CHAPTER ONE

Introduction

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Community ecology is experiencing a resurgence, driven in part by its central importance in addressing critical applied problems, ranging from the control of pest and invasive species, to the wise harvest of natural resources, to projecting the impact of global climate change. A fundamental tenet of community ecology is that species do not exist in isolation: they are directly, and more importantly, indirectly interconnected with myriad other species. The essential 'glue' that holds communities together and that makes them more than the haphazard sum of individual species is the nexus of indirect interactions among three or more species that emerges from direct interactions such as predation, competition and mutualism between pairs of species. The recognition of indirect effects has triggered a rapid growth of empirical and theoretical research that aims to predict community-level dynamics under different contexts.

Indirect effects occur when the impacts of one species on another are influenced by one or more intermediate species. Indirect effects are diverse, but can be classified broadly as either (1) density-mediated or (2) trait-mediated. Density-mediated indirect effects (DMIEs) result from numerical responses of species to each other. For instance, a fox may kill rabbits, reducing rabbit population size, and so relaxing herbivory upon herbaceous plants. Hence, the fox's indirect effect on plants is mediated by density changes in rabbits; this is known as a trophic cascade. DMIEs, such as depicted by this trophic cascade, and other mechanisms such as apparent competition between prey mediated by the numerical response of a shared predator, have been well studied and have contributed to our understanding of community organization and ecosystem functioning in both terrestrial and aquatic systems (Holt and Lawton 1994; Polis *et al.* 2000; Terborgh and Estes 2010). However, the fox may not only kill rabbits, it may alter their behaviour and other traits. For instance, rabbits may hide more in the presence of foxes and so have less opportunity to feed on herbs. This

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indirect effect of the fox upon the plants could be strong, even though rabbit abundance remains high in the presence of foxes. In this case, it is a change in a rabbit's trait – altered behaviour to avoid predation – that determines the outcome of the predator–prey direct interaction and the nature of the indirect effect of foxes on plants. In this same food chain, consumption by the rabbit could change plant architecture and biomass, altering the exposure of the rabbit to capture. In principle, changes in traits of any species in a community could shift interactions among other species, as well as altering the interactions involving that species itself. The objective of this volume is to display the rich variety of ways such trait effects arise, and to examine the consequences of such trait effects for a wide range of ecological issues.

What do we mean by *trait*? Basically, we suggest that anything that can be measured about an individual organism or a strategy (sensu Vincent and Brown 2005) can be considered a trait. If we can measure it, then in principle other organisms can also measure it, and respond to this metric. As evolutionary biologists, the traits we most care about are typically those that are heritable and markedly affect fitness. In some cases, traits may be relatively independent of the environment, and of the sort that can be measured in museum specimens (e.g., body size and shape). Such invariance is indeed assumed in classical models in community ecology (in effect: seen one rabbit, seen 'em all). But in other cases, traits are highly plastic, varying in accord with changes in abiotic and biotic factors. Such traits can only be measured in a specific environmental context (for example life history traits, metabolic rates, or per capita attack rates by a predator upon its prey), and ideally would be described as functions of trait values against environmental variables, i.e., norms of reaction. If trait plasticity is an evolved state, it is reasonable to presume the trait in question is important in determining fitness, and that relative rankings of phenotypes by fitness vary with environmental circumstances.

Plasticity has long been of interest in evolutionary biology (e.g., Scheiner and Lyman 1991), but now community ecologists are increasingly aware that species traits and plasticity in traits can have multiple consequential effects for other species, not just for the species itself and its immediate interactors. These effects mean that the interactions determining community structure and dynamics can be much more pervasive than suggested by simple pairwise metrics such as niche overlap (permitting resource competition) and trophic transfers (comprising the links in food webs). Because trait effects are often large, trait plasticity implies that individuals in a given species have different direct and indirect effects in different situations. To the extent that these context-dependent effects are predictable, incorporating an understanding of them is essential to developing a predictive theory of communities. Such a trait-based approach also fosters the integration of evolutionary and community ecology.

Traditionally, theoretical models of ecology portraying the outcomes of interspecific interactions assumed that species have fixed properties.

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The variables at the core of community dynamics were then naturally the densities of each interacting species, possibly expanded to include different age classes. In recent years, it has become clear that theories based solely on density interactions provide an insufficient foundation for community theory. Parameters that govern interactions between a pair of species may depend not only on the traits of these species, but also on the traits and abundance of third (or more) parties. Because traits can be plastic or evolutionarily labile, they may themselves change on timescales commensurate with changes in density (Abrams 1995). If species B plastically changes a key trait in response to species A, this may influence the strength and even qualitative sign of interactions between species B and C. There is thus an emergent indirect interaction – a *trait-mediated indirect interaction* – between species A and C. The word ‘emergent’ reflects the fact that interacting entities can produce phenomena – higher order structures and functionalities – that are more than can be captured by a simple averaging of the properties of the entities considered apart (Page 2011). In other words, a trait-mediated indirect interaction (‘TMII’) occurs when species A indirectly influences species C by inducing a modification in the traits, such as behaviour, morphology and/or life history of species B. Two conditions must be satisfied for a TMII: (1) a species affects a trait of another species; (2) the latter species affects a third species, completing the indirect effect (Werner and Peacor 2003).

In general, a wide range of trait-mediated indirect effects (TMIEs) is possible via plastic shifts in behaviour, morphology, physiology and life histories of affected species. The recognition of TMIEs came to prominence first in predator–prey systems. For example, as in our fox–rabbit example, prey can avoid predation risk by altering their behaviours, morphologies and life histories in the presence of predators, leading to trophic cascades with enhanced primary production (Schmitz *et al.* 2004). More recently, TMIEs have received considerable attention in plant–herbivore systems because of the prevalence of herbivore-induced changes in plant traits (Ohgushi 2005). A change in leaf morphology, stem architecture or phenology of leaf production following herbivory can potentially alter the competitive efficacy of plants for light, and shift interactions with herbivores, pollinators, or seed dispersers, or even predators (Ohgushi *et al.* 2007). Such TMIEs can match or even outweigh classical DMIEs in determining community dynamics (Preisser *et al.* 2005; Trussell *et al.* 2006; Werner and Peacor 2006). The chapters in this volume demonstrate that ecological communities are replete with TMIIs, and that a deep understanding of such interactions is crucial for addressing many issues in both basic and applied ecology.

The richness of trait-mediated effects results in a far more reticulate pattern of linkages among species than do classical food web interactions, leading to emergent properties of communities that are hard to predict from analyses

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of individual species or species pairs (Ings *et al.* 2009; Beckerman *et al.* 2010). Phenotypic plasticity produces a complex tapestry of impacts on organisms, cascading upward and downward through trophic levels, and surprising chain reactions across entire communities. We believe the time is ripe for a synthesis of this new development in population and community ecology, leading to a fresh understanding of a wide array of ecological processes (including ecosystem dynamics), and this volume is a step towards such a synthesis.

The authors in this book emphasize conceptual issues and provide illustrative empirical and theoretical studies that highlight the central importance of TMIIs for ecological processes ranging from diffuse coevolution, to population dynamics, to community organization, to ecosystem functions. The chapters, we believe, collectively provide crucial steps towards an integrated perspective on the ecological and evolutionary consequences of TMIEs in a wide range of ecological systems, consequences linking evolution, community and ecosystem ecology. This perspective enhances our ability to answer basic ecological questions, foster the conservation of biodiversity, and project how ecosystems may respond to anthropogenic environmental changes.

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PART I

Community

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CHAPTER TWO

Perspective: kinds of trait-mediated indirect effects in ecological communities. A synthesis

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Introduction

Our assessment of the importance of trait-mediated indirect effects (TMIEs) relative to density-mediated indirect effects (DMIEs) in ecological communities continues to rise. It seems only yesterday that the landmark experiment of Beckerman *et al.* (1997) was published, showing that grasshoppers, in the presence of 'disabled' spiders incapable of consumption, were intimidated enough to reduce their feeding activity and thereby maintain strong trophic cascades to the producer level. The first comprehensive review, by Werner and Peacor, appeared 6 years later and summarized numerous studies of TMIEs, including some that were able to calculate the relative importance of trait versus density effects; they concluded 'trait effects are often as strong or stronger than density effects'. A short time before, the same authors published an experiment (Peacor and Werner 2001) on a community consisting of an odonate predator and two competing anuran prey species; the predator consumed and intimidated one of the prey species, reducing its competitive effect on the second anuran species. The impact via the trait effect was 76–86%, as compared to 14–24% via the density effect. A second review by Peacor and Werner (2004) concluded that the effect of predators on prey traits modifies the magnitude of an effect farther along the pathway by 20–90%. In the same year, Schmitz *et al.* (2004) published a review of TMIEs and DMIEs in trophic cascades, whose title gives the conclusion 'Trophic cascades: the primacy of trait-mediated indirect interactions'. Shortly after, Preisser *et al.* (2005) did a meta-analysis of trait and density effects, finding for simple predator–prey interactions that certain trait effects (which they call 'intimidation') were at least as strong as density effects (which they call 'direct consumption'), being 63% versus 51%, respectively; the density effect actually declined along tritrophic cascades, while the trait effect climbed to 85% of the total effect. More recently again, Creel and Christianson (2008) reviewed risk

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effects and concluded that they 'can be large, sometimes substantially larger than direct effects'. One of their examples was an elegant experiment by Pangle *et al.* (2007) showing that the risk effects of predatory water fleas on the population growth of their zooplankton prey were more than seven times larger than the consumptive (direct predation) effects. The only damper on the increasingly rosy assessment of TMIEs is from Abrams (2010) who writes 'empirical techniques used to compare the magnitudes of behavioural and non-behavioural responses to predation are likely to have overestimated the behavioural component'.

It is interesting to ask why trait effects might be expected in theory to be so large in comparison to density effects. Werner and Peacor (2003) argue especially for behaviour that trait changes are rapid so exert their influence over most of the time course of the interaction; density changes gradually, so its impact is typically weak at the beginning and is transmitted only in proportion to the individuals removed, not the entire population. This reasoning is so apparent a posteriori that it makes us wonder why the possible importance of trait effects was not recognized longer ago than it was. We think in part the answer is that the importance *was* recognized, but with respect to different kinds of traits than behavioural ones. One kind of trait change comprises the (nonlethal) effects of parasites or pathogens on their hosts, and these are well known to be frequent and often severe (e.g., Long and Hay, this volume). Such non-density changes must often have a major impact farther down the effect pathway. Indeed, expansion of the domain of traits beyond the behavioural allows inclusion of many other kinds of trait effects. The many cases of induction of plant defences by herbivores are all candidates for food-web effects (e.g., Ohgushi, this volume). More generally, Miner *et al.* (2005) document the breadth and commonness of plasticity, which they define as 'the production of multiple phenotypes from a single genotype' in ecological systems. However, in our enthusiasm to add to the catalogue of trait effects, we may sometimes go too far. For example, Werner and Peacor (2003) include as a kind of habitat or space-use trait change (see below for terminology) the subtidal study on apparent competition by Schmitt (1987), in which experimentally introducing a preferred prey caused a decrease in a non-preferred prey because of the increased immigration of predators – is this a trait change or a density change or something in between? Whatever the finer points, we have now accumulated in one place or another numerous examples of trait changes and their ecological effects. This sets the stage to ask three questions: (1) what are the axes along which trait-mediated effects can be classified? (2) what is the relative commonness and importance of the various kinds of effects? and (3) what kinds of effects are well covered by theory versus stand as grist for the theoretician's mill (sensu Paine 1988)? Our short synthetic chapter cannot come close to providing complete or even systematic answers to these questions; rather, we sketch out a framework taxonomy and hang some examples on it, many from this volume, and then give a few implications.