Chapter one

Tracking the tractable: using invasions to guide the exploration of conceptual ecology

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INTRODUCTION

Our understanding of the complex functioning of human physiology, neurology, and behavior has long been guided by the study of anomalies in these systems. When faced with a seemingly intractably complex system, it is at times easier to fathom its mechanisms by disrupting or disturbing it rather than trying to delicately explore the 'natural' entity. It has recently become clear to ecologists this tact of using the disruption or distortion of a system to better understand its normal workings can be applied to the study of the behavior, spread, and impact of non-indigenous species (NIS) on natural communities (Sax *et al.* 2005). The power of this view of NIS is that systems are inadvertently being perturbed all over the globe. What we can learn from the perturbations will not only advance the science of ecology, but also will allow ecologists to restore and rebuild these very systems. However, not all disruptions of a system are necessarily informative. Further, if the system as it normally functions holds some intrinsic value,

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as do invaded ecological systems, it is in the interest of the researcher to work to both understand invasions but also to correct or mitigate the damaging impact of non-native populations.

NIS pose a wide variety of threats to their non-native habitats through immediate and long-term influences on species composition and ecosystem functioning (Parker *et al.* 1999). Because the negative impacts of NIS are first, directly, and primarily ecological, ecologists and evolutionary biologists constitute the forward line in meeting the challenges posed by the introduction and spread of NIS. The many pathways through which an introduced population can affect non-native habitats and communities, however, are difficult to determine and predict. Which tools can the ecologist apply to the problem of NIS? Any solution must develop from a solid understanding of the following: 1) how populations intrinsically behave; 2) how populations influence the biotic and abiotic systems of which they are components; 3) how, conversely, an environment can influence a non-indigenous population; and 4) how NIS populations can change, phenotypically and genotypically, in new environments. Although all of these questions fall solidly within the tradition of ecological research, they demand, with a startling immediacy, capable answers culled from unresolved, ambivalent and even contentious ecological debate. While ecologists are at once well positioned to address the key elements that have arisen from the importance of NIS, our answers are likely to carry with them some of the struggles born of classic theoretical and conceptual debates in ecology and evolutionary biology. Here, however, the study of NIS may not necessarily suffer for these challenges.

The study of NIS, when approached from the realm of conceptual ecology, can act as interesting tests of competing ecological theories. This potential has long been recognized and more recently been promoted (Lodge 1993, Davis *et al.* 2001). Yet, not all ecological theory is applicable or appropriate for this type of test. Nor will the answers gained from all applications of ecological theory assist in improving our understanding, intervention, or prediction about actual colonizations of NIS. One of the key goals of this book is to better refine what ecologists believe the study of NIS can do for the field of ecology and, conversely, how conceptual ecology can advance our ability to explain and address the challenges posed by NIS. In this chapter we will organize some of the ways in which the study of NIS can advance conceptual ecology and vise versa, focusing on recent literature in the field and the ways in which the chapters of this book fit into that scheme. This chapter will also discuss how this book establishes guidelines not only for what we may learn from NIS, but for what we are unlikely to learn. Again, with imminent challenges and limited resources, understanding which scientific approaches, theoretical and applied, are intractable or impractical is as important to advancing this field as knowing which approaches show promise when confronting this complex problem.

TRACTABLE, INTRACTABLE, AND PRACTICAL STUDIES OF BIOLOGICAL INVASIONS

Although studies on the dynamics of invasive organisms demonstrate many research methodologies, three approaches are crucial to the advancement of our understanding of invasions; they are mathematical models, experiments (either manipulative or observational), and reviews or meta-analyses. The strength derived from exploring invasion dynamics through mathematical modeling is that scientists with expertise in a variety of theoretical applications can tackle the challenges of understanding biological invasions through novel techniques (Shea and Chesson 2002). Modeling suggests both possible dynamics, probable findings, and, perhaps more importantly, the limits to certain conceptual approaches to invasions (Harding *et al.* Chapter 17). It is broadly acknowledged that in order to better understand invasions, experimental approaches are crucial. There has been a growth of strong experiments in invasions, ranging from laboratory microcosms (Dick and Platvoet 2000), to field mesocosms (Dukes 2002), to large-scale manipulative field experiments (Tilman 1997). Many of the strengths of inferences derived from these studies, in order to be broadly appreciated, need to be reincorporated into mathematical models. Finally, meta-analyses and reviews provide a generalized assessment of the theoretical and empirical work that has collected over several years. The synthesis derived from these analyses can, as with the models, serve to inform, direct, or delimit the questions researchers ask about invasions (Cadotte *et al.* 2005). The dialectic derived from the complementary approaches of supposition, experimentation, and assessment offers the most efficient way to study invasions and draw broader understanding of ecological processes through the study of invasions. All three of these approaches are featured in this book, and in the following introduction to the themes of this book, we pay special attention to how this dialectic can guide important research and thinking on invasions.

The behavior of populations

Even in models of populations that do not include abiotic or interspecific environmental interactions, intraspecific population dynamics can illustrate important properties of invading populations through patterns of intrinsic population growth and spread (see Cadotte, *et al.* Chapter 21). Although a number of scales may ultimately prove important when assessing the arrival, establishment, growth, and impact of an NIS (Lloret *et al.* 2004, Hamilton *et al.* 2005), the population scale has long provided some of the clearest insights into the basic questions of invasion dynamics (Petrovskii *et al.* 2005, Thomson 2005). All of the features that figure prominently in population biology, from the role of carrying capacity to mortality and reproduction, provide a baseline understanding of how an NIS can be expected to behave when colonizing a new area. A key distinction when exploring these intrinsic properties lies in the different expectations of stochastic versus deterministic processes. Quite a few chapters in this book implicitly and explicitly address this important distinction.

Buckley and Metcalf (Chapter 5) review the role of density dependence in determining the population densities that can be reached by an invasive population and the influences of those densities on invasive success. They show how density dependence can delimit demographic parameters such as intrinsic rate of increase and dispersal ability. Using microbial microcosms, Warren *et al.* (Chapter 16) show that chance events play a key role in the establishment of an invader. Initial demographic stochasticity, propagule pressure, and the initial rate of increase all contribute to whether a population is able to establish in a community, but not necessarily persist in that community. Species-specific effects were also found to be important in both establishment and persistence, which indicates that careful characterization of the demographic qualities of an invading species may be important to understanding its potential impact.

What population-scale patterns do lead to persistence over time? Murrel (Chapter 7) takes a 'plant-eye view' in using simulations to show how the density and aggregation of a population can create a 'neighborhood' effect that determines ultimate population growth. This approach could be quite important in plant invasions, as intra-specific competition can determine ultimate viability and spread of a population. After the population is established, its dispersal becomes a crucial issue in anticipating the extent and impact of an invasion (Puth and Post 2005). Lewis *et al.* (Chapter 8) demonstrate a novel approach to modeling dispersal through two dimensions. Using kernel methods to incorporate long-distance dispersal into models and two-dimensional models to correct for biases in more commonly used one-dimensional models, a more accurate prediction of the dispersal behavior of an invading population can be made.

Metapopulation theory also emphasizes the role of dispersal in maintaining NIS persistence over time. Harding *et al.* (Chapter 17) show that for single NIS colonizing patchy environments, colonization success into empty patches must be greater than extinctions. This implies that species with strong dispersal may be predisposed to colonize. Combined with buffering life history traits, such as plants that can self-pollinate or vegetatively reproduce, a good dispersal mechanism can lead to successful colonization of a heterogeneous landscape.

Environment influencing NIS populations

Intrinsic population behaviors are clearly crucial to any understanding of the establishment and spread of NIS, but as with many ecological studies of populations, the behaviors of the population can depend on the biotic and abiotic components of the environment (Lodge 1993, Dukes and Mooney 1999, Holway *et al.* 2002). Incorporating the additional level of community complexity to population dynamics, however, can be daunting when determining the impact of NIS (Davis *et al.* 2000). The study of the establishment and spread of NIS can provide insight into how these more complex relationships develop, lending important case studies to the analysis of ecological communities. The complex and complicated dynamics of the environment also mean that these additional components can move problems from less realistic but tractable problems to intractable ones. Therefore, it is important to use studies of environmental influences on NIS to determine which approaches may be appropriate and which an inefficient use of time and resources.

A classic concept of how an environment can dictate whether or not a species can persist is that of the ecological niche. The idea that an environment is parsed into a finite set of niches has been an important one for the development of invasions biology (Cadotte Chapter 2). Vazquez (Chapter 14) uses a series of meta-analyses to explore how niche breadth and invasion success relate. When looking at fundamental niches (where species requirements are independent of community interactions) versus realized niches (where the suitability of an environment takes into account competition), the realized niche ultimately determines the success of an NIS. Vazquez points out that realized niches, however, are impossible to measure and warns against pursuing straightforward investigation into niche-based predictions of potential NIS success. This marks a powerful recommendation for invasions biology as a traditional line of inquiry into predicting the establishment of NIS has been the susceptibility of different habitats to invasions (Holway 1998, Levine and D'Antonio 1999).

In other circumstances, invasions can shed light on conceptual topics that are difficult to assess in natural communities. Duncan and Forsyth (Chapter 18) use historical records of bird invasions to test classic hypotheses of competition and community structure. Invasion records offer a unique way of discovering if invasions of bird species into certain types of environments are more likely to persist. They find that priority effects do occur, and that depending on circumstances, stochastic processes and deterministic processes (such as competition) can determine ultimate community composition. Sax and Gaines (Chapter 20) suggest that species rich communities are likely to be more susceptible to invasions (because conditions are favorable for many species). They argue, however, that this is true only up to a critical threshold (such as highly speciose tropical rain forests) at which point Elton's (Elton 1958) model, in which species rich communities have less available niche space unexploited by the best competitor, become applicable. Both Sax and Gaines (Chapter 20) and Smith and Shurin (Chapter 19) explain that heterogeneity within regional scales can mean that multiple processes (stochastic and deterministic) and multiple outcomes (invasion resistance and susceptibility) can be found in any one habitat. This indicates that even in unsaturated communities (where presumably there is ample niche space for well-dispersed invaders), invasion success is contingent on other factors. This role of contingency and complexity is becoming a common theme in both invasions literature and the empirical studies of community composition and assembly, and therefore points to an important area of reciprocal research.

Another example of the challenges inherent in complex community dynamics is illustrated in Harding *et al.* (Chapter 17). Although, as mentioned above, they show that metapopulations without competition rely on a simple strategy of colonization and buffers from extinction, adding even one more species into the model can radically change the number of population parameters and life-history traits that may ultimately dictate the successful establishment and persistence of an NIS. This complexity of potential outcomes indicates that metapopulation theory, as applied to multiple species living in subdivided habitats might be well applied to case studies, experiments, and management problems that offer specific species characteristics and robust estimation of population parameters. With such a meta-analysis, it may be possible to determine whether a metapopulation model can accurately describe and predict certain types of invasions.

Using microbial microcosms, Warren *et al.* (Chapter 16) reinforce this conclusion. In a series of ambitious experiments where different species are introduced into established communities, they show that predicting invasions can depend on a number of characteristics of the species involved as well as the community characteristics. Specifically, the intrinsic rate of increase (a simple population parameter) should be thought of as having as much to do with the interaction (contact experience) between an invader and a community as intrinsic properties of the invading population.

Demographic parameters (like the intrinsic rate of increase) themselves are not constant. These parameters can change stochastically due to both intrinsic demographic factors, such as random changes in birth or death rates. They can also change due to environmental stochasticity. Freckleton *et al.* (Chapter 6) distinguish demographic versus environmental stochasticity at different stages of an invasion (arrival, establishment, and spread). They show with mathematical models that stochastic processes influence these stages of the invasion in different ways and with different consequences. Stochasticity may be more important in phases with low densities (arrival and establishment), while density dependent behaviors may hold a greater influence on the spread of already established populations. Again, models like this can indicate when and how to proceed with an experimental program to test stochastic and deterministic components of invasion success.

Although direct agonistic interactions between species, such as competition and predation, have long been held as central to understanding the population structure of communities, indirect effects and mutualisms have recently been thrust into the forefront of thinking on a number of conceptual themes in ecology (Wootton 1994, Lortie *et al.* 2004), such as richness-productivity, population viability analysis, and invasions (Lach 2003). Vazquez (Chapter 14) shows in his meta-analyses of niche breath and invasions that the presence of mutualists and other niche categories that may be tricky to measure can have an important influence on the ultimate viability of a population in a new habitat. Thorpe and Callaway (Chapter 15) extend the discussion of mutualisms to the level of indirect mutualist interactions and feedback loops. Good experimental evidence has shown that presence of soil pathogens decrease NIS plant success in native range and absence of those pathogens increases NIS success in new range. Further, mutualist interactions can more easily create positive feedbacks in a new range, enhancing plant success. This conceptual approach to invasions might be well suited for a mathematical study, as feedbacks are both common in nature, yet difficult to tease apart from other community effects.

In addition to using analyses of environmental contexts to predict whether an NIS will successfully establish and persist in a novel environment, Gilbert and Parker (Chapter 13) and Satake *et al.* (Chapter 12) address how the environment can prevent an invasion or even reverse an already persistent NIS. Gilbert and Parker argue that the understudied role that pathogens play in plant population regulation can have important consequences in understanding, predicting, and mitigating or reversing high-density persistence of NIS. Satake *et al.* (Chapter 12) model 'classic' mast seeding, and show that when seed set is negatively correlated in time but positively correlated across space a system is most resistant to invading seed predators.

Phenotypic and genotypic change

A new and exciting theme in invasions biology addresses how populations of NIS may change in phenotypic expression (Schweitzer and Larson 1999) or genotype (Sakai *et al.* 2001) due to the novel environments they experience in their new range: this includes population changes inherent in a colonizing event such as founder effects or drift (Palumbi 2002, Cox 2004). Just as mutations in a virus within human populations can mean the difference between rarity and a pandemic, so too changes in NIS populations can turn a rare or isolated population into a pest. This can also be one of the major factors in creating create time lags between the arrival phase of an NIS and an outbreak (Mack *et al.* 2000, Byers and Goldwasser 2001, Memmott *et al.* 2004). New methods in genetics, life-history evolution, and coevolutionary theory can provide insight into and draw inference from the growing examples of NIS populations that have changed fundamentally since their arrival in a new range.

Evolutionary change in NIS populations can follow many possible pathways. Schierenbeck and Aïnouche (Chapter 9) emphasize that pre-adapted generalist genotypes will facilitate invasion success. Substantial genetic variation can provide the requisite genetic material for rapid evolutionary response to the novel environment, and Shierenbeck and Aïnouche (Chapter 9) point out that there are many pathways to this variation (heterozygosity, polyploidy, and perhaps now even extra-genomic genetic information (Lalle *et al.* 2005)). However, general genetic diversity may not alone be enough to influence invasion success (Herben *et al.* 2004). More importantly, how labile life-history traits are (phenology, clonal or vegetative reproduction in plants, mating behaviors, etc.) may mark the important genetic distinction. Buckley and Metcalf (Chapter 5) describe how life-history evolution due to unique forces at work in novel environments (different life-history strategies) may benefit NIS populations.

While life-history evolution may be responsible for rare large outbreaks, this would be difficult to test. Thorpe and Callaway (Chapter 15) explain that evolutionary response of microbial communities can happen so fast that this may mute or mitigate an NIS from long term dominance through positive soil feedback pathways. Because of a potentially rapid response and the short generation times of microbial communities, it may be possible to test soil systems for rapid evolutionary response to encouraging or mitigating the successful establishment of an NIS. NIS colonization, additionally, may provide ideal systems to research the stability of microbial communities as well as their relationship to the plants with which they interact through belowground pathways (Wardle 2001). Pathogens would also fit this model, and Gilbert and Parker (Chapter 13) describe the coevolution of plant-pathogen systems and maternally inherited induced resistance. The evolutionary response of an NIS to the biotic community may be crucial not only in the establishment, but in the resulting effect on the native biota. Kondoh (Chapter 10) models how contact experience, the previous evolutionary filtering from prior interactions between an NIS and related novel competitors, predators, and prey, can result in successful invasion. He describes how the contact experience, in many forms, can influence the specific components of contact between the NIS and novel biota as information retrieval (detecting the other species), processing (recognizing characteristics of that novel species), and behavioral response (being able to prey upon, escape, or compete with that species).

NIS populations influencing populations and environment

It should be noted that even identifying an invasive species can be problematic (Colautti and MacIsaac 2004, Murphy *et al.* Chapter 4). But regardless of definition, there is a general understanding among biologists that ultimately any invasive will in some key way be defined by its influence on the biotic and abiotic components of its new range. There may be millions of NIS propagules entering complex environments, but our concern for their range expansion is ultimately a function of their impact on other species in their new range, the ways in which they affect ecosystem processes, and how these changes may persist or increase over time.

Historically documented invasions can also provide insights into the pathways through which the context of and invading organisms can influence both persistence and the concomitant influence on native biota. Courchamp and Caut (Chapter 11) used models incorporating direct and indirect interactions to explain invasions, as well as show how the invasions themselves illustrate the complex and sometimes counterintuitive behaviors of interacting populations. Complex dynamics between populations may also mean that after an invasion it takes many generations for the effects of the new interactions to show their impact (Freckleton *et al.* Chapter 6).

Although documented changes in native biota or ecosystem function may be clear after an invasive becomes a damaging pest, predicting the ultimate impact of an NIS on native habitats is difficult. A number of factors, intrinsic to the invading population and due to the novel environment, can elicit complex responses to the non-native populations. Indirect effects on the environment are difficult to detect, let alone predict, yet may be among the more common and serious responses to NIS. Invasive plants can alter the soil nutrient feedback loops and render long term changes to the soil environment (Thorpe and Callaway Chapter 15). Mutualisms, such as pollination services, can be disrupted by invasives. Though the converse may occur. Non-native bees have been shown to increase pollination efficiency of some plants (Richardson *et al.* 2000), although the effect on native pollinator communities adds additional uncertainty to the diagnosis of these effects. Generalism versus specialism can be crucial to the extent of influence a non-native species may have in pathogen-host relationships (Gilbert and Parker, Chapter 13), pollinator systems (Vazquez, Chapter 14), and soil mutualisms (Thorpe and Callaway Chapter 15). The symmetry of these mutualist relationships is of further consequence (Vazquez, Chapter 14) when inferring the potential impact an NIS may have on novel systems.

Whether direct or indirect, the stochastic nature of population interactions can radically affect the ultimate consequences of a persistent NIS (Freckleton *et al.* Chapter 5, Warren *et al.* Chapter 16) especially as systems may contain nonlinear dynamics. A final level of complexity results from the many applications of our inference to political, social, and economic issues. It is broadly accepted that NIS can affect the inherent richness of native biota, specific endangered species, the ecosystem function of native habitats, as well as biota of economic importance. In their review of how NIS influence novel communities, Murphy *et al.* (Chapter 4) found a correlation between level of invasive on the SE scale and community impact, there was no correlation with economic impact. This may trouble our ability to apply a level of community change due to an invasive to some system of social or economic ‘importance’ of the invader.

CONCLUSION

Invasions biology is faced with many of the same struggles that have long faced mainstream ecology. Organisms show an array of intrinsic qualities that are both indicative of their population dynamics as well as responsible for those dynamics. Yet populations of organisms respond and influence their biotic and abiotic contexts, and they adapt phenotypically and genotypically to them. The problem of filtering that which is broadly important to populations from that which is idiosyncratic is highlighted in the study of NIS. We certainly need to develop a general understanding of the qualities of populations and habitats that can lead to invasion persistence and impact, yet we often find that the causes of any specific invasion can be unique to that specific species or habitat. A major goal of this book is to carefully assess when simplicity is informative (e.g., a population-level analysis of density dependence), when complexity is instrumental (such as when abiotic factors influence NIS persistence), and when generalization is not likely possible (such as the factors that make up the realized niche of an NIS).

One of the greatest challenges facing the study of invasions biology arises from species-specific characteristics. As is often shown in this book, a better understanding of the interface between intrinsic population properties and the stochastic context of a population is likely to provide important insights into NIS establishment and expansion. Frustrating many straightforward paths to invasion prediction is the combination of stochastic and deterministic processes that influence populations behaviors (Dennis *et al.* 2003). Mathematical models may help indicate which parameters under which assumptions can show a definitive influence on population dynamics. Thus, when entering an observational or manipulative experimental program, the theoretical literature can prove an important guide to developing hypotheses and testing them.

Reflecting recent conceptual advances in general ecological theory, often ignored processes such as mutualisms, intra-specific competition, and below ground processes are also likely to influence the potential impact of NIS (Callaway and Aschehoug 2000, Richardson *et al.* 2000, Parker and Haubensak 2002, Callaway *et al.* 2004) and mark potential pathways to bridge what appears to be idiosyncratic to more generalizable patterns. In these areas, the study of NIS may be well suited to inform our greater understanding of such complex and often masked mechanisms in general. Thus, not only is there a reciprocal interest in understanding traditional problems in ecology and invasions biology, these two approaches to natural systems should interact and inform each other as they advance in techniques, concepts, and understanding.

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