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CONNECTING THEORETICAL AND EMPIRICAL STUDIES OF TRAIT-MEDIATED INTERACTIONS

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Abstract. Trait-mediated interactions (TMIs), in which trophic and competitive interactions depend on individual traits as well as on overall population densities, have inspired large amounts of research, but theoretical and empirical studies have not been well connected. To help mitigate this problem, we review and synthesize the theoretical literature on TMIs and, in particular, on trait-mediated indirect interactions, TMIIs, in which the presence of one species mediates the interaction between a second and third species. (1) In models, TMIs tend to stabilize simple communities; adding further biological detail often reduces stability in models, but populations may persist even if their dynamics become mathematically unstable. (2) Short- and long-term changes in population density caused by TMIs depend even more on details, such as the curvature of functional responses and trade-offs, which have rarely been measured. (3) The effects of TMIs in multipredator communities depend in a straightforward way on the specificity of prey defenses. (4) Tritrophic and more complex communities are theoretically difficult; few general conclusions have emerged. Theory needs new kinds of experiments as a guide. The most critical needs are experiments that measure curvatures of trade-offs and responses, and experiments that (combined with theory) allow us to scale from short- to long-term responses of communities. Anecdotal evidence from long-term and large-scale studies suggests that TMIs may affect community dynamics at practical management scales; community models incorporating TMIs are necessary and require closer collaborations between theory and experiment.

Key words: community models; competition; empirical study; food web; foraging; indirect interactions; individual traits; long-term response; module; population density; trait-mediated interactions; trophic.

SPECIAL FEATURE

INTRODUCTION

The study of ''trait-mediated interactions'' (TMIs), in which trophic and competitive interactions depend on individual morphological, behavioral, or life-history traits as well as on overall population densities, is an increasingly rich subfield of community ecology. The literature of behavioral ecology amply demonstrates that organisms show adaptive changes in behavior, morphology, and life history in response to the pressures of starvation and predation. Emerging work shows that these changes can influence community dynamics in ways that are not predictable by classical population models (Sih 1997, Werner and Peacor 2003). Empiricists have shown short-term effects of behavior on foraging success and predation risk (Werner and Anholt 1993), while theoreticians have shown that adaptive trait change can alter the short- and long-term dynamics of communities under a broad range of plausible ecological scenarios. In particular, theoreticians have shown that trait modification can change the expected direction of species' density changes under community manipulations (Abrams 1992*b*); the population dynamics and persistence of communities (Murdoch and Oaten 1975, Abrams 1982, Holt 1984, Gleeson and Wilson 1986, Křivan 1996, 1997, Křivan and Sirot 1997, Schmitz et al. 1997, van Baalen et al. 2000); the relative strengths of direct and indirect interactions (Abrams 1995); and the number of interactions in food webs (Matsuda et al. 1994, 1996).

Despite this growing body of evidence, the importance of TMI has not been wholeheartedly accepted by community ecologists. Most, whether empiricists or theoreticians, continue to assume fixed traits and independent pairwise interactions in their models and experiments. Why? Three possible reasons are (1) the profusion of theory, which can be hard for a nonspecialist to assimilate; (2) the general focus of TMI theory and theory-testing experiments on short-term effects, and an accompanying tendency to neglect the community-level context of TMIs; and (3) the disconnection between TMI theory and its empirical base. This paper seeks to mitigate some of these problems. We provide a synthesis of the theoretical lit-

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erature on TMIs involving multiple species, supporting our argument that large portions of this literature are mature and ready to serve as a foundation for new and different kinds of studies. The review highlights opportunities for theorists and empiricists to work together to test TMIs in novel ways, using short-term measurements of critical parameters such as partial preferences or the curvature of cost and benefit functions to scale up to longer time scales at which many questions about the importance of TMIs remain unanswered.

We will concentrate mainly, although not exclusively, on trait-mediated indirect interactions (TMIIs), changes in the interaction between two species that result from changes in traits of another (third) species in the community. The classic example is trait-mediated indirect competition, in which induced morphological or behavioral defenses on the part of one prey species lead to heavier predation pressure on another prey species. We will ignore studies of indirect interactions, such as classical apparent competition (Holt 1984), that are mediated solely by density rather than depending ultimately on some combination of trait and density changes. We also neglect trait-mediated changes in isolated predator–prey systems, which are direct rather than indirect interactions. However, much of our discussion is relevant to direct as well as indirect trait-mediated interactions.

We first briefly review the various theoretical frameworks that have been used to incorporate trait modification into models of population and community dynamics, focusing on untested connections between theoretical frameworks and empirical data. These frameworks, and the categories of behavioral changes that they suggest, serve as the foundation for the main part of the paper, a review and synthesis of the many models of community dynamics with TMIs. Finally, we use this review to discuss the state of the field, and to suggest profitable directions for ecologists interested in TMI.

Two of the ingredients of a general understanding of TMI, short-term qualitative experiments and long-term strategic theory, are well in hand. The two missing pieces are knowledge of the shapes of response functions (as opposed to tests of significant effects of trait modification) and the ability to scale all the way from observed trait changes and short-term changes in predation rates to longer term effects on population densities. To fill these gaps, theoreticians and empiricists should collaborate on integrated studies. Examples of such studies that integrate adaptive individual-level mechanisms (whether they deal with TMII or not) with population dynamics are Tilman's work on plant communities (Tilman 1982, 1988) and McCauley and co-workers' studies of microcosm communities built around *Daphnia* (McCauley et al. 1999, Nelson et al. 2001). At the end of this paper, we sketch an outline for such a collaborative study on TMII.

Community ecologists lack the time to incorporate all possible factors in their models: the effects of stochasticity, spatial or size-structured populations, and genetics all compete for their attention. Integrated theoretical and empirical studies of focal systems are the next step toward establishing whether TMI matters to the broad sweep of community ecology, and which aspects of trait mediation are most important in natural systems. If theoreticians and empiricists interested in TMI can hang together instead of hanging separately, they will set an example for all ecologists of how theory and experiment can move forward and establish new ideas about the mechanisms driving ecological communities.

Incorporating Trait Modification in Models of Community Dynamics

In order to categorize theoretical results on the effects of TMI, we must define some basic categories of trait modification. For this purpose, we briefly describe how individual-level trait changes have been incorporated into population dynamic models; these models, which scale from individual traits to interactions between populations, are important components of the general theory of TMI. Some of these formulations are not specific to TMI, but also apply to direct interactions in predator–prey models. The status of these models (a well-worked-out theory, with many models and general tests, but few detailed tests that measure both the details of trait modification and their effects on population-level dynamics) resembles that of community models of TMI.

In the broadest sense, traits include any property of an organism that affects its trophic activity (foraging rate on prey or mortality risk from predation) or its life history. We will focus, as most TMI researchers have, on short-term plastic changes in behavioral traits, but at an ecological level, any trait change is expressed through its effect on life-history and trophic characteristics, and is constrained by the trade-offs between these characters, e.g., between predation risk from two different predators, or between predation risk and starvation risk (McPeek and Peckarsky 1998). Behavioral changes are plastic on a short time scale, which appeals to empiricists. However, the same kinds of trade-offs apply to morphological or life-history changes. For example, growing defensive spines could simultaneously reduce predation risk and incur a metabolic cost (Harvell 1998), leading to a fitness trade-off analogous to switching between a risky, resource-rich environment and a risk-free, resource-poor one. Similarly, metamorphosis can be treated as a drastic, irreversible form of habitat shift (Werner and Gilliam 1984). The appropriate time scale for incorporating behavioral shifts into models, whether organisms can be treated as optimizing their behavior instantaneously, and how this changes qualitative conclusions, is still an open question that will have to be settled on a case-by-case basis for specific systems (Ives and Dobson 1987, Abrams 1992*a*, Persson and de Roos 2003). We still expect that the broad general conclusions of the theory on the feedback between individual-level behavioral traits and community structure and dynamics should apply to long-term phenotypic trait changes as well, or even to evolutionary (genetic) trait changes.

We partition induced trait changes into three categories: diet selection, activity or time budgets, and habitat selection. We briefly discuss how each category has been incorporated into theoretical population dynamic models, and mention what (if any) quantitative tests have been applied to the models.

Although these categories are distinct in the empirical literature, the mathematical models that describe them are often conceptually, or even structurally, equivalent. For example, ''diet selection'' describes a consumer that can feed on multiple prey types within a single habitat, while one form of ''habitat selection'' describes consumers that feed on different prey types in different habitats (Lawlor and Maynard Smith 1977, Abrams 1987*c*). However, if the cost of travel (measured in time, energy, or risk) between habitats is negligible and prey encounter is sequential and random, then a single mathematical model describes both scenarios; the only distinction is the spatial scale of diet choice. Similarly, habitat selection and activity budgets are strongly correlated. One could describe hiding under a rock, which reduces both foraging rate and predation risk, either as a habitat choice or a reduction in activity. The two descriptions are equivalent if (1) there is no cost to changing habitats, and (2) risk and reward are both linear functions of activity, such as when activity level represents the fraction of time spent foraging.

Diet selection

Prey-switching models, the original framework for incorporating diet selection in population models, simply assumed that predators preferentially choose the most abundant prey item (positive switching), usually as a sigmoidal function of relative frequency (Murdoch 1969, Murdoch and Oaten 1975, Papaj and Prokopy 1989). Although empirical tests have found positive switching in some systems (Manly 1973, Murdoch and Oaten 1975), there are many potential complications such as simultaneous use of different resources (Murdoch and Oaten 1975), variation in prey quality (Werner and Gilliam 1984), and spatial heterogeneity (Schluter 1981).

Prey-switching models have been successful in predicting behavior, but they do not distinguish between different proximate causes of predator choice, nor are they easy to generalize across systems. In contrast, optimal foraging models address the evolutionary consequences of diet selection and include explicit behavioral rules for maximizing instantaneous fitness (e.g., Schoener 1971), based on some combination of the energetic content and handling time of resources (Belovsky 1986, Stephens and Krebs 1986). They predict optimal switching rules as a function of foraging trade-offs (MacArthur and Pianka 1966, Schoener 1971), or more generally allow diet choice to vary over time according to models of genetic or behavioral change (Abrams 1992*a*, 1999). The results vary according to the currency of maximization (energy or combinations of different substitutable, complementary or nonsubstitutable nutrients; Westoby [1974], Leon and Tumpson [1975], Pulliam [1975], Abrams and Shen [1989], Hirakawa [1995], Fryxell and Lundberg [1998]); maximization constraints such as time or digestive constraints (Abrams 1990*a*, Rothley et al. 1997, Schmitz et al. 1997, Abrams and Schmitz 1999); and foraging arena (sequential or simultaneous choice of food items).

Short-term empirical studies (reviewed by Stephens and Krebs 1986) have supported optimal foraging models. However, in some situations in which these models predict that consumers should take only one resource, partial preferences exist where consumers continue to take some of the less preferred prey type (Krebs et al. 1977, Hubbard et al. 1987). Partial preferences could result from constraints on predator choice such as required nutrients in the less abundant prey (nonsubstitutability), limited gut content (Abrams and Schmitz 1999), sequential choice, nonrandom prey encounters (Belovsky et al. 1989), limited perception of predators (Berec and Křivan 2000), or the need to sample prey periodically to update information about their value (Krebs et al. 1978). Alternately, they could represent true mistakes; experimental data suggest that mistakes in diet choice are most common when the opportunity costs of such mistakes are low (McNamara and Houston 1987; reviewed by Fryxell and Lundberg [1998]). More study of both the shape of partial preference curves and their underlying mechanisms is critical, because (as we will discuss) the difference between a sharp and a gradual transition in diet choice has implications for community dynamics. In order to generalize about the long-term importance of TMI, we would like to be able to scale all the way from predator decision rules, to the outcome in a diet choice experiment, to fitnesses and changes in population densities.

Activity and time budgets

Many prey species adjust their activity level in response to the presence of predators and the density of resources (e.g., reviews by Lima 1998*a*, *b*, Werner and Peacor 2003). A variety of behavior changes, including reductions in the rate of movement, increased use of refuges (Lima 1998*b*), and antipredator behaviors such as escape responses, have similar costs (reduced foraging, leading ultimately to reduced reproduction and increased risk of starvation) and benefits (reduced predation risk; Ives and Dobson 1987). One common limitation of these studies is that they have treated animals as completely inactive or active at any moment. Most animals, however, vary their activity levels more continuously (Lima 1998*b*).

Different assumptions about the mode of activity change are incorporated in models by specifying costs (reduction in birth rate or foraging success or increase in death rate) and benefits (reduction in predation rate) as a function of activity levels. Activity level can be assumed to be optimized instantaneously to maximize fitness (Ives and Dobson 1987); it can change at a rate proportional to the derivative of fitness in a way that reflects either genetic change or gradual learning (Abrams 1992*a*, 1999, Houston et al. 1993, Abrams and Rowe 1996, Abrams and Matsuda 1997) or it can be derived from a full dy-

namic optimization model (Werner and Anholt 1993, Crowley and Hopper 1994, Luttbeg and Schmitz 2000, Luttbeg et al. 2003). These models have been tested in experimental microcosms many times and have been found to predict (at least the sign of) behavioral changes of organisms under threat of predation (Anholt and Werner 1995, Johansson and Rowe 1999, Anholt et al. 2000, Richardson 2001; reviewed in Lima 1998*b*), but we rarely know how rapid the changes are and whether they conform better to an instantaneous or a gradual model. Differences in the details of how activity level is incorporated in theoretical models do, alas, affect their conclusions (Ives and Dobson 1987, Abrams 1992*a*). Once again, this implies that empiricists need to refine their experiments to guide theoretical models; is the assumption that prey instantaneously optimize their foraging rate sufficient, or should theoreticians continue to pursue models of more gradual change?

Habitat selection

Most information about habitat selection comes from tests of optimality that measure either fitness (Fretwell and Lucas 1970, Morris 1988) or components of fitness in different habitats (Werner and Hall 1976, Werner et al. 1983, Werner and Gilliam 1984). Functional responses representing optimal habitat selection behavior have been developed for single consumer species, competing consumers, and consumers that are preyed on by predators (Murdoch 1977, Abrams 1982, 1987*c*, van Baalen et al. 2000). Some of the important distinctions in determining an optimal foraging rule are the linearity of payoffs; whether predators have a bias in habitat preference; and whether habitat choice involves error (Murdoch 1977, Nisbet et al. 1993). As with diet selection and activity budgets, there are a variety of additional complexities that could be incorporated in population-level models. These include allowing individuals that arrive earlier at sites to defend them against individuals arriving later (ideal preemptive selection; Pulliam 1986); incorporating variation in individual abilities to defend or acquire resources (Parker and Sutherland 1986, Mc-Namara and Houston 1990); allowing for costs of changing patches (Charnov 1976, Rosenzweig 1981, Fryxell and Lundberg 1998); and adding other constraints on foragers such as interference competition and predation (reviewed by Rosenzweig 1991; Fryxell and Lundberg 1998).

Prey may also choose their habitat to evade predators. There is extensive evidence that habitat choice is influenced by predation risk (reviewed by Lima and Dill 1990; Fryxell and Lundberg 1998), and empirical studies show that species can balance risks of predation with the gains from foraging (e.g., Sih 1980). However, the precise forms of behavior that are included in functional responses (e.g., Fryxell and Lundberg 1998) and the forms of the resulting functions have not generally been tested.

The models of behavior discussed here serve as building blocks for the community models discussed in the next section. The qualitative predictions of the simplest models have been thoroughly tested with combinations of behavioral and population-level measurements, but quantitative data on the *shapes* of gradual responses, which make qualitative differences in outcomes at the community levels, are lacking (Abrams 1992*b*, 1995). Some of the more complex models also remain untested, simply because there are many possible factors (and factorial combinations) to explore both in experiments and in models. Surprisingly small details can be important, which makes it hard for empiricists to allocate finite research budgets, or for theoreticians to simplify and generalize models. Many quantities remain unmeasured in short-term empirical studies; integrated studies of focal systems will help us to decide which details are most important.

Community Dynamic Models

We now turn to the literature on the effects of TMI in multispecies communities. Because our main interest is in indirect interactions (sensu Abrams 1995), we restrict ourselves to studies of communities with at least three species. For this reason, we omit studies on the effects of trait-mediated effects in isolated predator–prey systems (Ives and Dobson 1987, Abrams 1992*a*), including a large literature on the effects of plant quality and tolerance in plant–herbivore or plant–pathogen–herbivore systems that suggests that plastic or evolutionary changes in plant traits can destabilize plant–herbivore systems (Edelstein-Keshet and Rausher 1989, Foster et al. 1992, Underwood 1999, Chase et al. 2000). We have also restricted our scope to models of classical behavioral ecology in which species traits do not evolve. In most, but not all, of the studies, adaptation is considered to take place by rapid behavioral changes, although there are reasons to expect short- and long-term evolutionary optima to be similar in many cases (Day et al. 1994, Losos et al. 2000, Richardson 2001). We similarly do not include any ''evolutionary game'' studies in which individuals have to take the strategies of conspecifics into account, or any models incorporating explicit population genetic models of behavior. In this paper we mostly consider ''top-down,'' population-based models, in which the effects of stochastic and systematic variation between individuals in a population are largely ignored, although we discuss these models briefly in the *Conclusions.*

A final omitted category is host–parasite systems, in which both empiricists and theorists have pointed out that sublethal infection may change host traits ranging from fecundity to predation risk (Hudson et al. 1992, Lefcort and Blaustein 1995, Marvier 1996, Murray et al. 1997, Mesa et al. 1998, Boots and Norman 2000, Myers et al. 2000), especially in systems where parasites are transmitted from one host species to another via predation (Lafferty 1992, Lafferty and Morris 1996). The indirect effects of parasites can range from destabilization of predator–prey cycles (Ives and Murray, 1997) to changes in the biodiversity and energy flow of ecosystems (Thomas et al. 1997, 1998).

TABLE 1. Theoretical literature on behaviorally mediated effects on community dynamics.

Diet selection	Habitat choice	Activity budget
A) One-predator–two-prey systems		
Murdoch and Oaten (1975), Tansky (1978), Teramoto et al. (1979), Holt (1984), Gleeson and Wilson (1986), Abrams (1987*c*, 1990*a*), Abrams and Shen (1989), Abrams and Matsuda (1993), Fryxell and Lundberg (1994), Křivan (1996), Schmitz et al. (1997), Abrams and Schmitz (1999), Boukal and Křivan (1999), Křivan and Sikder (1999), van Baalen et al. (2000)	Holt (1984), Křivan (1996, 1997), Abrams (1999), Boukal and Křivan (1999), van Baalen et al. (2000)	Abrams (1987*a*,*b*), Abrams and Matsuda (1993)
B) Two-predator–one-prey systems		
Not applicable	Matsuda et al. (1993), McPeek and Peckarsky (1998)	Lima (1992), Matsuda et al. (1993)
C) Tritrophic systems (including omnivory)		
Křivan (2000)	Schwinning and Rosenzweig (1990), Luttbeg and Schmitz (2000)	Abrams (1984, 1991*b*), Fryxell and Lundberg (1998), Luttbeg and Schmitz (2000)
D) Other systems: square; branch; longer chains		
Lawlor and Maynard Smith (1977), Abrahams (1986), Abrams (1987*c*, 1990*a*,*b*), Rothley et al. (1997), Schmitz (1998), Abrams and Schmitz (1999), Colombo and Křivan (1993)	Danielson (1992), Sih (1987), Colombo and Křivan (1993)	Colombo and Křivan (1993), Abrams (1992*b*)

We start with some basic definitions, both of the categories that we use to subdivide the literature (community structure and behavior type) and of the response variables that theoreticians typically look at to assess the effects of TMI (stability, population densities, trait dynamics). Using these categories and definitions, we provide a general discussion of the existing theoretical literature on TMI (Table 1).

Definitions

Trait effects.—We use the same categories defined in the previous section (diet selection, habitat choice, and activity budget) to organize theoretical studies. Where these categories are mathematically ambiguous, we list studies in both categories.

Community structure.—We also divide studies by community structure, or ''who eats whom.'' The most common structure studied, by a large margin, is a community with one predator and two prey species (Table 1, row 1). Other researchers have examined two predators competing for a single prey species (Table 1, row 2), tritrophic chains (Table 1, row 3), and four-species communities including a branch structure with three trophic levels and two bottom-level prey species: we lump all communities with more than three species into an ''other'' category. To our knowledge, no one has studied the dynamics of a diamond (three trophic levels with two intermediate species), even though these have formed the basis of a series of empirical studies (Werner and Peacor 2003).

Like the behavioral categories just defined, community structure can be ambiguous in theoretical studies. For example, suppose a focal species that preys on a lower trophic level has different mortality rates in different patches. We could model this as predation by predators with different (fixed) population sizes in different habitats (Matsuda et al. 1993), implying three trophic levels, or as a result of differing abiotic mortality risks, implying only two levels. Similarly, mortality rates that increase as a function of activity could result from exposure to predation, or from starvation caused by the metabolic costs of higher foraging rates. Species with different mortality rates could also inhabit different patches (Morris 1988). For this review, we have used a strict definition: all species must be explicitly included in the authors' description of a model.

Response variables

Persistence and stability.—Some of theorists' interest in TMI has come from the well-known discrepancy between simple multitrophic model dynamics, which can be unstable to the point of extinction, and the observed persistence and apparent stability of many predator–prey associations in nature. ''Stability'' can have many definitions (Grimm and Wissel 1997). The simplest mathematical measure of stability is the eigenvalue of the interior equilibrium, which gives the rate at which the community composition will move toward or away from the equilibrium point where all species are present. Two related (and more easily measured) measures are (1) permanence, the tendency of all species to increase in numbers when rare and, hence, to maintain the species richness of the community (Hofbauer and Sigmund 1984, Butler and Waltman 1986, Law and Morton 1996); and (2) the coefficient of variation (CV, standard deviation/mean) of fluctuations in population densities (Connell and Sousa 1983). In simple systems, these measures are re-

lated, but they need not covary in more complicated systems (Grimm and Wissel 1997). For example, adaptive changes in diet or habitat selection can increase the overall permanence of multispecies communities without stabilizing the community at an equilibrium (Abrams 1992*b*, Křivan 1996, 1997, 1998, Křivan and Sikder 1999, van Baalen et al. 2000). Permanence without stability may be a general feature of models in which optimality criteria lead to sudden changes in behavior. One challenge for theoreticians is to find ways of analyzing models in terms of permanence and CV, and understanding when these more useful measures accord with simpler mathematical stability criteria (Nisbet and Gurney 1982).

Population densities.—Current research in community ecology focuses as much or more on long-term differences in (equilibrium) biomass or productivity as on stability. Empiricists usually design their field studies to measure short-term changes in population densities under different conditions. Most theoretical studies of TMI have focused on stability without exploring effects on equilibrium densities (which may be meaningless in unstable systems). In contrast, Abrams and coworkers (1982, 1984, 1991*a*, 1992*b*, 1993, 1995) have often analyzed changes in fitness or instantaneous population growth rates when population sizes are held constant. These measures are essentially the same as the short-term density changes observed in experiments; if we consider a very short experimental period, any changes in population density should be proportional to the instantaneous growth rate.

The two different time scales of (short-term) instantaneous growth rates and (long-term) equilibrium density changes should set bounds on the results of experiments. Short- and long-term dynamics will not always be directly related, and sometimes even the signs of changes in density and instantaneous growth rate may change with time scale (Matsuda et al. 1993). As we will discuss, translating between short- and long-term effects is one of the most important open problems in TMI theory.

Population density changes are also correlated with the stability properties mentioned in the previous section. For example, in two-predator–one-prey systems, indirect mutualisms (positive indirect effects between predators sharing a common prey species) are strongly associated with stabilization of the three-species equilibrium and permanence of the three-species community. Of course, these associations are not perfect; the same caveats that we have discussed with respect to the connections between stability, permanence, and CV apply.

Trait dynamics.—Several researchers (Schwinning and Rosenzweig 1990, Abrams 1992*a*, 1999) have studied trait dynamics, the changes over time in behavioral or morphological characters that modify trophic interactions. These studies have highlighted the potential for complex dynamics, and raise questions about both theoretical and empirical studies that assume instantaneous changes in trait values. There is very little empirical work evaluating the role of short-term trait dynamics in natural food webs, although evolutionary changes in behavioral traits are well documented (Boonstra and Boag 1987, Rijnsdorp 1993). The observation of complex behavioral trait dynamics affecting community dynamics, even without experimental manipulations, would be exciting.

Results

This section gives a broad overview of the results of existing theoretical studies of TMI.

One-predator–two-prey systems

Communities with one predator and two prey species are by far the best studied case of higher order interactions. In particular, diet selection studies, in which the trait that changes is the predator's probability of attacking each prey species, have a long history. Early studies (Murdoch and Oaten 1975, Tansky 1978, Holt 1984; see also Abrams and Schmitz 1999), which focused on a tradeoff between consuming low- and high-abundance prey in one patch or in different patches (including the switching models previously discussed), found that prey-switching behavior stabilized communities, enhanced prey coexistence, and generated indirect mutualism between the prey species. If one prey type or one patch type was sufficiently rare, then adaptive predators would switch to the other type, allowing depleted prey species to return to higher densities.

Studies that allow predators to follow optimal foraging rules weaken the conclusion that TMI is stabilizing. Systems are stable (in the sense of eigenvalues) if predators completely exclude low-quality prey from their diet (Gleeson and Wilson 1986, Fryxell and Lundberg 1994, 1998), but may not be otherwise. Direct comparisons between predators that follow simple rules and those that optimally choose prey types suggest that adaptive choices may destabilize dynamics (Mangel and Roitberg 1992, Křivan 1996). Different foraging scenarios such as nonsubstitutable resources (Abrams and Shen 1989) or joint feeding-time and digestive constraints (Abrams 1990*a*, Rothley et al. 1997, Abrams and Schmitz 1999) can lead to multiple stable equilibria or unstable dynamics. Other elements of biological realism, such as partial preferences (Fryxell and Lundberg 1994) or competition between prey (Gleeson and Wilson 1986, van Baalen et al. 2000), slightly stabilize communities. TMI can also increase permanence without increasing stability; all species may persist indefinitely (Křivan 1996, 1997, Křivan and Sikder 1999, van Baalen et al. 2000), even though the community does not reach a stable equilibrium. Community stabilization by adaptive behavior is context dependent and depends on the biological details of the system (Table 2).

In addition to the main thread of research on stability of shared-predator systems, Abrams (1987*b*) examined the effects of adaptive trait changes on (short-term) instantaneous population growth and (long-term) equilibrium population size. As with all of these models, adaptive trait changes in both the predators (diet selection) and prey (activity level) lead to a variety of indirect effects on instantaneous population growth. The net effects are

TABLE 2. Factors tending to increase or decrease stability, community persistence, and indirect mutualism.

Increase	Decrease
Coarse-grained/patchy prey distribution: either patch quality (e.g., foraging efficiency) varies or each prey species is confined to separate patches (Holt 1984, Abrams and Schmitz 1999).	Fine-grained/random prey distribution: all prey are available at all times.
Models of prey switching based on prey density only (Teramoto et al. 1979, Murdoch and Oaten 1975, Tansky 1978).	Models of optimal foraging based on quality and density (Gleeson and Wilson 1986, Fryxell and Lundberg 1994) [but permanence increases: Křivan (1996), Křivan and Sikder (1999)]
Predators only limited by feeding time.	Predators limited by digestive constraints and/or feeding time (Abrams 1990*a*, Schmitz et al. 1997, Rothley et al. 1997, Abrams and Schmitz 1999), nonsubstitutable resources (Abrams and Shen 1989).
Interspecific (Lotka-Volterra) prey competition (Gleeson and Wilson 1986).	Intraspecific prey competition (prey grow logistically in absence of predator) (Fryxell and Lundberg 1994).
Partial preferences (Fryxell and Lundberg 1994, van Baalen et al. 2000).	
	Adaptive dynamics (Abrams 1992*a*, Abrams and Matsuda 1997, Abrams 1999*b*).

complex, but depend on the curvatures of the cost and benefit functions. If the predator's population size is relatively independent of the prey population size because it is limited by other prey or by additional factors, then the short-term and long-term indirect effects between prey types are largely similar. Otherwise, apparent competition is the most likely long-term outcome of such interactions between prey species. However, if the presence of a predator stops prey from overexploiting resources, increased densities of one prey type can cause the density of the other prey type to increase (Abrams 1992*b*, Abrams and Matsuda 1996). Because predator pressure allows increased productivity of the resource, adaptive trait change can lead to apparent mutualism in a two-prey–one-predator system.

Two-predator–one-prey systems

If two predators share one prey species, antipredator behavior by the prey leads to indirect effects between the predators. In contrast to the one-predator–two-prey case, theoretical studies of this scenario are relatively rare, perhaps because it was long assumed that two predators could not coexist if they both depended on a single prey species (Armstrong and McGehee 1980, Sih 1997). However, the large empirical literature on multi-predator communities (Sih 1997) has given rise to at least a few theoretical studies (Lima 1992, Matsuda et al. 1993). Perhaps because there have been so few studies, the results are straightforward. The specificity of prey defense governs the outcome of multi-predator–single-prey interactions. If prey defenses are effective against all predators (e.g., a refuge from all predators, or reduced activity), then predators will have an indirect, trait-mediated negative effect on each other (indirect competition) beyond the effects of exploitation or interference competition (which is a positive indirect interaction between predators and their prey). This indirect competition tends to reduce the chances for predator coexistence and stability of the three-species community. If prey defense is species specific, however, then the indirect effect between predators is positive and tends to increase persistence and stability.

Tritrophic interactions

In tritrophic interactions with a predator, a consumer, and a resource, behavioral changes by the consumer lead to indirect interactions between the predator and the resource. The predator may also be an omnivore, feeding on the resource as well as the consumer. Relatively few studies have explored this category, largely because of its analytical complexity. Tritrophic interactions can be very unstable, making it hard to assess either relative stability or relative density with and without trait-mediated interactions. With nonlinear trophic links (e.g., Holling type II functional responses), tritrophic systems (even without adaptive behavior) show chaotic behavior for a wide range of parameters (Hastings and Powell 1991, Abrams and Roth 1994, McCann and Yodzis 1994). Besides being notoriously difficult to quantify in natural systems (Ellner 1991), chaotic dynamics also rule out many of the more straightforward analyses of equilibria and stability.

There are three ways around this problem: the first two are to look at chains with linear functional responses, which elucidates basic mechanisms but runs the risk of missing important nonlinear dynamical effects, or to fix population dynamics and look only at trait dynamics or population distribution in space (Abrams 1984, Schwinning and Rosenzweig 1990, Abrams 1991*a*). The results again are complex and depend on the curvatures of the foraging cost and benefit functions of the middle species in the chain. Abrams (1984) also finesses this problem, in a different context, by making the bottom species an "abiotic" resource that increases linearly rather than exponentially at low densities; this change simplifies the dynamics.

The third way of coping with analytical complexities is to sidestep analysis completely and explore models numerically (Ives and Dobson 1987, Luttbeg and Schmitz

2000). Fryxell and Lundberg (1998:62) show an example of a numerical model in which behavioral trade-offs made by the middle species in a three-species chain are weakly stabilizing, in the sense that the CV of population density decreases slightly.

Larger communities (four or more species)

The argument that indirect effects make it difficult to generalize results of pairwise studies to three-species interactions also applies to larger communities; we are still not sure whether there are new qualitative features of indirect interactions in larger communities, or whether we will be able to generalize from the dynamics of three-species modules. One solution is to search for repeating patterns as the number of species within a system increases in certain ways. In non-TMI models, for example, Oksanen et al. (1981) found a systematic effect of the number of trophic levels on the response of density within trophic levels to nutrient enrichment. Because of the additional complexity of many-species interactions and the aforementioned difficulties of complex dynamics in systems with more than two trophic levels, most studies of larger communities (1) restrict themselves to communities with two trophic levels (but many species); (2) examine numerical rather than analytical results; or (3) hold population densities constant and examine trait dynamics or instantaneous effects on fitness or growth rate.

Abrams (1992*b*) analyzed a four-link food chain with adaptive traits in the middle two species. The results are complicated, but the main point is that indirect effects, which are necessarily trait-mediated rather than density-mediated because population densities are held constant, can be large relative to direct effects. The signs as well as the strengths of trophic interactions can also change, depending on the shapes of the foraging cost and benefit functions. For example, when both intermediate species in the chain increase effort with resource density and decrease effort with predator density (linear benefits, nonlinear costs), prey have a positive effect on their predators' predators, which can lead to counterintuitive scenarios where increasing prey density decreases predator fitness. If nonforaging prey can still be caught by predators, or if optimal foraging effort declines with increasing prey density, then there are fewer surprises: direct effects dominate, and the usual signs of effects (negative between prey and their predators, positive between prey and their predators' predators) hold.

The final thread of research in more complex communities uses more general models to explore community persistence. Colombo and Křivan (1993) proposed some general methods for incorporating behavior in models of larger communities, but have not analyzed them, while two papers by Matsuda et al. (1994, 1996) explored the structure and persistence of communities with two trophic levels and more than three species. Their models allowed prey defensive traits and predator foraging traits to evolve, and found that predator-specific defense increased community connectivity and stability (Matsuda and Namba 1991).

Discussion: Where Do We Go Next?

Conclusions from existing theory and experiments

The fundamental reason that community ecologists should care about TMI is the possibility that they have strong and widespread effects, which we must understand and incorporate into our models if we are ever to understand the dynamics of natural communities. In natural systems, we rarely expect to see densities changing while traits remain fixed or vice versa; the only reason to introduce ''risk'' predators in experiments is to demonstrate and quantify the importance of trait-mediated effects. We want to learn how to measure and model trait effects so that we can understand existing community structure and dynamics or predict the effects of changes on the community.

There is some evidence that the long-term dynamics of systems such as the boreal lynx–hare cycle or fish populations in stocked lakes are partly controlled by TMIs (Hik 1995, Werner and Peacor 2003), but these stories are still incomplete. As discussed in the *Introduction*, the theoretical and experimental work that has been done to date has fallen short of providing a convincing case for the long-term, broad-scale importance of TMI. The missing links in the argument for the importance of TMI are not the lack of short-term empirical tests or qualitative theory, but rather the difficulty (and futility) of constructing a completely general theory and testing it in the field. We will argue for collaborations between theoreticians and empiricists on longer term studies of particular systems as the best way to document the importance of TMI.

Despite the large, varied, and sometimes contradictory body of theoretical work on TMI, we can extract some generalizations about the various components of the theory that we have discussed.

1) *Incorporating behavior in models.* Reasonable formulations exist for incorporating many kinds of adaptive trait change into population- and community-level models. Despite the large number of qualitative tests of these models, quantitative tests of the details (attempts to test the shapes of functional forms, or distinguish between different optimization rules) are often lacking.

2) *Short-term dynamics.* The general conclusion of Abrams and co-workers on this topic is that strong indirect interactions can occur in a wide variety of situations. These interactions increase the number and variety of interactions in communities and, in some cases, can generate counterintuitive results such as predator populations that decrease in the short term when prey populations increase. Most importantly, sorting out the details of these variable outcomes requires measurement of the curvatures of cost and benefit functions, which, as pointed out by Abrams (1992*b*, 1995, 2001) and this paper have not been done.

3) *Stabilization.* Although many kinds of adaptive change (predator-specific defense, switching based on prey density, etc.) can stabilize community dynamics, it is clear that this is not a hard and fast rule. Nevertheless, based on the literature, we can make some generalizations about the tendencies of particular behavioral mechanisms to stabilize or destabilize community dynamics (Table 2). Because of the long time scales and intensive manipulation required to test theories of community dynamics, these models remain untested (Brown et al. 1986, Holt and Lawton 1994).

In all three of these areas, we have enough qualitative conclusions to make strong plausibility arguments for the importance and generality of TMI in communities. We now know that behavioral changes do have detectable short-term effects on population growth in a wide variety of systems (Werner and Peacor 2003). We know how to incorporate these effects into population models. We know, in theory, that these effects have strong effects for a wide range of plausible biological parameters. Finally, we know, theoretically, that, in the long term, they can have strong effects on community stability. Rather than construct the myriad models that would fill in all the gaps of Table 1 (cf. Hethcote 1994), it is time to review broadly what has been achieved with these studies,what has not been done, and where researchers should invest their time and energy next.

Integrated short–long term, theoretical–empirical studies

The biggest gaps in our understanding of TMI are the differences between qualitative and quantitative tests of theory in the short term, and between short- and long-term dynamics. Only by closing the first gap (by testing and parameterizing detailed short-term models) can we possibly close the second. The first step will be, as Abrams has suggested, to measure the curvatures of cost–benefit functions that theorists have identified as being important: ''much can be deduced about the nature of indirect effects with a little knowledge about the shapes of foraging cost-and-benefit functions'' (Abrams 1992*b*; see also Abrams 2001). The degree of nonlinearity of these curves and whether they curve up or down (the sign and magnitude of their second derivatives) should predict most of the short-term effects of experimental manipulations. Measuring curvature will require at least three levels per factor (resource or predator densities). These experiments will show what kind of cost–benefit curves really occur and will test predictions of middle-consumer responses to changes in predator and resource densities.

For example, consider a short-term, intensive study of refuge use behavior by a consumer in the middle of a (predator–consumer–resource) tritrophic chain. Three or four levels of fixed resource density in the absence of predators would establish the baseline functional response of the consumer; three or four levels of fixed predator density in the absence of a refuge would establish the baseline functional response of the predator. One could then come up with a basic idea of the appropriate trade-off structure (given a completely effective refuge that also prevented foraging), which would balance resource acquisition against mortality probability as a function of resource and predator levels (Werner and Anholt 1993, Anholt and Werner 1995, McPeek and Peckarsky 1998). Running experiments at the same levels of resource and predator in experimental arenas with refuges available would then test whether consumers were actually using refuges in a way conforming to theoretical expectations.

The next question, and the next stage of the experiment, would be to test whether the fitness trade-offs actually corresponded to the implicit growth–mortality trade-off. Four experimental treatments would correspond to (1) risk predators; (2) true predators; (3) either nonrisk predators (experimental removal at rates matching true predation) or the absence of a refuge; and (4) control (no predators). For univoltine animals, one could assess relative fitness by clutch size at the end of the season; consumers that mistakenly performed antipredator behavior (in the risk treatment), or were unable to perform antipredator behavior (in the nonrisk treatment) could be compared to predator-free or adaptively behaving consumers. In addition, one would know the fitness of (also univoltine) predators, and the relative abundance of the resource. It would be convenient to use an aquatic system where consumers responded to chemical cues, which would be the easiest form of ''risk'' treatment to maintain over time; however, one would have to check for acclimation of consumers to the stimulus. One could also use this experiment to check for plastic traits other than the focal trait (e.g., changes in morphology, differential habitat use other than refuge use).

These intensive short-term experiments, which would be made easier by video monitoring of marked individuals or other technological shortcuts, would in turn be coupled to a longer term, less intensive series of treatments at different resource levels (e.g., nitrogen or phosphorus concentrations) to determine the long-term dynamics and stability of the system. Presence and absence of refuges and predators in these treatments could be maintained over time without too much effort. Quantitative models calibrated from the previous experiments could suggest the qualitative behavior and time scale of expected dynamics, and the resource levels necessary to observe differences in trait- vs. density-mediated effects. Even if the experiment were run over only a few seasons, one could test the qualitative match of observed vs. expected trends and dynamical summaries such as CV (either a classical replicated design or some form of before–after design [Osenberg et al. 1994, Underwood 1994] could be used).

Such a design would test whether TMIs are necessary to describe the long-term dynamics of a system, or whether simple demographic and density-mediated effects are adequate. In addition, it could be used to partition the variance in densities across resource levels into density-mediated effects, trait-mediated effects, and interactive effects. In the long run, we need to develop theoretical and empirical frameworks for partitioning the variation in density in less tractable systems, where long-term manipulations are impossible. This kind of combined experimental and theoretical work, closely linking theoretical models with manipulative experiments and parameterizing models from field data, has been tremendously successful in other areas of ecology where experiments are difficult because of large spatial scales and long time scales (Thrall and Antonovics 1995, Pacala et al. 1996).

On the theoretical side, this project requires an explicit theoretical framework for extrapolating from within-season to between-season dynamics. Most existing TMI models assume continuously reproducing organisms for analytical convenience; in contrast, most animals that have been the focus of TMI studies (and the ones that would be most appropriate for the experiments just described) reproduce seasonally. (Abrams [1992*b*] assumes constant conditions within a season so that the resulting model can still be analyzed as a modified continuous-time model.) For quantitative comparisons between models and data, we need a model that allows continuous predation and behavioral change within a season, but discrete changes in population size between seasons. Such models are a straightforward extension of existing models: they just separate the within-season adaptive rules from the relationships between (e.g.) final size and reproductive output carried over to the next year (Mangel and Roitberg 1992, McPeek and Peckarsky 1998). Even in the absence of closely coupled experiments, developing such models would help to explore the connections between short- and long-term theoretical predictions, which is one of the major gaps in the theoretical literature; few studies have addressed both time scales in the same model framework (Abrams 1987*b*, 1995).

A final set of open theoretical questions, which we have neglected in this review, has to do with the connections between the general theoretical ''top-down'' models (*p* state), which are defined in terms of populations and average states, and ''bottom-up'' (*i* state) models that forego aggregation in favor of a detailed description of individual states and behaviors. Although individual-based models have been immensely successful in describing particular systems (Rose et al. 1993, Fahse et al. 1998, Gaff et al. 2000, Schmitz 2000; reviewed in Grimm 1999), they have rarely been integrated with the top-down models that form the bulk of the theory of TMI. The shortcomings of bottom-up models include a tendency toward overparameterization, and the difficulty of drawing broad conclusions that extend beyond a particular system, but they will form an essential ingredient in connecting observations of natural and manipulated empirical systems with top-down analytical models.

Conclusions

The simple fact that adaptive trait changes switch the signs of density changes in short-term experiments is both scientifically and practically important. Scientifically, it ties behavioral ecology to community ecology, encouraging behavioral ecologists to think about population dynamics and evolutionary biologists to think about community ecology. Practically, it may be important in managing populations at all trophic levels, from algal blooms to sport fish.

Although these short-term effects are important, we cannot say how they extend to longer time scales (McPeek and Peckarsky 1998). Are they strengthened or weakened by feedbacks between traits and reproductive success? If an animal stops foraging to avoid predation, will it fail to reproduce and hence produce the same expected number of offspring as if it had risked being eaten in the first place? Answers to this kind of question are important both for the broader theory of community dynamics and for practical long-term management (although we can already begin to apply the lessons of TMI to short-term management such as the maintenance of stocked fisheries). Short-term experiments on TMI are tools for investigating the structure of communities, not direct tests of ecological questions about the observed abundance and distribution of species. Extrapolation is important: one of the frontiers in the study of TMI is finding ways to make and test predictions about long-term ecological dynamics. Theory's great strength is in evaluating the consequences of local, short-term rules on the long-term structure and dynamics of communities. Theoreticians can also help empiricists to understand what data are required to provide solid foundations for long-term forecasts, and to find feasible ways to test these predictions.

The best way to catch the attention of community ecologists is to show them that TMIs answer outstanding puzzles in community dynamics: for example, that the paradox of enrichment and the controversy over trophic cascades can be understood by incorporating behavior in our models of communities (Abrams and Walters [1996] explore these problems with a model incorporating behavioral, but direct, interactions). If TMIs can solve otherwise impossible problems in community ecology, they will definitely emerge into the mainstream of ecology. We believe that progress hinges on collaboration between empirical and theoretical ecologists.

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