concepts, and vocabularies (e.g. Drossel *et al.* 2001, 2004; Brose *et al.* 2003; Kondoh 2003a, 2006, 2007; Beckerman *et al.* 2006; Uchida & Drossel 2007; Uchida *et al.* 2007; Guill & Drossel 2008; Staniczenko *et al.* 2010). Given the major influence that adaptive behaviour likely has on the functioning, stability, and persistence of natural communities, we undertook a review and synthesis of theoretical work dealing with the consequences of individuals' adaptive behaviour on the structure and dynamics of complex food webs, discussing current approaches, their strengths and limitations, and questions ripe for future research.

Adaptive foraging (AF) exhibited by top predators has recently been proposed as an important driver of community persistence, through consumers' coupling of fast and slow trophic pathways in the community as related to the abundances of their resources (Rooney *et al.* 2006, 2008). However, not only top consumers behave as adaptive foragers (Stephens & Krebs 1986). There are numerous empirical studies giving evidence that grazers and secondary consumers engage in AF; for example, planktonic micro-crustaceans (DeMott 1989) and benthic invertebrates (Taghon 1982) in aquatic ecosystems, as well as birds (Shochat *et al.* 2004), small mammals (Giraldeau & Kramer 1982), and insects (Scheirs & De Bruyn 2002) in terrestrial ecosystems. Given the likely importance of top predator AF for community dynamics and the apparently widespread occurrence of AF across trophic levels and ecosystems, it may be a key aspect of how consumers interact with their

resources within food webs, and a major ecological process that enhances the stability and persistence of complex natural communities.

In addition to AF by consumers, organisms can respond adaptively to their consumers, both at ecological time scales in terms of the presence and abundance of consumers (Harvell 1990; Lima & Dill 1990), and at evolutionary time scales in terms of the strong selection pressure that consumers can exert on their resources (Lind & Cresswell 2005). We refer to changes in resource behaviour in response to consumers as adaptive resource responses (ARR). Many types of ARR have been reported in the ecological literature. For example, organisms make behavioural decisions that take into account the current level of predation risk, affecting where and when they feed, reproduce, hide, and flee (Lima & Dill 1990). Environmental cues associated with changing levels of predation risk can trigger phenotypic changes in resource organisms (e.g. inducible defences; Harvell 1990). Effective ARRs can significantly decrease the strength and rate of consumption (Lind & Cresswell 2005) and therefore are likely to alter dynamics of trophically interacting populations (McCann *et al.* 1998), with impacts on community stability and persistence.

Thus, within any food web, in which most taxa play both consumer and resource roles, particular organisms will act both as adaptive foragers and as resources that avoid their consumers through adaptive responses. This widely distributed adaptive trophic behaviour (ATB), the fitness-enhancing changes in individuals' feeding-related traits due to variation in their trophic environment may play a key role in modulating the structure and dynamics of feeding relationships among populations within natural communities. In what follows, we show that addressing the consequences of ATB for food-web structure and dynamics gives insights into at least four core topics in community ecology, with important implications for conservation biology: (1) the incorporation of individuals' traits into understanding the features of food webs (DeAngelis & Mooij 2005; Woodward *et al.* 2005), (2) the potential mechanisms underlying the structure of empirical food webs (Pimm 1982; Williams & Martinez 2000), (3) the classic debate about complexity–stability relationships within communities (McArthur 1955; May 1972; McCann 2000), and (4) the biotic properties that support resilience and resistance of ecosystems to anthropogenic and other perturbations (Westman 1978; Levin & Lubchenco 2008). In the next section, we present a unified framework for assessing the most prominent approaches to including ATB in complex food-web models, providing insight into topic 1. Then, we synthesize the theoretical results concerning the role of ATB in food webs in terms of its consequences on the structure and dynamics of those ecological networks,

providing a way to link ATB with topics 2, 3, and 4. We finish by offering some perspectives on how the incorporation of ATB into food-web structural and dynamical analysis and modelling opens new directions for research that will advance ecological theory and its applications for conservation biology.

MODELLING ATB WITHIN FOOD WEBS: THE INTERPLAY BETWEEN ADAPTIVE TRAITS DYNAMICS AND POPULATION DYNAMICS

Food webs are ecological networks that denote who eats whom within communities (Pimm 1991). Form and function of food webs can be characterized, respectively, by their topology and dynamics. The topology of food webs consists of the set of species that belong to the community, together with the architecture of trophic interactions linking them (Dunne 2006). Food-web dynamics can refer to either the temporal changes in abundance or biomass of their constituent populations (i.e. population dynamics), or sequential changes in the topology of the network as nodes and/or links appear or disappear (i.e. structural dynamics; e.g. Staniczenko *et al.* 2010).

When researchers mathematically model population dynamics of food webs, their equations usually take the form:

$$\frac{\mathrm{d}N_j}{\mathrm{d}t} = r_j N_j + \sum_{i \in R_j} e_{ij} g_{ij} N_j - \sum_{k \in C_j} g_{jk} N_k, \qquad (1)$$

where N_j is the population size of species j, in units of individuals number, biomass, or density. Functions r_j, g_{ij}, and e_{ij} are the intrinsic growth rate, functional response, and conversion efficiency of species j consuming species i, respectively. Function r_j is generally set to zero for non-basal species. The biomass intake of species j that is converted into units of its population size is the sum of the intake from all of its food resources, $\{R_j\}$. Conversely, the population outflow is the sum of losses due to predation by all of its consumers, $\{C_j\}$.

Many implementations of this type of dynamical model treat species' traits as static. There are a number of dynamical food-web modelling studies that allow for consumers to switch among resource species according to their relative biomasses, for example, through the implementation of a Type III multispecies functional response (e.g. Brose *et al.* 2006; Williams 2008; Berlow *et al.* 2009; Brose & Dunne 2009). However, this is a form of passive resource switching that does not reflect explicit adaptive dynamics. As discussed previously, the traits and behaviours of organisms in the context of complex trophic interactions often change adaptively in response to their interactions with (or even the presence of) other organisms. Such ATB can result in a full array of organismal changes from

behavioural change, through developmental plasticity, to changes in gene frequency (Abrams 2005). Despite the scant attention that it has received historically by community ecologists (Abrams 2001, 2005), adaptive trait dynamics may influence population dynamics of interacting species by affecting interaction strengths (Houston & McNamara 1999; Abrams 2001, 2005) and therefore community structure and stability (McCann 2000). Like other adaptive traits, ATB may influence food-web dynamics on both ecological and evolutionary timescales (McCann *et al.* 1998; Abrams 2005). At the same time, ecological and evolutionary dynamics can influence the evolution of traits. Most foraging and anti-predator adaptations are frequency-dependent processes (Abrams 2005) as they depend on the relative frequencies of the interacting phenotypes. As a result, changes in population densities cause the fitness optima for trait values to vary, thus promoting trait evolution (Abrams 2005). Therefore, traits and population dynamics shape each other at multiple time scales (Houston & McNamara 1999; Abrams 2001, 2005).

One of the first approaches to modelling adaptive trait dynamics was developed by Lande (1976). He generated phenotypically based quantitative genetics models consisting of simple recursive relationships of the form $Z = h^2 S$, where Z is the population mean trait value, h^2 is the heritability of the trait, and S is the differential of selection for the trait in the population. However, the incorporation of frequency dependence in these models makes their analysis complicated (Day & Taylor 1996). Fortunately, there exists an approximation to this recursion that has a simple form and allows for frequency dependence. This function defines the rate of change of Z varying at a rate proportional to the slope of fitness W with respect to the value of an individual's trait z (i.e. the fitness gradient or marginal fitness; Abrams 2005):

$$\frac{\mathrm{d}Z}{\mathrm{d}t} = c \frac{\partial W_j}{\partial z}. \qquad (2)$$

Although the choice of which specific trait z is considered will depend on the questions at hand and the modelling strategy, a recurring candidate in studies that include ATB is the amount of energy or time that individuals allocate to consuming resources (i.e. foraging efforts; e.g. Drossel *et al.* 2001; Kondoh 2003a) or avoiding consumers (i.e. anti-predator efforts; e.g. Matsuda *et al.* 1996; Uchida *et al.* 2007). Both effort types affect the consumers' capture efficiency of resource (Stephens & Krebs 1986; Harvell 1990; Lind & Cresswell 2005). The higher the foraging effort invested in a particular resource, the larger the capture efficiency is of that resource (Stephens & Krebs 1986). Conversely, the higher the anti-predator effort of a resource against a consumer, the lower the capture efficiency of that consumer (Harvell

1990; Lind & Cresswell 2005). Hence, these efforts modulate the functional responses of consumers within a community. This modulation may be incorporated into a Type I or a Type II functional response as

$$g_{ij} = a_{ij}f_{ij}(1 - v_{ji})N_i, \tag{3a}$$

$$g_{ij} = \frac{a_{ij}f_{ij}(1 - v_{ji})N_i}{1 + \sum\limits_{i \in R_j} h_{ij}a_{ij}f_{ij}(1 - v_{ji})N_i}, \tag{3b}$$

respectively, where the capture efficiency $a_{ij}f_{ij}(1 - v_{ji})$ is composed of the potential encounter rate a_{ij}, the foraging effort of species j on their resource i, f_{ij}, and the anti-predator effort of i against j, v_{ji} (Uchida & Drossel 2007).

Combining eqns 1, 2, and 3a or 3b to model the interplay between ATB and population dynamics makes it possible to address the temporal changes of foraging and anti-predator efforts as a function proportional to the fitness gradient, taking the per capita population growth rate $G_j = \mathrm{d}N_j/N_j\,\mathrm{d}t$ as a measure of fitness W, that is,

$$\frac{\mathrm{d}f_{ij}}{f_{ij}\mathrm{d}t} = \kappa_j \frac{\partial G_j}{\partial f_{ij}}, \tag{4a}$$

$$\frac{\mathrm{d}v_{kj}}{v_{kj}\mathrm{d}t} = \kappa_j' \frac{\partial G_j}{\partial v_{kj}}, \tag{4b}$$

where κ_j and κ_j' are the adaptation rates of foraging and avoidance efforts of species j, respectively. If $\kappa_j > 1$ or $\kappa_j' > 1$, adaptation is slower than population dynamics and the shift of strategies reflects changes in the gene frequencies within the population j, whereas $\kappa_j > 1$ or $\kappa_j' > 1$ represents faster adaptive trait changes acquired through behavioural responses (Guill & Drossel 2008).

However, system (4) is incomplete because it ignores constraints on natural selection (*sensu* Lloyd & Venable 1992). A fundamental constraint is represented by allocation costs (Futuyma 2001), derived from the impossibility of individuals infinitely and simultaneously assigning energy and/or time to every task, as they have a finite available total effort to allocate across their activities. This constraint can be expressed as

$$\sum_{i \in R_j} f_{ij} + \sum_{k \in C_j} v_{jk} = 1. \tag{5}$$

The combined system (4) and (5) represents rules of evolution for AF and anti-predator efforts. Obtaining the optimal set of these efforts represents a constrained optimization problem, which consists of finding the set of foraging $\{f_{ij}^*\}$ and anti-predator $\{v_{kj}^*\}$ efforts that maximize the corresponding fitness gradient in eqn 4 restricted to eqn 5, and following population dynamics rules of eqn 1 with functional responses (3a) or (3b) (Matsuda *et al.* 1996;

Uchida *et al.* 2007). The available mathematical technique for solving this problem is the Lagrange multipliers, which results in a system of replicator equations (Lloyd & Venable 1992; Matsuda *et al.* 1996; Uchida *et al.* 2007)

$$\frac{\mathrm{d}f_{ij}}{\mathrm{d}t} = \kappa_j f_{ij}\left(\frac{\partial G_j}{\partial f_{ij}} - \gamma\right) \tag{6a}$$

and

$$\frac{\mathrm{d}v_{kj}}{\mathrm{d}t} = \kappa_j' v_{kj}\left(\frac{\partial G_j}{\partial v_{kj}} - \gamma\right) \tag{6b}$$

with $i = 1, 2, ..., \#R_j$ and

$$\gamma = \sum_{i \in R_j} f_{ij}\frac{\partial G_j}{\partial f_{ij}} + \sum_{k \in C_j} v_{kj}\frac{\partial G_j}{\partial v_{kj}}. \tag{6c}$$

System (6) is an optimal strategy, which defines that each f_{ij} and v_{kj} grows whenever its fitness gradient is higher than the fitness gradient averaged over all of js efforts, γ, and decreases when it is lower than γ. In that context, individuals of population j will increase their foraging efforts on i or their anti-predator efforts against k if their payoffs are higher than increasing their efforts on any other resource or against any other consumer. These adaptive dynamics will reach an equilibrium (i.e. $\mathrm{d}f_{ij}/\mathrm{d}t = \mathrm{d}v_{kj}/\mathrm{d}t = 0$ for every i and k) when the marginal fitness of all efforts become equal; that is, when there are not potential changes in any effort that will enhance the per capita growth rate of the population. In this way, the equilibrium solution $\{f_{ij}^*\}$ and $\{v_{kj}^*\}$ of system (6) is both the solution of the constrained optimization problem and an evolutionary stable strategy (ESS) (Hines 1987; Lloyd & Venable 1992; Matsuda *et al.* 1996; Uchida *et al.* 2007).

Note, however, that the population dynamics described by eqns 1 and 3a incorporating both AF and ARR determine that all $\{v_{kj}\}$ go to zero as the per capita population growth rate G_j is always negative unless no effort is being allocated to consumer avoidance (Uchida *et al.* 2007). Thus, under the framework of eqn 1 with linear functional responses (3a), we can only model AF or ARR, but not both simultaneously. Nevertheless, positive values of $\{v_{kj}^*\}$ are ensured, even in the presence of AF, when assuming that foraging contributes to the growth rate in a nonlinear way, that is

$$\frac{\mathrm{d}N_j}{\mathrm{d}t} = B\left(\sum_{i \in R_j} a_{ij}f_{ij}(1 - v_{ji})N_i\right)N_j - \sum_{k \in C_j} g_{jk}N_k. \tag{7}$$

with $B(z) > z$ (Uchida *et al.* 2007). This condition is achieved by $B(z) = \beta z/(1 + \beta z)$ (i.e. Type II functional response) or $B(z) = \sqrt{z}$, whenever $0 < z < 1$ (e.g. Matsuda *et al.* 1994, 1996), which reflects the fact that the use of food becomes inefficient when large quantities are consumed. Another way to ensure positive values of $\{v_{kj}^*\}$ is to

assume nonlinear constrains in the allocation cost of eqn 5, that is,

$$\sum_{i \in R_j} f_{ij}{}^x + \sum_{k \in C_j} v_{jk}{}^x = 1, \tag{8}$$

where $x > 1$ represents that consumers have access to other resource while they are searching for a specific one, and that specific anti-predator responses may also allow the avoidance of attacks by other consumer species (Table 1).

Besides the optimal strategy based on the replicator equation described in eqn 6a, other ways have been developed for incorporating AF into the dynamics of complex food webs (Table 1). For example, Drossel *et al.* (2001) assume that the total foraging effort of any species j is allocated so that the gain per unit effort g_{ij}/f_{ij} is equal for all $\{R_j\}$. This is satisfied by the expression

$$f_{ij} = \frac{g_{ij}}{\sum_{i \in \{R_j\}} f_{ij}}. \tag{9}$$

Note that Drossel *et al.* (2001) *a priori* assume that consumers exhibit an ideal-free distribution across resources (Fretwell & Lucas 1970), which requires a continuous

updating of the efforts values in eqn 9 that depends recursively on the functional response g_{ij} (Drossel *et al.* 2001; Quince *et al.* 2005b). In this way, eqn 9 also leads to an ESS (Drossel *et al.* 2001), an important feature of the ideal-free distribution (Fretwell & Lucas 1970). As the derivation of eqn 9 uses principles from game theory combined with ratio-dependent functional responses (see Drossel *et al.* 2001), we refer to this type of adaptive dynamics modelling as a game theory-based approach (Table 1).

Another approach used to include AF in complex food-web dynamics relies on optimal foraging theory (Stephens & Krebs 1986). Beckerman *et al.* (2006) employed the optimal diet breadth model (DBM) (Stephens & Krebs 1986) for projecting the instantaneous number of links that each species is expected to have within an empirical food web. This model defines how many resources should be optimally included in the diet of an individual of the species j, K_j, considering the net energy E_i, encounter rate λ_{ij}, and handling time H_{ij} that it experiences by consuming an individual of species i (Stephens & Krebs 1986; Beckerman *et al.* 2006). By sorting resources in a decreasing order of profitability (i.e. E_i/H_{ij}), the model projects the optimal value of diet breadth K_j that maximizes the per-capita total rate of food intake of j,

Table 1 Different combinations of adaptive and population dynamics modelling approaches used to include ATB (adaptive trophic behaviour) within complex food webs

Adaptive dynamics	ATB equations	Functional response	Constraints	References
Replicator-based	$\frac{\mathrm{d}x_{ij}}{\mathrm{d}t} = kx_{ij}(\partial G_j/\partial x_{ij} - \gamma)$	Type I	Linear allocation costs	Kondoh (2003a, **2007**)
		Type II or similar	Linear allocation costs	**Matsuda *et al.* (1996)**; Kondoh (2003b, 2005, 2006), Brose *et al.* (2003), Uchida & Drossel (2007), Uchida *et al.* (2007), Garcia-Domingo & Saldaña (2007, 2008)
		Nonlinear allocation costs		**Uchida & Drossel (2007)**, Uchida *et al.* (2007)
		Trade-off with intrinsic growth rate		**Matsuda *et al.* (1996)**
		Predator-dependent	Linear allocation costs	Guill & Drossel (2008)
Game theory-based	$f_{ij} = \frac{g_{ij}}{\sum_{k} f_{kj}}$	Ratio-dependent	Linear allocation costs	Drossel *et al.* (2001, 2004), McKane (2004), Quince *et al.* (2005a,b), Powell & McKane (2008), Powell & Boland (2009)
Solitary optimal-based	$\frac{\sum_{i=1}^{k} \lambda_{ij} E_i}{1 + \sum_{i=1}^{k} \lambda_{ij} H_{ij}}$	Type II	Animal and mathematical assumptions	Beckerman *et al.* (2006), Petchey *et al.* (2008)

In bold are the few works that have modelled ARR (adaptive resource responses). x represents both effort types f_{ij} and v_{kj}.

$$G'_j = \frac{\sum_{i=1}^{K_j} \lambda_{ij} E_i}{1 + \sum_{i=1}^{K_j} \lambda_{ij} H_{ij}}, \qquad (10)$$

where λ_{ij} is defined as the product between the attack A_{ij} and the resource density N_i. In this way, population density of resources but not that of consumers determines λ_{ij} (Stephens & Krebs 1986; Beckerman *et al.* 2006), and hence this model assumes that there is not frequency dependence. This point constitutes the biggest difference between game theory and optimality theory approaches (Giraldeau 2008), as that optimal value does not necessarily constitute an ESS.

In summary, three major approaches have been used to model AF within complex food webs (Table 1). The game theory approach, replicator approach, and optimality theory approach form a frequency-dependence gradient. The replicator approach is the most general of the three approaches, as it converges to the same behaviour as the game theory approach (i.e. a long-term foraging effort allocation leading to an ideal-free distribution across resources) when the foraging effort is frequency dependent. The replicator approach converges to the same behaviour as the optimality theory approach (i.e. consumers feeding on the most profitable resource) when the foraging effort does not depend on the dynamics of the entire food web (Uchida *et al.* 2007). As the replicator equation is based on fitness gradients, it is useful for modelling a broad array of traits (e.g. anti-predator effort), a property that is not shared by the other two approaches.

Extensions to the theory presented above include the incorporation of other costs of ATB, such as a trade-off between anti-predator efforts and intrinsic growth rate of resources (Matsuda *et al.* 1996; Table 1), the consideration of different functional responses (Table 1), and the modelling of ARR that are effective against many consumer species, for example

$$\frac{dv_j}{dt} = \kappa'_j(1 - v_j)v_j \frac{\partial G_j}{\partial v_j}, \qquad (11)$$

which assumes that the defence v_j is effective against all of j's consumers (e.g. Matsuda *et al.* 1994, 1996; Kondoh 2007).

CONSEQUENCES OF ATB ON THE STRUCTURE AND DYNAMICS OF FOOD WEBS

Based on an analysis of the dynamical properties of the models presented above, there are a number of theoretical studies that have addressed the consequences of ATB for the structure and dynamics of complex food webs. In spite of some differences in the modelling and analytic approaches adopted by different researchers, there are some

central points of convergence in their findings about the results of ATB. These points are: (1) ATB promotes the complex structure of those networks, (2) ATB increases the stability of their dynamics, (3) ATB inverts May's negative complexity–stability relationship, and (4) ATB provides resilience and resistance to ecological networks against external perturbations that generate changes in species composition or species abundances (Table 2). In this section, we synthesize the main results of studies addressing these issues.

Structural consequences

Since the beginning of ecology as a scientific discipline, the characterization and analysis of food-web structure has occupied a central place (e.g. Elton 1927, 1958; McArthur 1955; Watt 1964), and has provided a basis for assessing the relationship between community structure and community stability and function (Odum 1953; McArthur 1955; Elton 1958; Watt 1964; Pimm 1982, 1991; Dunne 2006; Stouffer & Bascompte 2010). Nevertheless, only recently have appropriate tools and enough computational power for dealing with complex communities been available to ecologists. In the search for simple rules of community structure that generate complex food webs with properties resembling those of natural ones, several simple, one-dimensional network models have been proposed (Cohen *et al.* 1990; Williams & Martinez 2000; Cattin *et al.* 2004; Stouffer *et al.* 2005). The niche model (Williams & Martinez 2000) and its variants (Cattin *et al.* 2004; Stouffer *et al.* 2005; Allesina *et al.* 2008) predict many aspects of food-web structure reasonably well (Williams & Martinez 2008; Stouffer *et al.* 2005; Allesina *et al.* 2008), but they are phenomenological and do not give a mechanistic basis for explaining structure (Loeuille & Loreau 2005). Other studies that we subsequently describe suggest that AF may be an explanatory mechanism underlying the structure of complex natural food webs. However, the comparison between predicted and observed structural properties has been confined to a small number of network properties, more limited than those analysed from networks assembled using the niche model and its variants.

Petchey *et al.* (2008) proposed an allometric diet breadth model (ADBM) for food-web structure based on solitary optimal theory (Table 1). The ADBM contains parameters representing species richness S, encounter rates, handling times, and energetic values of resources. That model uses eqn 10 to construct the network of interactions by assuming that every species in the network is a potential resource for every other species. Species richness S is obtained from the empirical food web, whereas the remaining parameters are calculated from body masses of consumers and resources through empirical relationships. This model, which incor-

Table 2 Structural and dynamical consequences of adaptive trophic behaviour in complex food webs

Consequences	Non-adaptive	Adaptive	References
Structural			
Number of species	Poorer	Richer	Guill & Drossel (2008)
Realized connectance	Equal to the potential one	Lower than the potential one	Kondoh (2003a,b, 2005, 2006, **2007**), Beckerman *et al.* (2006), Guill & Drossel (2008), Uchida *et al.* (2007), Uchida & Drossel (2007), Matsuda & Namba (1991)
	Equal to the potential one	Equal to the potential one (with nonlinear constraints on efforts)	Uchida *et al.* (2007), Uchida & Drossel (2007)
		Higher when defences are specific rather than general	**Matsuda *et al.*** (1994, 1996)
Number of trophic levels	Fewer than field food webs	Closer to field food webs	Drossel *et al.* (2004), Guill & Drossel (2008), Uchida & Drossel (2007)
Effect of enrichment	None	Increase the number of species	Guill & Drossel (2008)
Effect of body size	None	Increase the number of trophic levels	Guill & Drossel (2008)
Dynamical			
Stability	Less permanent	More permanent	Uchida *et al.* (2007), **Matsuda *et al.*** (1996)
	Less persistent	More persistent	Kondoh (2003a, 2005, 2006, **2007**), Brose *et al.* (2003), **Uchida & Drossel (2007)**
		Persistence is higher when resource's defences are specific rather than general	**Matsuda *et al.*** (1996)
Response to external perturbations	Fragile to species removal	Robust to species removal	Uchida & Drossel (2007), Quince *et al.* (2005)b
	Fragile to species invasion or speciation	Robust to species invasion or speciation	Drossel *et al.* (2001), Guill & Drossel (2008)
Stability–potential connectance relationship	Negative	Positive	Kondoh (2003a, 2006), Uchida & Drossel (2007)
	Negative	Negative	Brose *et al.* (2003)
	Negative	Unimodal (specific defences), negative (general defences)	**Kondoh (2007)**
Persistence-richness relationship	Negative	Negative	Uchida & Drossel (2007)
Robustness-richness relationship	None	Positive	Uchida & Drossel (2007)

In bold are the studies that have modelled ARR (adaptive resource responses). Stability includes both persistence and robustness.

porates AF, predicts 5–65% of the links in 15 empirical food webs. In addition, the model produces mean-standardized errors (MSE) for a set of 12 network structure properties (e.g. mean trophic level, mean path length, proportion of species that are omnivores, etc.) that fall within the range of MSE for the niche model for 12 of the 15 webs. Although not as simple as the prior structural models, the ADBM predicts specific links, reproduces the phenomenological

rules used in those models, and provides a mechanistic basis for suggesting that AF may underlie the generation of complex food-web structure-observed natural systems.

Beckerman *et al.* (2006) introduced the use of the solitary optimal model, but with a parameterization based on published Type II functional responses spanning a wide range of taxa, instead of allometric equations. This earlier DBM predicts species diet breadths that are similar to those observed in empirical food webs. In both the DBM and ADBM, the network of feeding interactions is created by successively applying eqn 10 to each species as a consumer, assuming that all individuals of each species are identical and that all food-web species can be preyed upon (Beckerman *et al.* 2006; Petchey *et al.* 2008). Therefore, the maximal potential diet breadth of each species is $S - 1$. However, eqn 10 restricts the resources that each species consumes to those that are the most profitable for the consumer. As a result, highly constrained values of food-web connectance ($C = L/S^2$) emerge as a consequence of individual optimal foraging behaviour (Beckerman *et al.* 2006). In this way, the DBM predicted well both the level of connectance and the relationship between connectance and species richness of empirical food webs. Note, however, that Allesina (2010) questioned the utility of ADBM and DBM as predictors of trophic relationships, demonstrating a strong similarity between the results of the ADBM and those of the niche model and its variants, which include fewer parameters. This analysis favours simpler models that may represent simpler mechanisms of community structuring (Allesina 2010). Nevertheless, it is plausible that AF might be the biological mechanism underlying the rules of simple models, which have been criticized as lacking of mechanistic basis for explaining structure.

The restricted connectance predicted by Beckerman *et al.* (2006) is a key outcome of most models that include AF in complex food webs, independent of the specific model in use (e.g. Kondoh 2003a, 2005, 2006; Uchida *et al.* 2007; Guill & Drossel 2008; Table 2). Generalist foragers are morphologically and physiologically able to consume various types of food items, but they are also able to choose a subset of them as a function of their profitabilities and abundances (Stephens & Krebs 1986). Therefore, AF constrains the diet breadth of consumers (Stephens & Krebs 1986), a constraint that scales up to the whole network, restricting the possible values of food-web connectance. It is possible to distinguish between potential and realized connectance (Kondoh 2003a, 2005, 2006), where potential connectance C_P considers those links representing the feeding interactions that each species is morphologically and physiologically capable engage in, whereas the realized connectance C_R only considers those links representing the interactions that actually occur (Kondoh 2003a, 2005, 2006; Table 2). When both popula-

tion and adaptive dynamics are explicitly modelled, which is the case for the replicator and game theory modelling approaches (Table 1), the potential number of links L_P are defined by a non-zero encounter rate a_{ij} in eqns 3a and 3b, whereas the realized links L_R are defined by a non-zero effort f_{ij} in those equations. This allows expressing C_R as L_R/S^2 and C_P as L_P/S^2.

Another important result regarding restricted C_R is what Matsuda & Namba (1991) found analytically. They demonstrated that L_R in a food web with Lotka–Volterra dynamics defined by eqn 3a and linear constraints on foraging effort as in eqn 5 is always smaller than $2S$ (Matsuda & Namba 1991). However, when relaxing the allocation cost of eqn 5 by the incorporation of nonlinear constraints on foraging efforts as in eqn 8 with $x > 1$, foraging efforts always increase when they become too small (Uchida & Drossel 2007; Uchida *et al.* 2007). In this way, at a fixed point all efforts are non-zero, and therefore C_R becomes equal to C_P.

Another key consequence of AF on food-web structure is the emergence of the heterogeneous distribution of link strengths, consisting of many weak interactions and few strong interactions. However, the studies that suggest a relationship between weak links and stability have relied on fairly low-dimensional systems (McCann *et al.* 1998; but see Wilmers *et al.* 2002) or on local stability results that suggest the importance of weak links in long cycles (Neutel *et al.* 2002). This has been shown to be negligible compared with shorter cycles and the sign of interactions (Allesina & Pascual 2008). Nonetheless, this distribution has been observed in experimental field food-web studies (Paine 1992; Goldwasser & Roughgarden 1993; Wootton 1997), and has been suggested as an important driver of the stability of complex food webs in nature (McCann *et al.* 1998; Neutel *et al.* 2002). Kondoh (2003a) and Quince *et al.* (2005a), respectively, using a replicator approach and a game theory approach (Table 1), suggest that AF is an explanatory mechanism for that interaction strength distribution. This result was achieved using foraging effort dynamics described in eqns 6a and 8, which resulted in most of $\{f_{ij}\}$ reaching low values and few of them reaching large values. Hence, the same foraging effort dynamics produced both a constrained C_R and a heterogeneous interaction strength distribution, which are key properties of empirical food webs. More results dealing with structural consequences of AF in complex food webs are given in Table 2.

With respect to ARR, there are few studies addressing its consequences on food-web structure (bold references in Table 2). Matsuda *et al.* (1994, 1996) studied the different structural consequences that specific (6b) and non-specific (11) anti-predator defences exert on food webs when they are modelled with species' population dynamics also incorporating AF. When ARR is modelled as non-specific defences, L_R is restricted to be lower than $2S$, but when it is

modelled as specific defences L_R does not have such a constraint (Matsuda *et al.* 1994). Furthermore, non-specific defences allow higher richness, diversity, and total abundance of consumer species, higher connectance, fewer isolated sub-webs, and lower total abundance of resources, as compared with non-specific defences (Matsuda *et al.* 1996). Thus, consumer-specific defences may promote more complex food webs than non-specific counterparts.

Dynamical consequences

The stability and persistence of ecosystems in response to perturbations has been a central concern for ecologists and conservation biologists for a long time (Pimm 1991; McCann 2000; Pascual & Dunne 2006a). Identifying the intrinsic factors that promote or enhance the stability and persistence of populations and communities is both a fascinating scientific challenge and a key issue for making management decisions in a rapidly changing world. Regarding food-web ecology, there is a long-standing and still active debate over what stabilizes complex communities (McCann 2000). In this section, we present results of studies that propose ATB as an intrinsic factor that stabilizes food-web dynamics, a process that can invert the negative complexity–stability relationship proposed by May (1972), and that can increase food-web resilience and resistance against environmentally driven changes in species composition or abundances.

Despite their central position in the ecological knowledge, the concepts of complexity and stability are used in a variety of ways in the ecological literature (Pascual & Dunne 2006b), which can lead to apparently contradictory conclusions when analysing the results of research that addresses their relationship (Pimm 1982, 1991). Below we summarize the different concepts of food-web complexity and stability used in research that studies the consequences of ATB, and then present the main related results and conclusions.

The measures of complexity mainly used in those works are connectance (e.g. Brose *et al.* 2003; Kondoh 2003a, 2005; Drossel *et al.* 2004) and species richness (e.g. Kondoh 2006 Kondoh 2007; Uchida & Drossel 2007). The stability definitions these studies employ can be grouped into three concepts: permanence, persistence, and robustness. None of them rest on the existence of a locally stable equilibrium for the entire food web, but instead consider whether species will remain in the system over a given time horizon. Permanence is often used when the dynamics of a system are analytically studied, and is defined by the existence of a positive boundary for population densities that repel them far from zero. Thus, a system is said to be permanent when there is some mechanism in the system of equations that ensure that species never go extinct (Krivan & Sikder 1999). On the other hand, persistence is assessed when using

numerical simulations for studying model dynamics, and it is defined as the number or proportion of initial species that remain in the system after a finite number of model iterations (e.g. Brose *et al.* 2003, 2006; Ramos-Jiliberto *et al.* 2009; Valdovinos *et al.* 2009). Finally, robustness is also used for numerical simulations and it focuses on the response of some feature of a system to a perturbation, particularly perturbations not common in its development or history (Jen 2003). For example, structural robustness of food webs has been characterized as the amount of secondary extinctions that result from sequential species loss of different types (e.g. Dunne *et al.* 2002; Srinivasan *et al.* 2007; Dunne & Williams 2009; Staniczenko *et al.* 2010). ATB has been shown to promote all three types of stability in dynamical food webs that incorporate AF (Table 2).

Adaptive foraging stabilizes food-web dynamics, in terms of increasing permanence and persistence, by allowing resources to recover their abundances when they become rare (Uchida & Drossel 2007; Uchida *et al.* 2007). This stabilizing mechanism is possible because adaptive consumers decrease foraging efforts against rare resources, provided that other resources are sufficiently abundant (Uchida & Drossel 2007; Uchida *et al.* 2007). This is a similar effect to what is achieved by using a Type III multispecies functional response, where passive switching based on relative biomasses of resources can result in reduced pressure on low abundance resources (e.g. Williams & Martinez 2004; Williams 2008; Berlow *et al.* 2009; Brose & Dunne 2009). Conversely, specific ARR increases persistence and may set permanence in food-web dynamics by enabling the recovery of rare consumers whose resources decrease their avoidance efforts against them (Matsuda *et al.* 1994, 1996; Kondoh 2007). In this way, foraging efficiency of rare consumers is increased until their abundances are recovered. Conversely, if defences are general (11), resources continue to defend against all their consumers whenever at least one of them is sufficiently abundant; therefore rare consumers are unable to recover their densities when competitors are abundant (Matsuda *et al.* 1994, 1996; Kondoh 2007). Those recovering mechanisms for both ARR (Matsuda *et al.* 1994, 1996; Kondoh 2007) and AF (Uchida & Drossel 2007; Uchida *et al.* 2007) can be seen as apparent mutualisms that emerge due to the inherent frequency dependence of ATB, as reported by studies that use replicator approaches to modelling (Table 1).

Another ATB mechanism that has been proposed as stabilizing food-web dynamics, in terms of persistence and robustness, is what we call fitness-enhancing decisions, i.e. the optimal allocation of effort, defined by their adaptive dynamics, which the organisms of a species distribute among their resources and consumers. Those fitness-enhancing decisions might ensure the necessary food intake and a sufficient reduction of consumption risk for a non-

negative population growth rate, even in a changing environment. This mechanism is the most widely proposed explanation for the enhancement of food-web persistence (Drossel *et al.* 2001, 2004; Kondoh 2003a, 2005, 2006; Uchida & Drossel 2007) and robustness (Quince *et al.* 2005b; Uchida & Drossel 2007; Guill & Drossel 2008) due to AF (Table 1).

Both stabilizing mechanisms mentioned above can be encompassed by the more general concept of flexibility of food-web structure (Kondoh 2003a, 2007). This flexibility concept considers a background architecture of interactions composed by the potential links that are activated or inactivated as the respective f_{ij} and v_{kj} become positive or zero. This results in a stabilizing effect on food-web dynamics that can be attributed to both the emergence of apparent mutualisms and fitness-enhancing decisions, keeping the realized connectance at low values (Kondoh 2003a, 2007). Note, however, that flexibility requires an adaptation speed sufficiently high to be effective in conferring stability to food webs, as it should induce food-web restructuring soon after the environmental changes occur (Kondoh 2003a). When modelling AF by means of the replicator equation (6a), adaptation speed of forager j is defined by the constant κ_j (see Modelling ATB within food webs: the interplay between adaptive traits dynamics and population dynamics section). The values of κ_j that have been studied are 0.0025, 0.025, 0.25 (Brose *et al.* 2003; Kondoh 2003a) and $\kappa_j = 2$ (Uchida & Drossel 2007; Guill & Drossel 2008), and it has been shown that the faster the foraging adaptation, the more persistent the food web (Kondoh 2003a). Conversely, the same analysis can be carried out when modelling ARR by means of the replicator equation (6b), where κ_j' determines the speed of species j for reallocating its defence efforts against its consumers. However, no study has addressed its consequences for food-web stability.

The flexibility of food-web structure due to AF may lead to a positive complexity–stability relationship whenever higher complexity implies an increase in potential resource species per consumer (Kondoh 2003a, 2006; Uchida & Drossel 2007). As more potential resources are available for a given species, it has more possibilities to optimally reallocate its foraging efforts after a perturbation. In this way, the higher the potential connectance of a food web, the higher is its flexibility and, consequently, the more persistent and robust it will be (Kondoh 2003a, 2006; Uchida & Drossel 2007). But this conclusion has been questioned. Brose *et al.* (2003) show that stability decreases with potential connectance if more realistic population dynamics are used, for example, a Type II instead of Type I functional response, and the more realistic niche model is used to generate the initial food-web structure instead of random or cascade (Cohen *et al.* 1990) models. Kondoh (2006)

countered this objection by suggesting that the niche model increases potential connectance and decreases the fraction of basal species, which in turn destabilizes the system. He demonstrated that if this confounding effect is removed, a population is more prone to persist in a more complex food web independent of the assembly and functional response models in use (Kondoh 2006). However, as noted above, the definitions of complexity and stability are crucial for understanding their relationship. When complexity is measured as species richness and stability is measured as persistence, their relationship is always negative regardless of whether AF is included or not in the food-web dynamics (Kondoh 2006; Uchida & Drossel 2007; Table 2). Nevertheless, the effect of species richness on stability is reversed when the stability is defined as community robustness (Uchida & Drossel 2007; Table 2). In short, the sign of the complexity–stability relationship arising from food-web dynamics including AF is dependent on the definitions used for these two properties. The relationship will tend to be positive either if complexity is defined as potential connectance, regardless the definition of stability, or if stability is defined as robustness, independent of the measure of complexity.

Regarding food-web flexibility due to ARR, generalized defences lead to a negative complexity–persistence relationship even when complexity is defined as potential connectance (Kondoh 2007; Table 2). However, specific defences lead to a unimodal relationship where the positive region can be explained by the increased extinction risk of consumers that depend on few resource species that likely allocate all their available defence effort against it. The incorporation of another consumer may result in the emergence of apparent mutualisms, allowing the recovery of the focal consumer. However, a high number of consumer species increases the likelihood that resource competition overcomes apparent mutualism, which explains the negative part of the unimodal relationship (Kondoh 2007).

Food-web flexibility is also a key mechanism supporting resilience and resistance of communities to external perturbations that generate changes in species composition or abundances. Among the several types of perturbation that could fall into this class, three of them have been studied for their consequences for food-web dynamics with AF: (1) species deletions (Quince *et al.* 2005b; Uchida & Drossel 2007; Guill & Drossel 2008), (2) species introductions (Drossel *et al.* 2001; Guill & Drossel 2008), and (3) random changes in vital rates, represented as parameter values into the models of population dynamics (Kondoh 2003a). The issue of resistance of food webs against species deletion was discussed previously, under the label of robustness. With regard to resistance of food webs to species introductions, the incorporation of AF into food-web dynamics enhances

robustness against species introductions via speciation or invasions (i.e. introductions of species drive fewer extinctions of native species; Drossel *et al.* 2001; Guill & Drossel 2008; Table 2). Less has been studied about the role of ATB in relation to resilience of food webs facing environmental perturbations, with one study demonstrating that higher values of adaptive rate κ_j of eqn 6a confer resilience to food webs subjected to random changes in populations' vital rates (Kondoh 2003a).

SYNTHESIS AND PERSPECTIVES

In a world experiencing profound changes at a fast rate due to anthropogenic impacts, a deep understanding of ecosystem complexity – what it means, how it emerges and evolves, and what intrinsic factors allow its maintenance – constitutes a critical and deeply challenging task (Pimm 1991). Throughout this review, we synthesized evidence demonstrating that ATB is a fundamental driver of key aspects of complexity in food-web structure, in particular constrained realized connectance (Kondoh 2003a, 2005, 2006; Beckerman *et al.* 2006; Uchida *et al.* 2007; Guill & Drossel 2008) and heterogeneous distributions of link strengths (Kondoh 2003a; Quince *et al.* 2005a). We described how these two structural properties lead to the emergence of stabilizing mechanisms for food-web dynamics. Although the stabilizing role played by heterogeneous link strength distribution for food-web dynamics has been reported elsewhere (McCann *et al.* 1998; McCann 2000; Neutel *et al.* 2002), the significance of constrained realized connectance has not been fully appreciated. Constrained realized connectance promotes the flexibility of food-web structure (Kondoh 2003a; Guill & Drossel 2008), ensuring the emergence of at least two stabilizing mechanisms, apparent mutualisms (Matsuda *et al.* 1994, 1996; Kondoh 2007; Uchida *et al.* 2007), and fitness-enhancing decisions (Drossel *et al.* 2001, 2004; Kondoh 2003a, 2005, 2006; Uchida & Drossel 2007). As at least some structural features that ATB promotes in model food webs match those observed in field food webs (Beckerman *et al.* 2006; Petchey *et al.* 2008), and as ATB is ubiquitous across organisms belonging to nearly every taxon and ecosystem type (Stephens & Krebs 1986; Lima & Dill 1990), its incorporation into models of food-web dynamics appears important for future model-based research. The incorporation of ATB into food-web dynamics highlights the interplay between adaptive and population dynamics, which can help advance more unified ecological theory.

The study of the consequences of ATB on community structure and dynamics has developed quickly in the last decade. However, the technical terminology and implementation of many of the relevant papers has unnecessarily limited their impact on important lines of research in ecology and conservation biology. We have attempted to present, using accessible language, the main insights thus far emerging from this type of mathematical, model-based research, as a means of increasing its utility for the development of both basic theory and better applied research related to complex ecological systems. The latter depends crucially on the former. It will take robust theories of the structure and dynamics of species interactions in ecosystems to forecast responses at multiple scales to changes in the environmental context with enough understanding of both the main drivers and the uncertainties to make appropriate decisions about conservation and management.

Although the explicit consideration of ATB in models of community dynamics offers important new insights on complex ecological structure and dynamics, it comes at the cost of additional model complexity, often driving the models into very high-dimensional space where thorough sensitivity analyses are difficult to implement. Another key challenge will be how to validate aspects of the dynamical models against empirical data. Such validation of complex models is challenging, but not impossible, as demonstrated for dynamical models without explicit ATB (Brose *et al.* 2006; Otto *et al.* 2007; Berlow *et al.* 2009). In addition, there are aspects of ATB that have not yet been addressed in current models that could be included in next-generation models. For example, current models do not consider evolutionary or structural constraints that impede organisms from reaching optimal states with respect to their interactions with every trophic resource or natural enemy. Organisms are unlikely to respond optimally in all circumstances. This issue may fundamentally alter the dynamics of ecological networks, and could change our understanding of the effects of species turnover driven by dispersal, anthropogenic perturbations, and other factors.

Complex dynamical models such as those described here that include ATB can generate qualitative predictions that are relatively robust to changes in parameter values, allowing the use of field data to evaluate contrasting predictions without the need to assume a fixed set of parameter values. The benefits of such models include the large array of important questions they open up to quantitative, computational analysis and more robust theory development and implementation. For example, which structural properties of communities composed of adaptive organisms confer more resistance or tolerance to species invasion? How does the decrease in the proportion of species exhibiting ATB, as expected from extinction of large-bodied predators driven by habitat fragmentation, impact the dynamics of communities and their robustness to environmental perturbations? How does the ATB of pollinators and seed dispersers shape the structure and dynamics of bipartite networks? These are just a few of the many open and important questions that

can be addressed by the next generation of dynamical models that include ATB.

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