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Biotic Invasion: A Global Perspective and Ecology of Invasion: Patterns and Perspectives

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Abstract

Interest in biotic invasions has grown as the entry, spread and proliferation of organisms beyond their native ranges is accelerating world-wide. The study of invasions can make use of these natural experiments for better understanding community composition changes, the rate and character of natural selection, genetic drift, and coevolution. Biotic invasions are part of the global change caused by man; in many cases they have created one or more serious environmental alterations: the loss of biodiversity, radical changes in the abundance and roles of native species, and attendant economic consequences, e.g. increased erosion, fire, and flooding. Papers were presented under six overlapping and interconnected categories: 1) assessment of invaders' new ranges and status, 2) characterization of invaders or their habitat, or both, 3) attempts to identify correlations among invaders, their habitats, or both, 4) experimental approaches to invasion, 5) modeling invasions, and 6) the prevention and control of invaders. The presentations ranged along multiple research fronts dealing with a taxonomically-diverse group of invaders world-wide. The characterization of invaders, assessment of their new ranges, and correlation are being now augmented through experimentation and modeling. Together these approaches are yielding results that unravel invasion processes while at the same time providing insights into the control of invaders.

Preface

Interest in biotic invasions, the entry, spread and proliferation of organisms beyond their native ranges, has grown in the past decade with an acceleration that mirrors the time course of invasions themselves. After a long-quiescent phase, there has been a rapid acceleration of growth in deserved attention in this topic. We are still early in the ascendancy of this wave of interest and clearly have not reached any "plateauing" of interest.

Reasons for this attention are becoming increasingly apparent. The entry of a species new to a range instantly creates the opportunity for new species interactions. Biotic invaders may be viewed as "probes" that trigger change in communities in ways that native species rarely cause. As a result, much potentially can be learned from these "natural experiments" about forces underlying community composition, the rate and character of natural selection, genetic drift, and coevolution.

In addition, there are compelling environmental and economic reasons to investigate biotic invasions. Few communities have not already been the recipient of alien species, and fewer still are so isolated or possess such unusual intrinsic features as to make alien species entry and persistence unlikely in the future. In many examples world-wide the persistence of biotic invaders has created one or more serious environmental alterations: the loss of biodiversity, radical changes in the abundance and roles of native species, and attendant economic consequences, e.g. increased erosion, fire, and flooding. Biotic invasions were probably the first global change caused by humans; their importance has only grown with the deliberate and accidental exchange in species world-wide. Consequently, these organisms and the phenomena they spark deserve increasing attention among ecologists.

Products of this increased attention were well illustrated at the INTECOL meeting in Florence by the vigorous hybrid of two symposia, "Biotic Invasions: a global perspective" and "Ecology of Invasion: patterns and processes." Through 25 oral presentations and more than a dozen posters, investigators from five continents reported their results of a taxonomically-diverse array of species that have slipped the ecological constraints on their abundance in native ranges by spreading, proliferating and persisting in new, often-distant, ranges.

The Presentations

At least two themes arose during the two-day combined symposium. (1) As the international representation of the participants illustrated, biotic invasions are truly global in their extent and consequences. No one continent has been either the sole recipient or the sole contributor of species that are today aggressive invaders elsewhere. (2) Progress in our understanding of biotic invasions is moving rapidly on a variety of interconnected fronts. Papers were presented under six overlapping and interconnected categories: 1) assessment of invaders' new ranges and status, 2) characterization of invaders or their habitat, or both, 3) attempts to identify correlations among invaders, their habitats, or both, 4) experimental approaches to invasion, 5) modeling invasions, and 6) the prevention and control of invaders.

Assessment of Invaders' New Ranges and Status

The distribution of invasions has long been a source of investigation: clearly, the areal extent, spatial abundance and reproductive status of invaders are high on the list of first needs in any investigation of an invasion. Invasion biology needs a temporal as well as a spatial context; tracking the rate and character of an invasion facilitates prediction on the susceptibility of potential new ranges and habitats. Leppakoski and Olenin pointed out that the Baltic Sea has been site of marine invasions for at least the last 7 centuries. Some erstwhile invaders have failed to persist (e.g. Pacific salmonids); others have been only too successful in occupying their new range (e.g. the soft-shell crab, *Mya arenaria* and the barnacle, *Balahus improvisus).* Not only are these invaders firmly established, they may also be altering basic ecosystem processes in the Baltic Sea. Occhipinti, a co-convener of the symposium, has assessed the rise and apparent decline in the status of the alien bryozoan *Tricellaria inopinata* in the environmentally-threatened lagoon of Venice. The continued status of this aggressive invader may be tied to water quality in the Lagoon; in the last 2 years the alien has declined (along with other bryozoans) in response to changes in water chemistry associated with remediation efforts. As with the Baltic Sea, predictions about the status of invaders in the Venetian Lagoon will emerge only through long-term assessment of both the invaders and characteristics of their habitat. Attempts to tie recent changes in the physical environment to the fate of an invader are also a concern of Maekawa, who has followed areal spread of the alien tree *Robinia pseudoacacia* in Japanese riverine ecosystems. Using an unusually long-term series of air photographs, Maekawa described the accelerating spread of *R. pseudoacacia* from small, disconnected patches to a more continuous distribution. The alien tree's spread has potentially serious consequences for the biodiversity of the invaded riverine communities.

Characterization of Invaders or Their Habitat, or Both

The global exchange of species has accelerated so rapidly, especially in the last 200 years, that documenting their occurrence has been both a requirement and a challenge. We still lack comprehensive knowledge of the spread of alien species introduced more than 100 years ago; detection of recent immigrants will likely be delayed decades. Galil and Boudouresque independently reported on different aspects of the massive biotic invasions into the Mediterranean Sea in the past 150 years, especially invasions via the Suez Canal. The consequences of the mid-19th century opening of the canal are still reverberating through the Mediterranean Basin as new introductions from the Red Sea (and eastward) appear routinely. The diversity of this alien "bestiary" is impressive: Boudouresque estimates that 70 plant and approx. 350 animal species (4-5 % of the Mediterranean current biota) is alien. Here as in the Baltic, concern grows as to the consequences of these invaders: competitive displacement of natives, alteration of basic ecosystem processes, even the replacement of native keystone species by aliens.

Characterization took another form in the presentations by Richardson *et al.* and Rejmanek. Mutualisms between native species have often been neglected as important determinants of community structure; Richardson *et al.* contend that mutualisms, including positive interactions between invaders and indigenous species, have also been underappreciated. The seemingly idiosyncratic fate of introduced species may be in part clarified by more careful attention to the presence (or absence) of the requisite mutualists for potential invaders.

Rejmanek has also been concerned with predicting the fate of immigrants. His approach is based on aspects of invaders' life history traits and features of the native environment compared to the new range. He finds that the likelihood of persistence in a new range may be tied to as many as eight criteria, including possession of phenotypic plasticity, low nuclear DNA content, small seed mass, vegetative propagation, and dispersal by vertebrates.

Correlative Attempts to Identify Commonality among Invaders, Their Habitats, or Both

Comparisons arise readily in studying invasions: e.g., comparisons between congeners that become invasive and those that do not, comparisons between regions that appear vulnerable to invasion (compared to those that seemingly display relative invulnerability). These comparisons have often become more formal presentations of hypotheses through correlation. The varied uses of correlation were well illustrated at the INTECOL meeting. Stansbury's study illustrates a common use of correlation: seeking similarity among features of the invaded habitats as a means to predict potential future distribution; the search for so-called "invasion criteria." His detailed examination of the current range of *Asparagus asparagoides* in Mediterranean climates in southwest Australia reveals that the alien plant has apparent environmental limitations in soil pH, temperature and nutrient status.

Pysek used perhaps the broadest correlational scale in his attempt to assess whether plant families differ in their "invasiveness." His first-approximation answer (based on his assessment of 26 regional floras comprised of 164 plant families) suggests that some families do indeed contribute a high proportion (and number) of species to naturalized floras world-wide, e.g. Caryophyllaceae and Asteridae. But as Pysek points out, there are numerous criteria by which such a question can be addressed and each potentially affects the answer. Some families contribute many members of alien floras because the families are simply exceptionally speciose, e.g., Gramineae, Compositae, Cruciferae. Pysek concludes that there is no simple morphological, physiological or ecological character that can be related to the invasive ability of any family. Both Klotz *et al.* and Daehler had objectives that sprang from the same general type of correlational analysis seen in Pysek's work. Their goal however was prediction of the current (and potentially future) invaders in Argentina and Hawaii, respectively. Klotz *et al.* concluded that those European species that have become naturalized in Argentina often display a strong association with sites of human disturbance or occupation (anthrophytes); these are short-lived, small ruderal species with high fitness. Daehler evaluated four schemes for predicting woody invaders into the exceptionally vulnerable Hawaiian environments. The large array of woody invaders already in Hawaii allowed him to evaluate retrospectively the predictive power of each scheme. He concluded that it may be possible to build quarantine restrictions in any region based on the traits of alien residents.

Correlation is perhaps most instructive when it guides experimentation. Crawley illustrated the potential value of this dictum in citing the striking similarity in physiognomy and relative abundance among the members of alien plant communities in temperate grasslands, tropical islands, and urban-waste sites in widely-separated locations as evidence that similar "assembly rules" may operate within alien communities. He proposed a series of testable predictions on the processes that could act as the "filters" separating persistent and extirpated immigrant species. Here again, biotic invasions may be the ideal phenomenon with which to examine fundamental topics in ecology and evolution.

Experimental Approaches to Invasions

In a sense, all the symposium participants reported the results of experiments since biotic invasions are on-going "natural experiments", i.e., invaders alter to widely varying degrees the status of the natives in new ranges and their environments. In addition, deliberate, manipulative experiments of biotic invasions were also well-illustrated in the symposium; cases in which investigators introduced alien organisms and

evaluated the consequences. Such experimentation has the advantage of documenting events in clear "before" and "after" (introduction) time frames.

Williams *et al.* and Baruch reported the results of ecophysiological investigations on pre-existing invasions in Hawaii, arid southwestern U.S., and Venezuela, respectively. They report that African grasses (e.g. *Pennisetum setaceum, Eragrostis lehmanniana,* and *Hyparrhenia rufa, Melinis minutiflora)* have been repeatedly successful in tropical and sub-tropical new ranges as a consequence of a variety of these invaders' traits, primarily their high allocation of plant biomass to leaves and rapid growth response when resources become available. Such an ecophysiological "advantage" compared to natives in a community is consistent with the long-proposed Empty Niche Hypothesis, i.e., that invaders possess one or more features (not necessarily in common with other invaders elsewhere) that facilitate persistence. Black illustrated four putative cases of invaders filling an empty niche in western North America and Hawaii. The circumstances that seemingly explain proliferation and persistence are not however similar: e.g. *Bryonia alba* (secondary plant substances that retard seed predators, grazers and parasites in the new range), *Centaurea solstitialis* (root exploitation at soil depths not occupied by the roots of native species). Commonality among explanations for persistence remains elusive.

Case and Minchinton and Bertness manipulated field situations to investigate the circumstances that permit the recent, rapid spread of the alien species *Conyza sumatrensis* and *Phragmites australis* in Britain and New England, respectively. Competition from either native species or mixtures of native and alien residents was a major focus of both experiments. Such manipulative experiments, unlike the monitoring of many natural experiments, are instructive because the immense potential number of confounding factors can often be minimized. Mack stressed the importance of experimentation in examining the basic causes of plant naturalizations. He contended that explanation for the idiosyncratic nature of invasions may lie more in the circumstances upon the entry of immigrants than in their life history traits or even the intrinsic features of their potential new range. Related to these events is the size of the founder population, which is often small, i.e., particularly sensitive to the vagaries that may befall immigrants and their immediate descendants. He reported preliminary experiments that examine the cumulative role of stochastic forces in a new range on small founder populations. He pointed out that for many founder populations, voracious seed predators in the new range may be only the first in a long series of barriers (or filters) preventing naturalization.

Modeling Invasions

Modeling invasions is an outgrowth of both correlation and experimentation. Invasion models can serve to predict the fate of invaders as well as direct future experimentation. According to Mollison, one limitation in the application of invasion models has been the often quite complex calculations of the velocity of spread. He reported on a simplification of these calculations using the reproduction and the "dispersal kernel" of the invader. Invasion models can provide important insight into the character (and potential control) for individual invasions. Shigesada *et al.* reported on their modeling of the Pine Wilt disease in pine forests along the northwest coast of Japan, a disease caused by the nematode, *Bursaphelenchus xylophilus,* and dispersed by its vector, the pine sawyer. Their model takes advantage of the detailed field information available for these organisms. They found (1) the minimum density of pines for spread of the pathogen, (2) the minimum threshold density increases disproportionately with an increase in the eradication rate, and (3) if the eradication rate is low, the probability that a healthy tree will escape infection until the invasion subsides is inversely proportional to the initial pine density. Lampo and De Leo also modeled a specific invasion - the spread of *Bufo marinus* in Australia - by drawing on mark-recapture data. They attempted to account for both the rapid spread of this toad and its surprisingly high densities in its new Australian range compared to its native range in South America. This higher survival appears tied strongly to the high sensitivity of adult equilibrium densities in Australia compared to South American populations.

Prevention and Control of Invaders

Biotic invasions are usually destructive of native biota and often have detrimental consequences for regional economies and even human health. Consequently, the prevention, control and even potential eradi-

cation of invaders are widely-held goals. A variety of tools have long been employed in combating invaders; biological control has been often championed as one of the most effective. Louda, in her examination of the effects of introduced insects for control of invasive thistles in the US, illustrates that use of these agents is not without risk. The introduced weevil, *Rhinocyllus conicus,* attacks native as well as alien thistles, and for one native it reduced seed set by 86%.

Clearly, the consequences of biological control agents must be carefully assessed before release. Finally, Hobbs considered the efficacy of control measures at a wide scale. He questioned the value and effectiveness of attempts to control large, conspicuous invasions - efforts that are often very expensive and often only temporarily effective compared with the prevention of the entry of potential invaders in a new range or the early detection of recent invasions, while still small and localized. He argued that on both environmental and economic grounds dealing with future invaders rather than sole emphasis on current conspicuous invasions was a more prudent policy.

Conclusions

These presentations collectively represent the current breadth and strength of investigations in biotic invasions along multiple research fronts dealing with a taxonomically-diverse group of invaders worldwide. It is apparent that progress in the long informative research arenas of the characterization of invaders, assessment of their new ranges, and correlation are being now augmented through experimentation and modeling. Together these approaches are yielding results that unravel invasion processes while at the same time providing insights into the control of invaders.