

Testing Basic Ecological, Evolutionary, and Biogeographical Principles Using Invasive Species

D. F. Sax, J. J. Stachowicz and S. D. Gaines (eds), *Species Invasions: Insights into Ecology, Evolution, and Biogeography*. Sinauer Associates, Inc., Sunderland, MA, USA, 2005, 480 pp, 56 illus, Casebound, US\$74.95, ISBN: 0-87893-821-4; Paper, US\$49.95, ISBN: 0-87893-811-7

Cynthia D. Huebner

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Sax et al. argue in *Species Invasions: Insights into Ecology, Evolution, and Biogeography* that species invasion is an on-going experiment and a research tool with which to test fundamental ecology, evolution, and biogeography tenets. The authors recognize the importance of the applied and single-species approaches that currently dominate invasion research, but state invasive species provide three unique characteristics that make them model research systems: (1) ecological processes can be observed in real time, (2) place, time, and characteristics of introductions are often known, such that rate processes can be followed, and, (3) because different species have been introduced in abundance in different locations, it may be possible to examine and compare such species-additions over a variety of spatial and temporal scales.

The book is organized in three sections—ecology, evolution, and biogeography. The five chapters in the ecology section focus on species interactions, niche saturation, induced changes in ecosystem processes, extinction, and infectious diseases, emphasizing that invasive species provide an opportunity to study each of these topics in real time. The section on evolution includes six

chapters with discussions on taxon cycles, genetic bottlenecks, random drift, hybridization, introgression, selection on environmental and additive and nonadditive genetic effects, niche evolution, sexual selection, evolution of reproductive isolation, and the adaptive significance of sexual reproduction as they relate to invasive species and rate processes. The biogeography section is organized around six chapters with discussions on unique geographic evolutionary trajectories, species homogenization over space and time, population spread and range expansion, scaling patterns, and species dynamics in terms of island biogeography theory.

The concepts covered are broad enough to be of interest to most researchers focusing on invasive species, even if their taxa of interest are not included as support for each concept. Several chapters in the evolution and biogeography sections include additional descriptions of basic concepts that may make them more accessible to ecologists, especially students, who may be focusing on more applied invasion problems. The biogeography section will be of most interest to landscape ecologists, with the chapter on population spread being the strongest. Kinlan and Hastings summarize several population spread models ranging from the linear rates modeled by reaction-diffusion equations to the accelerating rates of patchy spread defined by stochastic nonlinear integro-difference models as well as

C. D. Huebner (✉)
USDA Forest Service Northeastern Research Station,
Morgantown, WV 26505, USA
e-mail: chuebner@fs.fed.us

individual-based models for systems rich in data. Their summary integrates dispersal dynamics, demography, and shape and heterogeneity of invaded areas. In doing so, they postulate which life history traits (e.g., long-distance dispersal, lack of Allee effects, active dispersal) and environmental factors (e.g., homogeneous, two-dimensional areas) will result in the most rapid spread by comparing spread rates and dispersal distances of several taxonomic groups with a more detailed comparison of terrestrial and marine invasions. Labra, Abades, and Marquet's use of minimum spanning trees and the North American Breeding Bird Survey to show that invasive and native species respond similarly at variable scales will likely lead to analogous studies with other taxa. Sax, Brown, White, and Gaines use island biogeography theory to show that overall species richness (more so for vascular plants and less so for birds) has generally increased over the past few centuries. The latter may appear to negate homogenization via loss of native species as a consequence of invasion. However, McKinney and Lockwood summarize several studies that indicate increased species richness is likely to occur only at larger spatial extents; conversely, homogenization is more likely to occur in intensely disturbed sites, such as urban areas. Vermeij argues, albeit with somewhat limited support, that when homogenization and loss of native species do occur, they are only short-term consequences. He further states that invasion may one day be seen as essential to the long-term vigor of ecosystems as mutations today are seen as essential to the long-term evolution of species and populations. Such statements may motivate researchers to clarify the short- and long-term impacts of invasion on species dynamics and ecosystems.

Four chapters in the evolution section—(1) taxon cycles by Ricklefs, (2) genetic bottlenecks in alien plant species by Novak and Mack, (3) mechanisms of evolutionary change by Wares, Hughes and Grosberg, and (4) niche evolution by Holt, Barfield and Gomulkiewicz—are comprehensive and likely of interest to landscape ecologists who hope to improve predictions of species spread and understand the role of genetic versus ecological processes in invasion lag times.

Loss of genetic diversity in response to genetic bottlenecks or founder events appears to be uncommon in successfully established invaders, possibly due to multiple introductions. Resolving whether invasive species are responding primarily to Fisher's natural selection theory or Wright's random genetic drift theory (or, more likely, both) is a proposed endeavor. The relatively high genetic diversity afforded to invasive species indeed may be the key to their dominance over some native species, who may not be able to respond as quickly to short-term environmental changes and whose niches are not evolving.

While an interesting summary of allelopathy and soil microbial interactions, the chapter on evolutionary trajectories by Callaway, Hierro, and Thorpe appears to be out of place. Although it is clear that species located in geographically different places may have developed different species interactions, it is the evolution (not the location) of interactions (some of which may be classified as facilitative) between plant species and soil biota that is of most interest. Calling these interactions examples of coevolution or reciprocal evolutionary change may be questioned by the more conservative evolutionary biologists, but that is of less concern than the lack of a description for the geographic mosaic concept (aside from referencing its founder). This chapter, if placed in the ecological section, may have helped connect the chapters of this section with the other two sections.

The chapter on interactions in the ecology section by Bruno, Fridley, Bromberg, and Bertness summarized the need for further research on all types of interactions because the presumed importance of lack of predators on invaders and competitive superiority of invaders has been refuted by several studies and other research indicates facilitation deserves more intensive study. Unfortunately, Stachowicz, and Tilman's chapter on community saturation appears to ignore interactions other than competition by focusing on resource utilization as the key to understanding community saturation and the role of diversity. Likewise, Blackburn and Gaston's reminder that humans are perhaps the most detrimental of invaders is timely but focuses on the effects of one interaction (predation) on avian extinction.

Lafferty, Smith, Torchin, Dobson, and Kuris' chapter on infectious diseases is also a discussion of predator–prey (parasite–host) interactions, though the authors do briefly connect these interactions with evolutionary theory in terms of host resistance and speciation via enemy-release. D'Antonio and Hobbie's summary of invasion effects on ecosystem processes includes some potential challenges when using invasive species that the evolution and biogeography sections under-represent. These challenges include differentiating covarying environmental factors (e.g., human-mediated disturbance) from factors solely associated with the invasion. The chapters in the ecology section appear to be characterized by the species-specific approach that the authors wish to move beyond. However, it may be these species-specific approaches that make the challenges easier to discern.

A combination of reductionist (species-specific or applied) and holistic approaches may be

required to keep invasion research both grounded and progressive. While I was hoping the authors would more directly link, even hypothetically, species interactions and the consequent changes in ecosystem processes with native and exotic species evolution or distributions, the book motivates the readers to do so themselves. There are a few repetitive uses of examples (e.g., the large ground finch of Daphne Major) as well as claims of “beyond the scope” in several chapters, which are disappointing to come across because the subject in question could be included in the perceived scope of the book. Despite these relatively minor problems, I find the book well-written, informative, and idea-generating. Consequently, I recommend this book to anyone seeking new perspectives on invasion theory, including researchers with both applied and basic questions about native and exotic colonizers and invaders.