PART II

Insights into EVOLUTION

Mark Vellend, A. Randall Hughes, Richard K. Grosberg, and Robert D. Holt

The most dramatic examples of evolutionary change often occur when a lineage is faced with a novel set of biotic or abiotic conditions. The driving force may be local or widespread environmental change, such as when pollution altered the selection regime on melanism in peppered moths in England (Kettlewell 1955), or it may be a species' arrival in a novel geographic locale, such as the adaptive radiation of Darwin's finches following arrival on the Galápagos islands (Grant and Grant 2002). Our ability to study and understand the evolutionary consequences of species introductions in new regions is often limited because we must use indirect evidence to reconstruct the sequence of events connecting an initial introduction to the current distribution of phenotypes and genotypes in space. Thus, in order to evaluate evolutionary processes directly, we often resort to laboratory experiments in which conditions are greatly simplified. This simplification can create doubt as to the general applicability of the results to natural settings.

Ecological geneticists occupy a middle ground, measuring selection in natural populations in contemporary time (Endler 1986). Exotic species provide exemplary fodder for such studies. As pointed out throughout this book, exotic species introductions present an unprecedented number of natural experiments replicated across space (the same species is often introduced into multiple places) and across taxa (multiple species are often introduced into the same place). What can we learn about the evolutionary process from studying exotic species?

It is always humbling to revisit classic texts in evolutionary biology. The present volume finds several remarkable parallels in the 1965 symposium volume *The Genetics of Colonizing Species*, edited by Herbert Baker and G. Ledyard Stebbins. As described in the Preface to that volume, the symposium "had as its object the bringing together of geneticists, ecologists, taxonomists, and scientists working in some of the more applied phases of ecology … to present facts and exchange ideas about the kinds of evolutionary change which take place when organisms are introduced into new territories." Forty years later, we have assumed much the same objective. Many of the themes raised in the Baker and

Stebbins volume are echoed in the chapters of this and other sections of the book: changing evolutionary pressures during different stages of invasion (Huey et al., Chapter 6; Ricklefs, Chapter 7); genetic bottlenecks and the maintenance of genetic variation (Novak and Mack, Chapter 8; Wares et al., Chapter 9); the development of local adaptation and spatial genetic structure (Holt et al., Chapter 10; Huey et al.; Wares et al.); the elucidation of traits important for successful invasion via cross-species comparisons (Rice and Sax, Chapter 11); the role of hybridization and introgression in adaptive evolution (Rice and Sax; Wares et al.); and the evolutionary consequences of novel biotic interactions (Callaway et al., Chapter 13).

Despite foreshadowing many of the themes of the present volume, the participants in Baker and Stebbins' symposium largely had their hands tied by a lack of direct evidence. As Ernst Mayr put it in the volume's summary, "When it comes to actual observations of genetic changes in colonizing species, the number of clear-cut cases is disappointingly small." The past 40 years have seen tremendous progress in elucidating evolutionary changes following the introduction of exotic species, in many instances providing case studies destined to be textbook examples of fundamental evolutionary processes (Cox 2004). The following chapters summarize much of this progress and point to a range of new directions.

The Baker and Stebbins symposium occurred on the eve of the "molecular revolution," sparked in the late 1960s by the widespread application of protein electrophoresis to the study of natural populations (Hubby and Lewontin 1966). Molecular markers have thoroughly infiltrated a wide range of subdisciplines in evolution and ecology (Avise 2004), and their application to most of the evolutionary phenomena discussed here provides perhaps the most striking contrast with the contents of Baker and Stebbins' volume. Molecular markers have allowed enormous advances to be made in extracting evolutionary lessons from exotic species invasions. For example, John Harper suggested in 1965 that knowing the source of the propagules that start an exotic invasion was the key to unraveling subsequent evolutionary trajectories, but admitted that possession of such knowledge was "rarely the case." Molecular studies have helped pinpoint the source (or, just as often, the sources) of exotic introductions, knowledge that has indeed proven vital to studies of evolutionary change. In addition, hybridization and introgression, which frequently accompany exotic invasions, have been much more thoroughly characterized using molecular markers, providing a springboard for examining the evolution of particular traits as they enter novel genetic backgrounds. Putatively neutral molecular markers allow strong tests for genetic bottlenecks following invasion, and also provide a critical basis of comparison when testing for adaptive evolution in traits of presumed ecological significance. Finally, DNA sequence data add a temporal element when used to reconstruct phylogenies, allowing the study of the timing of particular colonization events. Advances on these fronts feature prominently in the following chapters, building on the foundation laid by the Baker and Stebbins volume.

This book also highlights research whose conceptual basis has emerged more recently. While there has long been interest in the manifold consequences of exotic species arriving in new territories, where they are free of many natural enemies, the coevolution of competitors *within* trophic levels has developed only recently as a topic of potential importance in invasion biology. Callaway et al. review compelling evidence that allelopathic chemicals in some exotic plants make a major contribution to their invasive success, providing novel insights into the importance of competitor coevolution in terms of evolved tolerance to allelochemicals. Huey et al. also present some compelling case studies of exotic species revealing the simultaneous predictability of evolution in some respects (e.g., comparable latitudinal clines have arisen repeatedly for independent introductions into different biogeographic regions) and its unpredictability in others (e.g., the developmental basis for a given phenotype may vary among regions).

Interestingly, a number of issues raised in 1965 remain major unsolved puzzles today, representing important future directions in evolutionary studies of invasive species. First, if populations of exotic species in their introduced ranges are genetically isolated from founder populations, can we expect a spike in the global rate of speciation? Polyploidy and hybridization in plants has provided some striking examples of novel species creation resulting in part from exotic introduction (Cox 2004), but in how many other cases is speciation underway? Second, invasive species often remain quite rare for a long time following their introduction before experiencing explosive population growth and expansion. How often is this "lag phase" a result of the time it takes for adaptive evolution to produce invasive phenotypes? Given that adaptation via natural selection is involved, what is the relative importance of adaptation to abiotic versus biotic factors in the environment? Finally, perhaps the greatest limitation to research on the evolution of exotic species is that we can study only those species that have successfully established. How often is the *failure* of exotic species to become invasive due to a lack of appropriate genetic variation and therefore evolutionary potential? At the moment, we simply don't know. Tremendous progress has been made in the last 40 years, but in many ways we have only scratched the surface of the potential for exotic species to provide fundamental lessons in evolutionary biology.

Literature Cited

Avise, J. C. 2004. *Molecular markers, natural history, and evolution*, 2nd Ed. Sinauer Associates, Sunderland, MA.

Baker, H. G. and G. L. Stebbins, eds. 1965. *The genetics of colonizing species*. Academic Press, New York.

Cox, G. W. 2004. *Alien species and evolution*. Island Press, Washington DC.

Endler, J. A. 1986. *Natural selection in the wild*. Princeton University Press, Princeton, NJ.

Grant, P. R. and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's Finches. Science 296:707–711

Hubby, J. L., and R. C. Lewontin. 1966. A molecular approach to the study of genic heterozygosity in natural populations. I. the number of alleles at different loci in *Drosophila pseudoobscura*. Genetics 54:577–594.

Kettlewell, H. B. D. 1955. Selection experiments on industrial melanism in the Lepidoptera. Heredity 10:287–301.