ECOLOGY

Learning from the Aliens

Michael J. Crawley

A grant application lands with a thump on your desk. You skip straight to the summary section: "This proposal involves the release of an alien disease onto a tropical archipelago with a view to measuring the impact of introduced pathogens on extinction rates of endemic island birds." As my Scottish uncle would have said: "Aye. Right." But this is exactly what happened when colorful but disease-ridden cage birds escaped in Hawaii. *Species Invasions* is a fascinating book that interprets the results of literally hundreds of intentional and unintentional introductions. Representing an extraordinary range of "natural experiments," such invasions by alien species provide unique insights into large-scale and long-term processes in ecology, evolution, and biogeography. We nevertheless need to be circumspect. As unplanned experiments, they lack randomization and there is seldom any data on initial conditions. On the other hand, the introductions were often very well replicated, both within and between different geographic regions. Most major alien pest species were introduced to new environments hundreds or even thousands of times.

Species Invasions
Insights into Ecology, Evolution, and Biogeography
Dov F. Sax, John J. Stachowicz, and Steven D. Gaines, Eds.
Sinauer, Sunderland, MA, 2005. 509 pp. $74.95, £48.99. ISBN 0-87893-821-4. Paper, $49.95, £31.99. ISBN 0-87893-811-7.

The advantages of studying species invasions are several. Ecological and genetic processes can be observed in real time, rather than inferred from the patterns they generate. Rates of spatial spread and genetic change can be estimated from known places and dates of introduction. Although the first paper on species invasions (*1*) appeared in 1919, study of the phenomenon is often traced back to Darwin's *Beagle* voyage, when he documented many European plants thriving as aliens in South America. He pointed out that escape from the parasites and diseases that attack them in their native range may contribute to the rapid spread of invading plants and animals. An influential 1964 Asilomar conference (*2*) and a SCOPE program (*3*) in the 1980s boosted interest in the topic. *Species Invasions* brings readers up to date. The contributors' informative mix of data and theory offers a distinctive perspective on invasion biology.

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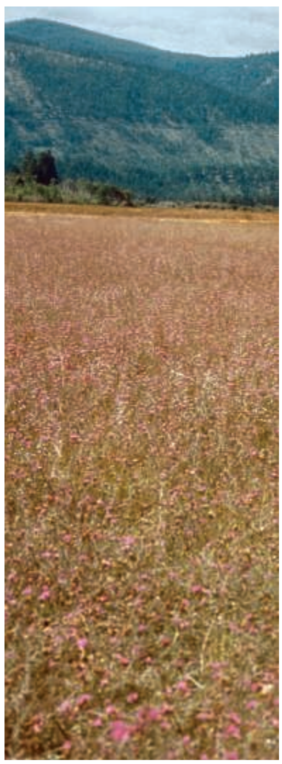
Species invasions can be used to address questions of community assembly and species packing. For instance, how does the establishment of an abundant alien species affect the number and relative abundance of native species that persist? Bruno *et al.* argue that competition is only one of several important factors that structure communities. I believe that, at least for plants, interspecific competition from established native species is the dominant force restricting invasion by aliens; other processes (like herbivory by native animals) typically become important only in places (or at times) where competition from the native vegetation has been reduced by some other means (e.g., increased soil disturbance by feral pigs in Hawaii). However, I agree completely that there is little evidence that competition from alien invasives has caused substantial (or even measurable) extinction of native species. As Sax *et al.* point out for vascular plants, rather than causing catastrophic loss of biodiversity, alien invasions almost always lead to increased total species richness. The majority of established alien plant species never become sufficiently abundant to have important negative impacts on ecosystem functioning or species interactions.

The effects of alien animals such as feral goats and pigs on oceanic islands are well known, but less is understood about the ways the presence of alien plants might alter the disturbance regime and hence influence ecosystem structure and function. D'Antonio and Hobbie address these questions in the context of alien plants that affect fire regimes or increase the rate of nitrogen supply.

Much of what we know about alien diseases concerns catastrophic infections like HIV, chestnut blight, or Dutch elm disease, but Lafferty *et al.* explore several more subtle, community-level effects of disease introductions. The case of the native Hawaiian avifauna is intriguing: there was no vector for the avian pox introduced by the cage birds until 1926, when an alien mosquito was introduced in the discarded bilge water of a visiting ship. From that point, the lowland native birds were rapidly eradicated. In other cases, introduced diseases can be agents of apparent competition, as in the United Kingdom where an alien nematode spread by introduced pheasants induces morbidity in the native gray partridge but not in the pheasants. Globally, however, most recent extinctions of bird species can be attributed to alien predators (e.g., rats and cats on oceanic islands) or habitat destruction by people. Blackburn and Gaston make the point that the particular set of native species that are lost depends on the set of introduced predators, so the attributes of the extinct bird species generally show no clear patterns (large-bodied ground-nesters on islands excepted).

Genetic bottlenecks occur when small numbers of colonists import only a tiny fraction of the allelic variation present in the parent population. However, as various contributors explain, serious reduction in genetic variability as a result of bottlenecks is observed in alien species much less often than was expected by the earliest workers in the field. For inbreeding species, the presence of high genetic variability in the invaded range is generally attributed to multiple introductions (e.g., the thousands of independent introductions for many of the weed species that arrived in the New World as contaminants in seeds from all over Europe and the Middle East). In the native range of inbreeding species, most of the genetic variation arises among populations, whereas variation within populations is typically very low. For outbreeding species, the genotypes of individuals are often sufficiently different that bottleneck effects are unlikely if hundreds (let alone tens of thousands) of individuals are introduced.

Alien species spreading through new environments encounter novel selection pressures; thus, they offer rich opportunities for studying the rate and predictability of



Weed with a biochemical weapon (spotted knapweed).

CREDIT: NORMAN E. REES/USDA AGRICULTURAL RESEARCH SERVICE, WWW.FORESTRYIMAGES.ORG evolution in the wild. Huey *et al.* discuss some wonderful examples of rapid evolution in the alien range. The classic example is provided by the fruit fly *Drosophila subobscura*, which was introduced repeatedly (and usually unintentionally) into both North and South America. It subsequently exhibited extraordinarily rapid evolution in such traits as wing size and chromosome inversions.

Rice and Sax consider the use of species invasions to test fundamental evolutionary questions, such as the benefits of sexual reproduction. For example, they discuss differences in the spread of introduced sexual and asexual species in two genera of grasses: terrestrial *Cortaderia* in California and marsh *Spartina* in New Zealand. In both cases, the sexual member of the alien pairs became more abundant, spread over a wider area, and occupied a greater range of habitats.

Invasion biology has helped reinvigorate entire subdisciplines within ecology. Allelopathy, the negative effect of one species on another mediated by the release of secondary chemical compounds into the environment, offers an excellent example. This topic had been left stone dead by John Harper's coruscating review (*4*) of a book by E. L. Rice (*5*), in which Harper argued that most if not all of the examples of allelopathy cited by Rice could equally plausibly be attributed to resource competition or to herbivory. As a result, a generation of ecologists steered clear of the difficult and intricately controlled experiments that were necessary to tease apart genuine allelopathy from the plethora of other possible plant-plant interactions. As Callaway *et al.* note, studies of exotic plants—especially the spotted and diffuse knapweeds, *Centaurea maculosa* and *C. diffusa*—have provided the most convincing demonstrations of the importance of allelopathy. In the Rocky Mountain states, these pernicious invaders exclude whole suites of native species to produce extensive monospecific stands. Their root exudates cause 100% mortality in native test plants but are not toxic to the *Centaurea* themselves. They are also much less toxic to coevolved plant species from the knapweeds' original European habitats, which suggests that long-term coexisting species evolve to tolerate each other's biochemistry. Adaptations to live with the allelopathic chemicals of all one's neighbors offer perhaps the best case of coevolutionary relationships within plant communities, relationships that are disrupted by the introduction of alien species.

Discussing the rates and spatial patterns of the spread of alien species, Kinlan and Hastings draw attention to the importance of the mode by which rare long-distance dispersal occurs. They also note the role played by life history traits that affect rates of population growth at low densities (Allee effects); after all, dispersal is only important if the dispersing organisms survive to reproduce in their new surroundings. And the authors' exploration of models and empirical data from various marine and terrestrial taxa reveals that feedback among migration, adaptation, and environmental structure is critical in determining the dynamics of range expansion by alien species.

The volume is more than a collection of case studies; it contains interesting new theory as well. Stachowicz and Tilman provide a lucid introduction to a stochastic model of community assembly, and they address the vexing question of whether the relationship between species richness and invasibility is positive, negative, or contingent. Holt *et al.* investigate evolution and niche conservatism in the context of theoretical models of source and sink populations in temporally variable environments. They point out that evolution can rescue an isolated but initially maladapted invading population from extinction, so long as evolution occurs rapidly enough. This "evolution outside the niche" defines the potential domain into which an alien species can expand. Their discussion also draws attention to the often-contrasting effects of migration on the potential for niche evolution in alien species: Migration provides opportunities for evolution by sustaining local populations in sites outside the initial niche (i.e., in sink habitats where population growth is negative); it increases local abundances, enhancing the opportunity for local mutational input; it alters density-dependent demographic processes; it introduces genetic variation from the source population; but it dilutes locally adapted gene pools, hampering adaptation.

My one serious reservation about the volume is its parochial focus. Virtually all of the authors and most of the examples are American. The editors claim that they "did not attempt to bring together the leaders in the field of invasion biology…but tried instead to draw together leaders and emerging leaders in the fields of ecology, evolution, and biogeography." Although that is fair enough, much of the best work on invasions has been carried out in South Africa, Australia, and continental Europe. Examples from these places, and the insights of the biologists who work there, do not get the coverage they deserve. It is instructive to recall that the major breakthrough in controlling the invasion of species-rich fynbos habitat in the Cape floristic region of South Africa (one of Africa's hottest biodiversity hotspots) did not come until it was pointed out that the invasive trees were wasting vast quantities of Cape Town's precious water supplies through excessive transpiration (*6*). As soon as serious financial resources were committed to the elimination of the alien species (using a combination of mechanical and biological control), large areas of species-rich fynbos were rapidly restored.

Species Invasions shows how far we have come since Elton's classic *The Ecology of Invasions by Animals and Plants* (*7*). The volume offers a fine compendium of ideas and examples that will be valuable to students for the number of doors it opens to scores of subdisciplines within ecology. For professionals, it represents a state-of-the-art overview of the issues involved in invasion biology.

BROWSINGS

What the Dormouse Said. How the Sixties Counterculture Shaped the Personal Computing Industry. *John Markoff.* Viking, New York, 2005. 336 pp. $25.95. ISBN 0-670-03382-0.

LSD trips, Ken Kesey's Merry Pranksters, Stewart Brand and the *Whole Earth Catalog*, musicians who became the Grateful Dead, communal living, antiwar protests, and Pentagon-funded research all appear in this exploration of the origins of personal computing. Markoff covers events between 1960 and 1975 in the area that would become known as Silicon Valley. He highlights the philosophical clash between two innovative, unconventional labs that shared a hacker culture and antiauthoritarian outlook: While John McCarthy and his Stanford Artificial Intelligence Laboratory sought ways to replace humans with machines, Douglas Engelbart recruited a "lunatic fringe" to the Stanford Research Institute to develop human-centered computing. (In a legendary December 1968 talk, Engelbert unveiled a system that included on-screen text editing, hypertext links among documents, and windows that allowed one to mix text, graphics, and video.) Another narrative thread concerns the conflict between open and proprietary software. The social, political, and cultural connections revealed in Markoff's captivating stories demonstrate the surprising importance of sixties counterculture to the development of today's computing world.

References and Notes

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7. C. S. Elton, *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).

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