

## CHAPTER EIGHT

# The implications of adaptive prey behaviour for ecological communities: a review of current theory

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### Introduction

The overarching goal of community ecology is to address broad problems, from predicting the effects of species' invasion and loss to understanding the processes affecting the diversity, resilience and robustness of ecological systems. Ecological theory addresses these questions through the development of models that examine how species interact within food webs, and how those interactions give rise to the community-level properties we observe in natural systems, such as the relationship between complexity and stability, and the distribution of links across the food web. We argue here that current theory in community ecology is limited in its ability to address these fundamental questions, because it has largely ignored the role of species to modify their traits in response to their environment. This oversight is especially evident from the paucity of theory that considers how the broad problems outlined above are affected by the ubiquitous ability of prey to modify their traits to balance the trade-off between foraging gain and predation risk (Lima and Dill 1990; Lima 1998; Werner and Peacor 2003).

The traditional approach to community ecology is focused largely on linked pairwise interactions between populations, whether through competition, exploitation, or mutualism (May 1973; Pimm 1982; Bender *et al.* 1984; Yodzis 1988; Schoener 1993). These pairwise interactions are treated as building blocks upon which our understanding of larger ecological communities can be built, with the implicit assumption that pairwise interactions are independent of the ecological context in which they are embedded (Wootton 1994; Abrams 1995; Werner and Peacor 2003). A critical evaluation of this assumption began to emerge in the late 1960s. Vandermeer (1969) introduced the notion of 'higher-order interactions' (HOIs) wherein the

interaction between two species is modified by other species in the system. While early attempts to test for HOIs were equivocal (Wilbur 1972; Neill 1974; Werner and Peacor 2003), the idea that species' interactions were not fixed began to gain wider acceptance through the development of foraging theory in the 1970s and 1980s.

Foraging theory was the first formal theory to suggest that the interactions between a consumer and its resources might be altered by ecological context (MacArthur and Pianka 1966; Murdoch 1969; Schoener 1971; Charnov 1976). This theory assumes that consumers optimize their diet depending on the abundance and quality of available resources. Though not reported as such until much later, this was the first ecological theory that included HOIs: a consumer's foraging behaviour, and the strength of the interaction between it and its resources, varied with ecological context (i.e., the abundances of *other* resources in the system). This theory has been widely tested (Stephens and Krebs 1986) and the consequences of flexible foraging by predators for dynamics and structure are now a well-studied problem (McCann and Rooney 2009; Abrams 2010a, b; Beckerman *et al.* 2010).

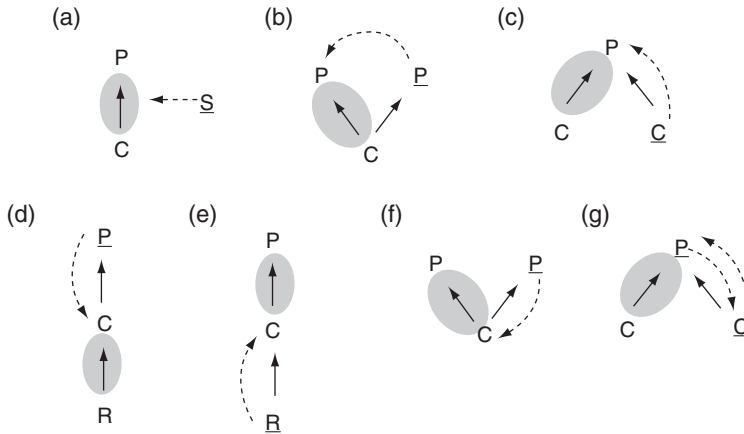
The insights of foraging theory were extended to consideration of how species might adjust their behaviour to balance the benefits of foraging gain against predation risk through the theoretical work of Peter Abrams (Abrams 1984, 1987, 1992). There is abundant evidence that this expression of phenotypic plasticity is common in many taxa, spanning diverse habitats (Lima 1998; Agrawal 2001). Abrams' work predicted that changes in a species' traits could affect not only the interaction of that species with its own predators and resources, but also impact the interactions among other species in the community. Perhaps the most surprising result of this work is that the indirect effect of one species on another, mediated only through trait change in an intermediate species (so-called trait-mediated indirect effects), can have magnitudes equal to, or even larger than, the magnitude of the direct and indirect interactions arising from consumptive effects (Abrams 1984, 1995). Theory developed since this early work has begun to explore the dynamical and structural consequences of trait modification (reviewed in Bolker *et al.* 2003; Abrams 2010b). Nevertheless, despite the mounting theoretical and empirical evidence suggesting that adaptive prey trait modification (hereafter, APTM) can affect ecological dynamics, APTM is seldom incorporated into general ecological theory (Bolker *et al.* 2003; Abrams 2010b), and we therefore know little about its potential influence on many fundamental ecological problems.

We review the theory addressing the influence of adaptive response of prey to predators on the structure and dynamics of food webs. We provide a broad discussion of the importance of HOIs in ecology in order to provide context for the theory on APTM, and because of the potential congruence between the influences of different HOIs. We then discuss the various approaches and

decisions that must be made in order to incorporate APTM into theory. We follow with a review of existing theory on the consequences of APTM for food web structure and dynamics, and highlight how inclusion of APTM can modify canonical predictions regarding apparent and exploitative competition, trophic cascades and the paradox of enrichment, and the relationships among diversity, stability and connectance in food webs. This review of theory provides a basis for an evaluation of the evidence for and against the need to consider APTM to achieve an understanding of ecological communities. Current theory and empirical work strongly suggests that APTM is critical, but current theory and empirical work are not sufficient. We identify key gaps in current theory: the role of environmental variability; the dependence of APTM on system dynamics; and our understanding of the influence of APTM in food webs larger than those typically studied ( $N = 3$ ), and suggest future directions in theory to address these gaps. Finally, we second previous arguments that the most conclusive evidence that APTM is crucial to food web theory will come from studies that integrate theory and experiment, and suggest directions we argue are particularly important in this endeavour.

### HOIs in food web theory

An examination of HOIs provides context for the study of APTM, and may also provide clues to the potential influence of APTM. Several disparate mechanisms lead to HOIs (Fig. 8.1). First, one species, denoted an ecological engineer (a conspicuous example being beavers), may modify the environment in a way that affects the interactions between other species (Fig. 8.1a). Second, predator interference may lead to one predator affecting the predation rate of a second predator on a prey (as in the Beddington–DeAngelis functional response, Beddington 1975; DeAngelis *et al.* 1975) (Fig. 8.1b). Third, predator switching occurs when predator preference for a given prey type is affected by the density of a second consumer prey (Fig. 8.1c). Fourth, predators may become satiated by consuming one prey type, affecting consumption rate of a second prey type (Fig. 8.1c). In both these latter cases a HOI results from one prey species affecting the foraging behaviour of a predator and consequently affecting the interaction between the predator and the second prey. However, the different equations used to describe these HOIs have important consequences for model predictions (reviewed below). Finally, modification of prey traits can lead to a variety of higher-order interactions (Fig. 8.1d–g). In a tritrophic food chain, a predator can indirectly affect a resource when the prey modifies traits in response to changes in predation risk (i.e., predator density, Fig. 8.1d). Conversely, a resource can indirectly affect a predator when the consumer modifies traits in response to changes in resource levels (Fig. 8.1e). In two-predator–one-prey systems, a prey response to one predator may affect predator risk to a second predator (Fig. 8.1f). Lastly, there can be



**Figure 8.1** Schematic representations of the most commonly studied processes leading to HOIs, in which one species affects the interaction between two others. R, C, P and S represent resources, consumers, predators and species with no trophic significance, respectively. Solid arrows represent trophic consumptive interactions, dotted arrows represent induced trait changes, and the grey ellipses represent the pairwise interaction that is a function of a third species. (a) Predator–consumer interaction is a function of another species (e.g., an ecological engineer) that affects environmental conditions that affect the interaction. (b) Predator–consumer interaction is a function of a second predator in the environment that interferes with the focal predators ability to forage. (c) Predator–consumer interaction is a function of a second consumer’s density due to predator satiation or predator switching. In (d–g) HOIs arise from adaptive prey trait modification. (d) A consumer trait-response to reduce predation risk affects the consumer–resource interaction. (e) Consumer trait-response to changes in resource level affects the predator–consumer interaction. (f) A consumer response to a change in one predator’s density affects its interaction with a second predator. (g) A consumer modifies its traits to changes in the predator density. In addition to density changes in the consumer as in (c), these trait changes feed back and in turn affect predator traits (foraging preference).

complex interaction between HOIs if both prey and predators can modify their traits in response to changes in density and traits of the other; here prey adjust traits in response to both predator density and foraging behaviour, and the predator’s foraging behaviour responds to both the density and traits of prey (Fig. 8.1g).

The different HOIs have received varying amounts of attention in the theoretical literature. Whereas they all have a qualitatively similar representation in ecological theory (i.e., species-pair interactions that are dependent on the density of other species in the food web (Dambacher and Ramos-Jiliberto 2008)), we are unaware of any review that has examined the commonalities and contrasts of their effects. It is clear, however, that the inclusion of some HOIs

can strongly influence theoretical predictions. A prominent example is the classic study by McCann *et al.* (1998). In this case, high densities of one resource reduce the consumption rate on a second resource, effectively leading to a sigmoidal (and hence stabilizing) functional response between consumer and resource. While attention to this study has primarily focused on the relative magnitudes of interaction strengths, (i.e., ‘weak interactions’), the higher-order nature of the interaction is key to the stabilizing effect found. Similarly, predator switching has also been shown to have large effects on system stability in small food webs (reviewed in Bolker *et al.* 2003; Abrams 2010b) and on basic food web properties including stability and structure in large webs (Kondoh 2003, 2006; Uchida and Drossel 2007).

### Terminology

The terms used to describe many HOIs, or subsets thereof, are many and often used differently. ‘Trait-mediated indirect effects/interactions’ (TMIE, TMII) (Abrams *et al.* 1996; Peacor and Werner 1997, also behaviourally mediated indirect effects, Miller and Kerfoot 1987) occur when one species affects another species by inducing a modification in an intermediate species’ phenotype, such as behaviour, morphology and/or life history. This would include all of the HOIs described in Fig. 8.1, except for ecological engineers. This term was created to distinguish them from the indirect interactions typically described in theory, termed ‘density-mediated indirect effects’ (DMIE), in which one species indirectly affects a second species by changing the density of an intermediate species (Abrams *et al.* 1996). ‘Nonconsumptive effects’ (NCEs) (Abrams 2008), also termed ‘nonlethal effects’, occur when the predator causes a TMII through inducing changes in prey traits, as in the interactions depicted in Fig. 8.1d–g. In some of the HOIs, there is adaptive predator behaviour (Fig. 8.1b, c, potentially g), and in some others there is adaptive prey trait modification (Figs. 8.1d–g). The term ‘interaction modifications’ (Wootton 1994) has been used to encompass the general effect of one species affecting the interaction between two others, and may refer to any of the HOIs in Fig. 8.1. To investigate the literature in the area, all of these terms should be used as keywords.

### Approaches to modelling adaptive prey trait modification

#### **Methodology for incorporating traits into models: a specific example**

In this section, we review the major approaches that have been taken towards representing APTM in models. As we note above, prey can modify many traits in response to predation risk, including behaviours, such as activity level or habitat choice, morphology, such as the growth of defensive spines, or life history, such as size or reproductive strategy (Tollrian and Harvell

1999). Regardless of the trait under consideration, the fundamental constraint is that modification of the trait involves balancing a fitness trade-off (Bolker *et al.* 2003). The fitness benefit of the type of trait modification addressed here is increased survivorship due to a reduction in predation risk, but this modification carries a fitness cost such as reduced growth or reproduction (e.g., due to reduced foraging) or increased predation risk from another predator (Fig. 8.1d, f).

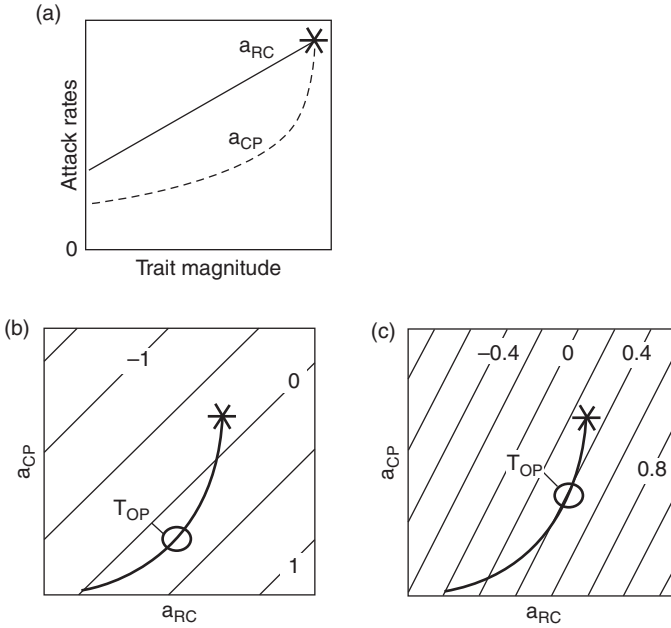
The typical approach to incorporating APTM in a model is to define functions relating prey trait expression to both fitness cost and benefit. As we review below, the shapes of these cost and benefit functions are crucial to determining the effects of APTM. To help provide intuition for this consideration, we review a specific model of Abrams (1984). This model examines indirect interactions in a tritrophic chain in which the intermediate consumer (prey) species ( $C$ ) can adjust its phenotype ( $T_{op}$ ) to changes in predator ( $P$ ) and resource ( $R$ ) density (as in Fig. 8.1d and e).

$$\begin{aligned}\frac{dR}{dt} &= rR\left(1 - \frac{R}{K}\right) - a_0CRT_{op} \\ \frac{dC}{dt} &= b_0a_0CRT_{op} - a_1PCT_{op}^2 - D_1C \\ \frac{dP}{dt} &= b_1a_1PCT_{op}^2 - D_2P.\end{aligned}\tag{8.1}$$

Here  $r$  and  $K$  are the logistic growth parameters,  $a_i$  are predation rate parameters,  $b_i$  are conversion efficiencies of the resource to prey and prey to predator, and  $D_i$  are background mortality rates.  $T_{op}$  is a flexible trait, defined as the optimal fraction of time the consumer spends foraging, although this term could be used to describe the expression of other traits that affect consumption rates. In this model, the cost and benefit of modifying  $T_{op}$  are specified by the functions describing the dependence of consumer–resource attack rate and predator–consumer attack rate, respectively, on  $T_{op}$ .  $T_{op}$  is defined as the time spent foraging that maximizes consumer (prey) per capita growth rate, and thus

$$T_{op} = b_0a_0R/2a_1P.\tag{8.2}$$

Thus an increase in predation risk will lead to a reduction in the optimal foraging time. Key to the subject of this chapter, using this equation for  $T_{op}$  makes the loss term of the per capita resource growth rate equation  $a_0C(b_0a_0R/2a_1P)$ . Adaptive prey foraging therefore makes the resource growth rate equation a function of the predator density, and therefore an example of a HOI since the resource–consumer interaction is now a function of a third species. Similarly, the predator functional response now depends on resource density, leading to another HOI. The nonlinearities introduced by these HOI underlie the unique and key role that APTM has on the system.



**Figure 8.2** Graphical representation of the incorporation of adaptive trait modification in ecological models. These figures correspond to adaptive prey behaviour in a tritrophic chain (Equation (8.1)). (a) A trait change is presented in models as affecting the interaction coefficients between each species pair. The star represents no trait change (e.g., maximum foraging time). A reduction in fraction of time foraging (moving toward origin on  $x$ -axis) more strongly reduces the attack rate on the consumer than it reduces the consumer’s attack rate on the resource. (b–c) Representation of the consumer growth rate and trait change as a function of the attack rates. The straight lines represent the per capita consumer (prey) growth rate isopleths. Without plasticity, as in traditional theory, the potential attack rates are constrained to a point (corresponding to the star in (a)), whereas with adaptive foraging (trait modification), the potential attack rate combinations are constrained to a line. In (c) the resource density is higher than in (b), making the growth isopleths denser and steeper.  $T_{op}$ , the optimal trait modification, occurs at the trait change that maximizes growth rate (indicated by a circle).

To clarify and emphasize the multiple processes and modelling decisions made in this analysis, we use a diagrammatic representation (Fig. 8.2). In conventional theory, the attack rate describing predator–prey interactions is either a constant or a function of one or two of the interacting species. For clarity, we build upon the linear case presented in Equation (8.1). We represent the attack rates (which are proportional to interaction strengths) in a two-dimensional plane, in which the  $x$  and  $y$  axis represent the consumer–resource and predator–consumer attack rates, respectively. In conventional theory (i.e., no trait modification), the trait magnitude equals a constant and

the combination of attack rates would be a single point in this plane, which we indicate by the star. In contrast, with adaptive prey behaviour, the prey can modify the trait magnitude, leading to a range of possible attack rates. Fig. 8.2a illustrates the dependencies shown in Equation (8.1), wherein the consumer–resource and predator–consumer attack rates have a linear and stronger-than-linear dependence on the trait value, respectively. We can translate the two curves in Fig. 8.2a to a single curve illustrating the relationship between the two attack rates, given their functional dependence on the plastic trait (Fig. 8.2b). We can also superimpose the consumer growth rate as a function of the interaction strengths on this figure, as indicated by the parallel isopleths in Fig. 8.2b.  $T_{op}$ , as defined by Equation (8.2), occurs at the point on the curve where the growth rate is highest, indicated by the circle (Fig. 8.2b and c). To illustrate the interplay between the prey’s trait expression and system dynamics, consider how modifying parameters to lead to a higher resource level will affect  $T_{op}$ , which in turn feeds back to affect species abundances. A higher resource level will shift, change the slope, and change the density of the growth rate isopleths, leading to a smaller trait change (i.e., the circle indicating maximum growth rate at the optimal trait change is closer to the star at the trait value in the absence of the trait change). Comparing Fig. 8.2b and c, we see that an increase in resource level increases the per capita growth rate of the prey for both the non-adaptive (compare values at stars) and adaptive (compare values at circles) cases, but that this difference is much smaller in the adaptive case.

### **Methodology for incorporating trait modification into models: general considerations**

As noted above, a key factor in models with APTM is the shapes of the fitness cost and benefit functions, which depend on the assumptions of the modeller. The manner in which cost and benefit functions have been represented in models can be broadly divided into four categories. First, the functional relationship can be explicitly derived from foraging theory (Werner and Anholt 1993; Krivan and Sirot 2004). Second, biologically reasonable relationships that satisfy specific dynamical properties, such as leading to a stable equilibrium, can be chosen (Abrams 1984, 1995, 2003). Third, rather than using explicit equations, only the signs of the derivatives are defined, thereby defining the curvature of the functions (Abrams and Vos 2003). Lastly, equations are used that forgo an explicit representation of traits. In these models, the interaction strength between two species is a direct function of the density of a third species (Arditi *et al.* 2005; Goudard and Loreau 2008). Whereas the approach of forgoing traits can provide a general framework for studying the effects of HOIs by abstracting out the mechanisms that underlie HOI, it is difficult to relate model results with the natural processes that underlie the HOI.



The shapes of the fitness cost and benefit functions have been shown to be absolutely critical to determining the ecological effects of APTM, and many combinations of linear, nonlinear accelerating, and nonlinear decelerating forms have been explored (Abrams 1984, 1992, 2000, 2004, 2007; Ives and Dobson 1987; Schwinning and Rosenzweig 1990; Abrams and Matsuda 1997; Křivan 1997; Křivan and Sirot 2004). We are unaware of any successful attempts at measuring the shapes of these functions empirically, a situation that has been lamented repeatedly in the literature (Abrams 1995, 2001b, 2008; Bolker *et al.* 2003). We address this gap in the Discussion.

### **Modelling the dynamics of trait change**

Once the trait has been incorporated through the specification of fitness cost and benefit functions, a decision must be made regarding the time-scale of prey response, relative to population dynamics. Many studies have assumed that trait modification is instantaneous, as in the example shown above (Abrams 1984; Křivan 1997, 2007). In such models, the trait is essentially represented as a parameter, as in Equation 1, that instantaneously takes on the value that maximizes fitness or maintains an ideal free distribution (Abrams 1984; Schwinning and Rosenzweig 1990). However, this assumption strikes many as too unrealistic (Bolker *et al.* 2003; Abrams 2010b). The most common alternative formulation borrows an approach from quantitative genetics and assumes that the rate of trait change is determined by the steepness of the fitness gradient with respect to the trait (Abrams *et al.* 1993; Abrams 1999, 2001a). A second alternative formulation specifies the rate of trait change as a function of the environment, e.g., predator density, without any reference to fitness (Vos *et al.* 2004a, b). In the two alternative formulations, the trait becomes a state variable with an explicit dependence upon the environment (e.g., the densities of other species), and trait dynamics and population dynamics occur simultaneously. The difference between assuming instantaneous trait change versus specifying a dynamical equation for the trait is not trivial, as a number of studies have shown that different assumptions can produce qualitatively different effects; for example, instantaneous change is often stabilizing, whereas trait change proportional to the fitness gradient can be de-stabilizing (Abrams 1999, 2001a, 2003; Ma *et al.* 2003).

Theory must also consider prey perception of environmental change. Most studies assume that prey trait modification is 'perfect', that is, APTM always increases fitness. However, studies that have introduced error into trait modification, through e.g., imperfect information or limited perception, have shown that this can have large effects on system dynamics (Luttbeg and Schmitz 2000; Abrams and Matsuda 2003; Kimbrell and Holt 2004; Abrams 2007). For example, both Luttbeg and Schmitz (2000) and Kimbrell and Holt

(2004) show that the degree to which prey are able to perceive their environment has important consequences for system persistence.

### **Adaptive prey trait modification in food web theory**

In this section, we review theory on how APTM affects long-term dynamics in small ( $N \leq 3$ ) and large food webs, and identify mechanisms that have consistent effects on food web dynamics. First, we briefly review results from two-species predator-prey systems to provide some context for the considerations of larger webs. We then consider the three basic three-species food web topologies, laid out above, that include APTM (Fig. 8.1d-g). These topologies are the focus of most theoretical studies because they are the simplest systems that can exhibit indirect effects: in one-predator-two-prey systems, the focus is on apparent competition between the prey; in two-predator-one-prey systems, the focus is on exploitative competition between the predators; in tritrophic chains, the focus is on trophic cascades and the paradox of enrichment. For each topology, we address the mechanisms that induce stability or instability, with a special focus on the ecologically relevant indirect effects observed in traditional ecological models. Finally, we review the few studies that have incorporated APTM into larger food webs.

### **APTМ in predator-prey models**

Ives and Dobson (1987) provided one of the first analyses of long-term dynamics in systems with APTM, and suggested that prey trait modification increased stability. Since this paper, studies have altered assumptions about the shapes of the fitness cost and benefit functions and the timing of trait change. In general, instantaneous responses to predation tend to be stabilizing (Ives and Dobson 1987; Křivan 1997, 2007; Cressman *et al.* 2004), whereas incorporating lags can be de-stabilizing. When predation risk increases at a decreasing rate with increasing trait value (i.e., predation risk saturates at high levels of the trait), the effect is often de-stabilizing (Abrams *et al.* 1993; Abrams and Matsuda 1997). This is especially true when the trait is incorporated into the Type II functional response of a predator. De-stabilization results from 'chase' cycles generated by the interaction between prey behaviour and predator satiation: when prey are abundant, predators are satiated; this leads to a reduction in prey defence, which leads to an increase in predation and a declining prey population, which causes prey to increase defence levels. As long as prey and/or predator behavioural responses are not instantaneous, this can lead to unstable population dynamics, though it may not alter the effects on system persistence (Abrams 2000, 2003). However, when risk increases linearly or superlinearly with increasing trait value, this tends to stabilize dynamics (Ives and Dobson 1987; Křivan 1997, 2007; Křivan and Sirot 2004; Cressman *et al.* 2004). Coevolution of prey and predator foraging traits also tends to increase stability (Křivan 2007; Mougi and Nishimura 2008).

### **APTМ in tritrophic food chains**

The tritrophic chain topology (Fig. 8.1d, e) was studied by Abrams (1984) in the first paper introducing the notion of indirect effects arising from prey behaviour (i.e., TMIEs). Abrams documented that interactions arising from trait modification could be of larger magnitude than those arising from consumptive effects (DMIE). Trophic cascades and the paradox of enrichment have been the focus of most of the dynamic studies since that time.

There has been considerable theoretical interest in the effect of APTM on the magnitude of trophic cascades, perhaps motivated by empirical work suggesting that TMII may be the most important cause of such cascades (Schmitz *et al.* 2004). Traditional ecological theory (Oksanen *et al.* 1981) predicts that density-mediated trophic cascades will have consistent effects on species in the chain: in particular, enriching the system will have no effect on the middle consumer, because any increase in prey abundance will be countered by an increase in predator abundance. However, several theoretical studies have shown that APTM in the middle consumer can lead to an increased abundance of the middle species in response to enrichment (Abrams and Vos 2003; Křivan and Schmitz 2004; Křivan and Sirot 2004; Vos *et al.* 2004a, b; Ramos-Jiliberto *et al.* 2008). Abrams and Vos (2003) use a very general framework to show that, depending on the shapes of the fitness cost and benefit functions, each species' equilibrium abundance can change in either a positive or negative direction, emphasizing that including APTM leads to model results that contrast with traditional theory (see also Abrams and Matsuda 2005; Abrams 2009).

The paradox of enrichment (Rosenzweig 1971) describes how increasing the carrying capacity of the basal species de-stabilizes the dynamics of a tritrophic system; increasing basal carrying capacity leads first to cycles, and ultimately to chaotic dynamics (Hastings and Powell 1991). Several studies have shown that APTM tends to be stabilizing (Fryxell and Lundberg 1998; Rinaldi *et al.* 2004; Vos *et al.* 2004a; Ramos-Jiliberto *et al.* 2008); APTM reduces the amplitude of fluctuations, preventing the transition to chaos and stabilizing the persistence of the system.

### **APTМ in two-predator-one-prey webs**

A dominant paradigm in ecology is that two predators cannot coexist on a single prey (Armstrong and McGehee 1980). However, Matsuda *et al.* (1993) showed that coexistence was possible if APTM reduced susceptibility to one predator, while enhancing susceptibility to the other, i.e., if trait modification is predator-specific. This specificity generates a mutualistic TMII between the predators that opposes the density-mediated competitive interaction, enhancing coexistence of all three species. Generalized defensive traits that are equally effective against both predators, on the other hand, promote instability and reduce the likelihood of coexistence. Matsuda *et al.* (1994, 1996) and Kondoh (2007) have extended this finding to show that

predator-specific trait modification is stabilizing, whereas generalized trait modification is de-stabilizing, even when this topology is embedded in more complicated topologies.

### **APTМ in one-predator-two-prey webs**

One-predator-two-prey webs were the focus of much of the early theory on the effects of predator foraging behaviour on ecological dynamics (Murdoch 1969), and recent theory has considered how the inclusion of APTM with predator behaviour can alter standard predictions. In traditional ecological theory, one-predator-two-prey systems are characterized by the negative DMII between the two prey, known as apparent competition, that is expected to lead to competitive exclusion, analogous to exploitative competition (Holt *et al.* 1994). However, if predators alter their foraging behaviour in response to prey density, either through predator switching, diet choice or satiation, the intensity of apparent competition tends to be reduced, permitting coexistence of all three species (see reviews in Fryxell and Lundberg 1998; Bolker *et al.* 2003; Abrams 2010a).

Abrams and Matsuda (1993) were the first to explore the consequences of adaptive foraging in both prey and predators. They showed that this interaction could produce either positive switching (predator preference for most abundant prey, as in predator switching models) or negative switching (predator preference for the less abundant prey), but that the overall result was a mutualistic TMII between the prey. Later studies using similar methodologies (i.e., ordinary differential equation models), but with different assumptions about shape of fitness cost and benefit functions, have confirmed this basic result. In general, APTM tends to reduce the intensity of apparent competition between the prey, making coexistence more likely (Abrams and Matsuda 1996; Abrams *et al.* 1998; Abrams 2000; Yamauchi and Yamamura 2005). Whether APTM is also stabilizing seems to depend upon modelling assumptions related to the shapes of the fitness cost and benefit functions and the relative speed of adaptation (Abrams 2000). Studies of this topology using individual-based modelling further suggest that APTM can lead to stable coexistence. Kimbrell and Holt (2004) allowed prey to evolve modified behaviour to predators (sensitivity) and predators to evolve preference behaviour. They showed the prey sensitivity alone was stabilizing, and that if both prey and predator traits were adaptive, the system was more stable than a system without adaptation.

### **APTМ in larger systems**

There have been very few studies of APTM in larger food webs (Matsuda *et al.* 1994, 1996; Dambacher and Ramos-Jiliberto 2007; Kondoh 2007). Kondoh (2007) examined the influence of APTM on community-level stability metrics in food webs of 3–12 species with multiple trophic levels and different levels

of connectivity. In this model, prey could modify a trait to reduce predation risk, at the cost of reduced reproduction (for non-basal species) or reduced intrinsic growth rate (for basal species). Trait modification was either general (reduced risk from all predators) or specific (reducing risk from one predator led to increased risk to other predators). When models were constrained to two trophic levels, APTM led to HOIs of the form shown in Fig. 8.1f and g; for more than two trophic levels, all of the HOI caused by APTM shown in Fig. 8.1 are possible. Predator-specific APTM led to increased community persistence as the fraction of adaptive species or the rate of adaptation was increased. Further, a positive relationship between the number of connections and the stability of the food web was observed in simulations with few species, while a unimodal connectance–stability relationship was observed for webs with many species. In contrast, generalized trait modification decreased persistence and led to negative connectance–stability relationships. The mechanism underlying these effects was a trait-mediated ‘rescue effect’ explored by Matsuda and colleagues (Matsuda *et al.* 1993, 1994, 1996). In this case, when a prey adapts its trait to a more abundant predator, this increases susceptibility to rarer predators, thereby increasing those predators’ growth rates and ‘rescuing’ them. The decrease in stability as connectance increases in large webs is attributed to increased competition between predators for the same prey. However, if predators were also allowed to forage adaptively, as in Matsuda *et al.* (1993, 1994, 1996), this pattern might change, as adaptive foraging by predators can generate positive complexity–stability relationships (Kondoh 2003, 2006; Uchida and Drossel 2007). Furthermore, the contribution of the HOI caused by APTM in a tritrophic interaction (Fig. 1d, e) was not discussed, and therefore the contribution was not clear.

## Discussion

We have examined adaptive prey traits within the broader context of higher-order interactions and reviewed the most common approaches to incorporating APTM into population models and the theoretical literature concerning the effects of APTM on long-term ecological dynamics. Many studies show that APTM tends to increase system persistence (the coexistence of all species). The qualitative effects of one species on another (for example, the sign of the interaction between them) are often modified by the inclusion of APTM; this is often the mechanism leading to coexistence (Abrams and Vos 2003). APTM is also frequently predicted to have a stabilizing effect on dynamics, preventing large amplitude fluctuations (Abrams 2000; Vos *et al.* 2004a; Yamauchi and Yamamura 2005; Ramos-Jiliberto *et al.* 2008). However, across simple predator–prey, one-predator–two-prey and tritrophic systems, it has been predicted that APTM can de-stabilize system dynamics if the predator has a Type II functional response (Abrams and Matsuda 1997; Abrams 2000, 2003, 2007).

This is a result of 'chase' cycles generated by the interaction between prey behaviour and predator satiation: when prey are abundant, predators are satiated; this leads to a reduction in prey defence, which leads to an increase in predation and a declining prey population, which causes prey to increase defence levels. As long as prey and/or predator behavioural responses are not instantaneous, this can lead to unstable population dynamics, though it may not alter the effects on system persistence (Abrams 2000, 2003).

The current body of theory therefore elucidates important considerations for the incorporation of APTM in theory, and makes clear that APTM can strongly influence model predictions. However, crucial issues remain. In particular, the overarching question of whether APTM is necessary to understand ecological systems has not been definitively answered. We suggest that the evidence from existing theory and experiment is strongly suggestive, but nevertheless equivocal. The current theory has not included factors that are intrinsic to the evolution and expression of APTM and therefore potentially omits processes crucial to understanding their influence in food webs, including environmental stochasticity and trait expression based on system dynamics. Furthermore, APTM studies have largely been restricted to small webs, and it is unclear how the results of these studies will scale up to larger webs. We next discuss these needs in more detail and suggest future directions for addressing them. Finally, we argue that the strongest case for the importance of APTM will be made by studies that bridge the gap between theory and experiment, and discuss particularly profitable directions in this area.

### **Evidence, pro and con, for the need to include APTM in ecological theory**

The broad goals of ecological theory are to understand dynamical and structural properties of food webs that affect basic properties including stability, ecosystem function, diversity and the cascading effects of species introductions and removals. Empirical work strongly indicates that APTM affects the very nature of the interactions between species that forms the cornerstone of ecological theory. A large body of empirical work shows that APTM contributes substantially to the net effect of the predator (reviewed in Werner and Peacor 2003; Schmitz *et al.* 2004; Miner *et al.* 2005; Ohgushi 2005; Creel and Christianson 2008; Heithaus *et al.* 2008; Peacor and Werner 2008; Peckarsky *et al.* 2008). Further, empirical work has supported some counterintuitive theoretical predictions such as a predator having a positive effect on its prey's growth rate (Abrams 1987; Peacor 2002). However, the great majority of empirical studies have addressed short-term effects on fitness correlates, rather than long-term effects on demographic properties including population dynamics, stability and abundance. We address this disconnect between theory and empirical work below, in the section 'Bridging the gap between theory and experiment.'

We argue that the theoretical evidence for the need to include APTM is equivocal: theory to date suggests that APTM should have a strong influence, but there are also crucial elements missing from current theory.

There are two arguments stemming from theory that suggest APTM is crucial to food web theory. First, given the importance of other HOIs in ecological theory (reviewed in section ‘HOIs in food web theory: various mechanisms including APTM’), it is plausible that the HOIs arising from APTM will be similarly influential. Second, the general conclusion of all of the studies summarized here is that APTM appears to have very large effects on system dynamics. In addition to altering the net influence of one species on another, theory predicts that APTM can even change the sign of the interaction between them, and can affect food web properties, such as stability and connectance (Matsuda *et al.* 1994, 1996; Kondoh 2007).

Despite the suggestion that APTM will be important, there are a number of reasons to temper this suggestion. First, the results summarized above are highly dependent upon the assumptions made about the shapes of the fitness cost and benefit functions and the timing of defence expression, and there is very little empirical work that could guide modellers (Abrams 2010b). Second, current theory has largely failed to consider a number of aspects of APTM that are crucial to its role in natural systems. Finally, ecological theory of APTM has almost been exclusively restricted to the study of simple three-species systems, but the translation of these results to large food webs is tenuous. We discuss these three issues in the next section.

### **Future needs for theory of APTM**

#### *Environmental stochasticity*

Despite the recognition that a variable environment is fundamental to the evolution and expression of phenotypic plasticity, including APTM, existing theory examining the influence of APTM has largely ignored environmental stochasticity. This stochasticity can be caused by spatial variability faced by individuals from the same population, or temporal variability due, in large part, to abiotic factors. A winter freeze kills fish in some ponds, differentially and dramatically altering predation risk for many species. An invasive species modifies the environment as an ecological engineer, or has strong influence on a predator’s dynamics, strongly influencing predator-induced effects on prey. It is this type of environmental variability that empiricists are familiar with, and that most empirical studies simulate. However, there are almost no studies of APTM that include such exogenously driven variability. Indeed, not only is stochasticity excluded, but most theory on the effects of APTM is conducted at equilibrium (e.g., Abrams 1984, 1992, 1995; Křivan 1997; Abrams and Vos 2003; Křivan and Sirot 2004).

The incongruence of the importance of environmental stochasticity as a driver of APTM and its absence in ecological models raises concern as to whether existing theory represents APTM accurately enough to give meaningful predictions. Take, for example, studies that examine whether the addition of APTM is stabilizing. We know from long-term observational studies that environmental variation can have large effects on species densities (Werner *et al.* 2007a, b), suggesting that systems may rarely be near equilibrium. Moreover, environmental stochasticity can interact with nonlinearities in ecological models (such as those introduced by APTM) to produce dynamics that would not be predicted through a study of the underlying deterministic model (Coulson *et al.* 2001; Rohani *et al.* 2002). Therefore, analysis done near equilibrium, with the associated assumptions required, may not be relevant. Similar issues may exist in studies that compare the relative magnitudes of DMIEs and TMIEs near equilibrium using the approach, outlined above, of perturbing the system away from equilibrium (Abrams 1984). Small perturbations made near equilibrium may not be representative of the time-integrated influence that APTM has under varying conditions far from equilibrium. Furthermore, stochasticity has the ability to modify the strength of ecological interactions. For example, whereas stochasticity could weaken indirect effects, due to stochastic extinction 'short-circuiting' chains of interaction (Schoener 1993), studies of apparent competition have shown that environmental stochasticity can actually amplify the strength of DMIEs (Holt and Barfield 2003; Brassil 2006).

There are at least three distinct approaches to modelling environmental stochasticity that could potentially be used to examine ATBP. The first adds stochasticity to an existing deterministic model. Coulson *et al.* (2004) review a number of different treatments of stochasticity in these cases, such as adding stochasticity as 'noise' around the deterministic dynamics or in such a way that it can interact with nonlinearities in the model. The second approach treats one of the populations in the system as a stochastic variable (Peacor *et al.* 2006). The third approach uses individual-based models, wherein all of the species are dynamically linked, but the encounters between individuals are stochastic (Luttbeg and Schmitz 2000; Ovadia and Schmitz 2004). There are trade-offs between these different approaches. The first approach can uncover important feedbacks between stochasticity and deterministic dynamics (Coulson *et al.* 2001; Rohani *et al.* 2002), but is challenging to formulate and analyse correctly. The second approach is easier to formulate, but does not include potential feedbacks between populations, as one variable is no longer impacted by others in the system. The third approach is computationally intensive and connecting model predictions to model assumptions can be challenging.

We are aware of only a few studies that have considered environmental stochasticity. In one theoretical study, predator dynamics are modelled as a



forcing function independent of prey dynamics and predator presence varies stochastically (Peacor *et al.* 2006, 2007). APTM strongly influenced system stability by a mechanism that required strong fluctuation in predator density that would not be represented in equilibrium studies. While this study is suggestive, we argue that the inclusion of environmental stochasticity is required for the theory on APTM from first principles, as environmental stochasticity is the dynamical process underpinning APTM.

### **Adaptive prey response to system dynamics**

The existing theory of APTM typically assumes that prey alter traits to maximize instantaneous fitness (Abrams 2010b). Implicit in this assumption is that prey response depends only on the current environmental state. This has the strength of allowing trait change to happen on the same timescale as system dynamics. However, it does not account for the extensive evidence from behavioural ecology demonstrating that prey response is shaped by myriad aspects of both individual state and the environment, including aspects that depend on time horizons of predation risk, life history strategy and length of the growing season (Abrams 1991; Rowe and Ludwig 1991; Lima and Bednekoff 1999; Van Buskirk *et al.* 2002; Pecor and Hazlett 2003). An explicit example of this is the adaptive response of organisms inhabiting ephemeral ponds that must metamorphose before emergence. In this system, the APTM strategy will depend on pond duration (Relyea 2007), so that species or populations in pond types with different durations will respond differently to identical resource and predator densities. From this example, it is clear that assuming APTM depends only on current environmental state can make misleading predictions. Instead, theory must consider how APTM is shaped by natural selection to respond to the dynamics of the system over longer time horizons. There are currently very few studies that optimize APTM over the lifespan while simultaneously allowing APTM to affect system dynamics, likely because the inherent feedback between trait change and the dynamics of the environment makes this a very challenging optimization.

One approach to this problem finds the optimal APTM strategy using iterative techniques, such as state variable dynamic modelling (Mangel and Clark 1989), genetic algorithms (Luttbeg and Sih 2004; Cressler *et al.* 2010) or neural nets (Strand *et al.* 2002). All of these techniques determine the set of 'rules' that maximize expected fitness over a specified time horizon (e.g., the lifespan of an individual or the length of a season). The ecological consequences of this strategy are then found by inserting these rules into a dynamic model. The strength of these approaches is that optimal rules can depend upon any number of factors, including time horizons, individual state or future environmental state. However, it can be difficult (but not impossible) to incorporate population- and community-level effects into these models (Mangel and Clark 1989). Luttbeg and Schmitz (2000) use a state variable

dynamic model to determine optimal prey foraging behaviour, and the consequences of flexible behaviour and imperfect information on system dynamics. In their model, behaviour determined prey fecundity and predator-dependent mortality, and was influenced by the prey's perception of their environment. Prey behaviour fed back on system dynamics through its effect on predator foraging success and reproduction. Given a constraint set (fixed/flexible behaviour/perception), the behavioural strategy that maximized reproductive output was determined and then integrated into a dynamical model of the abundance of the predator and prey over multiple seasons (for another example using this approach, see Takimoto 2003).

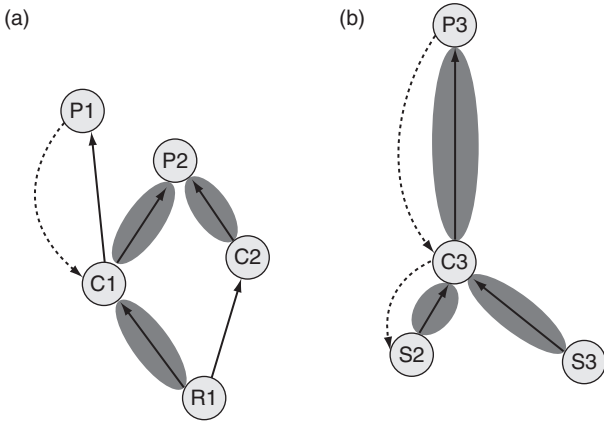
A second approach to incorporate dynamics-based APTM uses computational optimization algorithms to find ('evolve') the optimal foraging strategy of individual foragers (Kimbrell and Holt 2004; Luttbeg and Sih 2004; Peacor *et al.* 2006, 2007). Each individual in the population initially possesses a unique strategy. These individuals are then placed into a dynamic environment (often using an individual-based model) and allowed to grow, reproduce, and die, each according to its strategy. Reproduction between strategies creates new strategy variants, as in evolution, and over time, the biased reproduction of more fit individuals leads to a strategy with high fitness (Holland 1992). The difference between this approach and the one illustrated in the previous paragraph is that here optimization and dynamics occur simultaneously and population- and community-level dynamics are an emergent property of the foraging strategy that evolves. For example, Peacor *et al.* (2007) compare the optimal behaviour of a focal prey in a predator-prey system and in a one-predator-two-prey system. In the latter system, the focal prey cannot perceive the presence of the competitor, but base their behaviour only on resource and predator densities. The growth rate and the optimal behavioural response of the focal prey to identical environmental conditions differ between the two systems due to the long-term effects the competitor has on resource levels. Although not presented, the optimal behaviour was also a function of the time period of predator presence and absence (Peacor, unpublished data). Using a similar approach, Kimbrell and Holt (2004) found that the sensitivity of the prey to predation risk strongly affected the stability of a one-predator-two-prey system.

#### *Scaling up insights from small webs to large webs*

Ultimately, we need to understand the effect of APTM in large food webs to understand their influence on fundamental ecological questions. The majority of studies have, however, focused on low dimensional systems, which can represent 'community modules' (Holt 1997) of strongly interacting species that may be useful as building blocks in assembling complex communities (Bascompte and Mélian 2005; Stouffer *et al.* 2007). Thus, we are closer to an

understanding of the full complexity of ecological systems if the effects observed in small webs persist when these webs are embedded in more complex networks. Existing theory gives conflicting answers to this question. For example, small webs exhibiting chaotic dynamics are stabilized by inclusion into larger webs (Fussmann and Heber 2002). Similarly, unstable trophic modules are stabilized when connected to stable trophic modules in a model of a Caribbean food web (Kondoh 2008). On the other hand, keystone species effects are maintained when keystone systems are embedded into more complex webs (Brose *et al.* 2005).

The attempt to scale inferences from small food web studies of APTM to larger food webs is complicated by two related challenges: the superposition of webs and the interaction of APTM with other HOIs. As reviewed herein, current theory has shown that APTM can have a wide variety of effects, depending on the food web structure and the model assumptions. This makes inference difficult when multiple community modules are superimposed on one another. Consider, for example, the food web shown in Fig. 8.3a. Predator P1 induces APTM in consumer C1. Thus, we can consider at least two modules: the



**Figure 8.3** An heuristic diagram of a large food web. Panel (a) depicts the trait-mediated indirect effects arising from adaptive change in consumer C1’s foraging behaviour. This modified C1’s interaction with its resource, R1. It also affects the interaction of C1 with its second predator, P2. Depending on the shapes of the cost and benefit functions, it is possible for either, both or neither of the modules P1–C1–R1 and P1–P2–C1 to be stable, thereby making it difficult to predict the stability of the P1–P2–C1–R1 system. Panel (b) shows the indirect effects arising from the interaction of multiple APTMs: species S2 can adjust its traits in response to C3, and C3 can adjust its traits in response to both P3 and S2. This leads to trait-mediated indirect effects of P3 on S2 and P3 on S3 (Fig. 8.1d), S2 and S3 on P3 (Fig. 8.1e), and S2 on S3 (Fig. 8.1g). As above, it is impossible to predict, a priori, what effect these TMIs will have on the overall stability of the P3–C3–S2–S3 system. See colour plate section.

tritrophic interaction between P1, C1 and R1, and the two-predator-one-prey interaction between P1, P2 and C1. The APTM of C1 generates a positive TMII between P1 and R1, an effect that has been shown to be stabilizing (Vos *et al.* 2004a; Ramos-Jiliberto 2008). However, if this APTM is effective against predator P2 as well, the P1-P2-C1 system is predicted to be unstable (Matsuda *et al.* 1993). It is unclear whether the P1-P2-C1-R1 system will be stable or unstable. Furthermore, given the ubiquity of APTM, in any given community there will likely be more than one species reacting to the environment through modified traits and therefore multiple interacting HOIs (Fig. 8.3b; Abrams 2010b). This can produce similar problems with inference to those presented by a single instance of APTM leading to multiple TMIIIs. Moreover, work by Abrams (1992) on a four-species chain with two species employing APTM has shown the possibility of highly nonintuitive outcomes.

The inclusion of other processes leading to HOIs in large webs is also limited but informative. The emerging consensus is that they are critical to food web structure, as has been found for predator satiation and predator switching (reviewed in 'HOIs in food web theory: various mechanisms including APTM'). We simply need more work incorporating APTM into models of larger food webs to know if the same will be true for prey trait modification.

Existing studies provide contrasting approaches to incorporating APTM into food web models that can be used as starting points for further theory. The study of Kondoh (2007) is a straightforward extension of the most common approaches reviewed above for small webs, wherein traits are explicitly considered and each species' traits change in the direction of increasing fitness. This study fixed the properties of the web, such as the number of species and connectance, and then studied the dynamics. Arditi *et al.* (2005) and Goudard and Loreau (2008), on the other hand, considered only generalized HOIs, where pairwise interaction strengths depend upon the densities of other species in the web, and take a food web assembly approach, so that the properties of the web are not fixed. The general framework presented in these studies could be adapted to investigate specific APTM, for example by constraining the possible signs of the interaction modification and/or including HOI in specific links (see Dambacher and Ramos-Jiliberto 2007).

### **Bridging the gap between theory and experiment**

There is a large gap between theoretical and empirical work in the study of the effects of APTM (Bolker *et al.* 2003; Abrams 2010b). There are presently hundreds of studies in diverse systems that have demonstrated direct effects of APTM on prey demographics and indirect effects (i.e., TMII) on species interacting with the prey (reviewed in Werner and Peacor 2003; Schmitz *et al.* 2004; Miner *et al.* 2005; Ohgushi 2005; Peacor and Werner 2008). Many new avenues are being explored, including how environmental context

(such as refuges: Grabowski 2004; Trussell *et al.* 2006a, or resource dynamics and experimental duration: Turner 2004; Werner and Peacor 2006) can affect the relative magnitude of TMIs, how APTM can affect ecosystem processes (Trussell *et al.* 2006b; Schmitz *et al.* 2008) and the feedback effects of prey and predator responses to each other (Lima 2002; Luttbeg and Sih 2004). However, despite the profusion of activity in this area, theoreticians' calls for empirical measurement of certain relationships, and for more integration between theory and empirical work, have not been addressed. We are aware of several ongoing investigations moving in this direction (Trussell and Luttbeg, pers. comm., Vandermeer and Baskerville, pers. comm.). We repeat the call of earlier reviews for the need for integration of theory and empirical work here (Abrams 1995, 2001b, 2008, 2010b; Bolker *et al.* 2003).

One critical need is empirical measurement of the relationship between trait expression and fitness costs and benefits (Fig. 8.2). The review above makes clear that varying the shapes of the cost and benefit functions strongly influences theoretical predictions of the effects of APTM (Abrams 1984, 1992; Abrams and Vos 2003; Křivan and Sirot 2004), suggesting an accurate empirical description is necessary. Many biologically reasonable shapes have been proposed (Werner and Anholt 1993; Abrams 2003; Křivan and Sirot 2004), and, theoretically, differentiating between these shapes should be possible based on the results of short-term experiments (Bolker *et al.* 2003). However, surprisingly, we are not aware of a single study that has documented these relationships. A number of studies have shown how different levels of predation risk lead to continuous changes in trait expression (reviewed in Peacor and Werner 2008), but this does not yield the information required. A clear impediment is that the fitness cost curve is inherently difficult to measure; predator presence will affect prey traits, but predation rates must be measured as a function of trait values. There are likely creative ways around this problem, at least in some systems. For example, McCoy and Bolker (2008) quantified the effect of prey size and experience on predator functional response. While not explicitly measuring the shape of the fitness cost and benefit functions (because only two levels of trait modification were considered), the authors do examine the interaction of multiple factors on the strength of ecological interactions and their methodology could potentially be extended to consider cost and benefit functions explicitly.

In addition to the need to measure the functional relationship between trait modification and fitness costs and benefits relationship, is the measurement of the magnitude of the predator effect on consumer (prey)-resource interaction. This parameter is critical to any theory on APTM (representing the predator effect on the second and first terms in the resource and consumer growth rates in Equation (8.1), respectively). In an analysis of empirical studies, Peacor and Werner (2004a) found that induced effect of predators on

consumer (prey) traits commonly modifies the consumer-resource attack rates, a component of interaction strength, in the range of 20–90%. These magnitudes are clearly of an order to be important to dynamics. It would be helpful if empiricists measured the effect of trait modifications on interaction strengths alongside studies of indirect interactions and other responses; e.g., did the large indirect effects reported in a given empirical study arise from a 10% or 50% change in the interaction strength? We are aware of only a few studies that address this problem (McPeck and Peckarsky 1998; Peacor and Werner 2004a; Pangle *et al.* 2007; Creel and Christianson 2008). Furthermore, theoretical studies also seldom investigate how much the interaction strengths varied to produce the results reported. Did they require a 99% change in interaction strengths, which are likely biologically implausible? Attention to this factor by both empiricists and theorists would help to close the gap between empirical and theoretical studies.

We second the call by Bolker *et al.* (2003) in their review of theory of TMIs to integrate theory with empirical studies of the influence of APTM in food webs. There are a number of studies that have begun to move in this direction. The model of Vos *et al.* (2004a, b) was explicitly parameterized from laboratory data and was studied in an attempt to explain a pattern observed in experimental data (Verschoor *et al.* 2004). The individual-based model of Schmitz and colleagues (Schmitz 2000; Ovadia and Schmitz 2004) was calibrated from a mechanistic understanding of a particular field system (Beckerman *et al.* 1997). The short-term model output was then compared against experimental data before using the model to make predictions over longer time periods.

What is needed now is a comprehensive programme that combines theory, laboratory studies and field studies, as has been successfully applied to the study of other processes (Werner 2001). Laboratory (or very controlled field) studies will provide an understanding of the adaptive prey responses and enable the development of theory to form predictions for experiments with multispecies assemblages. Field experiments can then be used to test these predictions. An integrative process between laboratory studies, modelling and field work will yield the manner in which APTM affects the system dynamics. Studies of the context dependence of TMIEs of predators on resources (Peacor and Werner 2000, 2004b; Turner 2004) may be considered an example of a first step in such a research programme. For example, Peacor and Werner (2000) examined the effect of predation risk on an assemblage of tadpole species and size classes. Laboratory experiments yielded information on the APTM of the different tadpole species and size classes. They used this information to build a very simple model that accurately predicted the effect of predator-induced modification of prey behaviour on competition, and predicted how environmental factors (such as growing versus nongrowing resources) influenced the magnitude of predator-induced changes in prey

growth rates. This validation of short-term predictions is an important step, as the results are complex and require a model to help interpret them (Ovadia and Schmitz 2004). For example, under certain conditions, predator-induced changes in prey behaviour may have no effect on the prey's growth rate, but a strong indirect effect on the growth rate of the prey's competitors (Peacor and Werner 2000). Ultimately, what is required are quantitative predictions of the influence of APTM over longer (multigenerational) timescales in systems with many species. Experiments in controlled venues (e.g., mesocosms) will be helpful to develop this approach and yield insights into the processes, but ultimately, field-based studies using this approach will have the highest impact.

An alternative approach to integrating theory and data is the re-examination of existing time series data. A number of 'classic' ecological patterns, such as the cycles between lynx and hare abundances in the Arctic and cycles in Scandinavian voles, occur in systems in which APTM is hypothesized to be operating (Sundell *et al.* 2004; Peckarsky *et al.* 2008). These time series have been the subject of extensive modelling efforts, and so, for many of these systems, parameterized models already exist (Turchin 2000; King and Schaffer 2001). A profitable direction may be to revisit some of these time series and quantitatively test whether the inclusion of APTM into existing models is able to better explain the observed patterns. Such an indirect test was performed in the study of Dambacher and Ramos-Jiliberto (2007), who showed that by extending a previously published model for a lake food web by including APTM, they were better able to predict observed patterns of clear water phases.

## Conclusions

A principal goal of our review has been to address whether the adaptive response of a species to predation risk, herein denoted adaptive prey trait modification, is required for ecological theory to address adequately fundamental questions in community ecology, such as the relationship between stability and diversity, community resilience and robustness, and predicting the effects of species' invasion and loss. We argue that the current theoretical evidence is suggestive, but not definitive. This assessment is based on the exclusion of important processes intrinsic to APTM and the limited amount of theory in larger systems. On the other hand, APTM will likely strongly influence theory based on first principles: empirical studies have shown that the basic building blocks of food web theory, pairwise species interactions, are greatly impacted by changes in food web context and the consequent TMIs observed in many systems are testament to the influence of APTM. The underlying mechanism for such TMIs, phenotypic plasticity in traits involved in fitness trade-offs, has been documented in hundreds of species. Further, existing theory in simple systems supports the supposition that APTM is

critical by demonstrating that its inclusion has dramatic effects on standard outcomes in each of the classic configurations examined, and inclusion of other forms of HOIs has large impacts on theoretical predictions (Kondoh 2003; Uchida *et al.* 2007; McCann and Rooney 2009; Abrams 2010a; Beckerman *et al.* 2010). Yet despite this evidence, even theoretical studies that demonstrate the important of interaction strength in dynamical models (e.g., Neutel *et al.* 2002; Pawar 2009) are not considering the potential implications of the dynamic nature of these interaction strengths introduced by APTM (Kondoh 2007). We therefore argue that theory in large, complex systems that include APTM is needed, and that there is much to be garnered to inform such studies from present studies in small systems. What is most essential is much tighter integration of theory and data than has been achieved heretofore. Many of the above-mentioned gaps in current theory will likely be addressed by coupling system-specific models with empirical studies that examine systems with more (i.e.,  $N > 3$ ) species over long timescales and measure relevant parameters and functional shapes needed for close integration with ecological theory. Such a research programme will go a long way towards answering the question of whether APTM is critical to the structure and dynamics of ecological systems, and given the overwhelming evidence of the potential importance of APTM to fundamental ecosystems properties, we expect much empirical and theoretical activity in this area in the coming decades. We second the call of previous reviews (Bolker *et al.* 2003; Abrams 2010b) for these activities to be done in tandem.

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