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EDITORIAL

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Invasion science, ecology and economics: seeking roads not taken

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Introduction

As members of the editorial board of Neobiota who, for various reasons, didn't get our names on the original editorial (Kühn et al. 2011), we would like to add a coda to it. Even though there were 38 bullet points listing areas in invasion science where more work is needed, we would like to mention additional areas that we hope would be addressed in future issues of Neobiota. Like the other editors, we would like this innovative and exciting new journal to lead the way in all areas of invasion science. As the graphs in Gurevitch et al. (2011) and Kühn et al. (2011) show, the literature on invasions has been increasing almost exponentially since the early 1980s and so we cannot expect any list of areas of interest to stay complete and up to date for very long.

Three areas that we would like to stress are the interaction between invasion science and economics and the role that invasion science should play in advancing pure ecology in two areas, population dynamics and ecosystem ecology. Neither ecology nor economics appears as a word in the original bullet list, but many of the topics are obviously ecological while none are obviously economic. For economics, we want to point out its relevance to invasion science and the feedback between the two disciplines, particularly in a rapidly changing world with powerful new emerging economies. For ecology, we want to emphasise not what ecology tells us about invasions but what invasions reveal about ecology and evolution at two scales.

Economics

There are two recent multi-author books that show the extent and variety of the interaction of economics with invasion science (Keller et al. 2009, Perrings et al. 2010) and also the variety of approaches to tackling these problems, though in this field models are almost always important. Both books also cover management and policy. As any manager knows, finance, either explicit in income or implicit from volunteers etc., determines what can be done and which problems can be tackled. But economics is about much more than costs. Economic analysis and theory are important in developing policy for dealing with invasive problems and serve as motivators for both the public and private sector to take action.

The ecological and economic dimensions of the problem of invasive species are connected at different levels. Many of the changes that lead ecosystems to be more vulnerable to the impact of invasives (e.g. fragmentation, disturbance, loss of diversity, pollution) are direct consequences of economic behaviour. The ecological mechanisms affecting invasives, such as functional diversity and dispersion, are correlated with trade, transport and travel. The consequences of the reduction in ecosystem functionality and the ability to provide ecological services have direct implications for the value of the output and ecological capital of the system.

At every level, the ecological impacts of economic activities are incidental to and usually ignored by the actors concerned. These impacts are externalities of the market transactions; they are not taken seriously by those making the transactions perhaps because they are not held legally responsible for the impacts nor are the markets directly affected by these impacts. Instead these impacts are often borne by those who receive little or no benefit from the market transactions. In addition, quantifying some ecosystem services (and disservices) is difficult and approaches to do so vary necessarily by scale, type of service, and region (Meyerson et al. 2005). Therefore, the major economic problems of invasions are first to understand the nature of invasive species externalities, second to evaluate the consequences they have for well-being, and third to develop policies and instruments for their internalisation.

Ecology

The intimate relation between ecology and invasion science is well known. Less recognised is that invasions throw light on some ecological processes that can be more difficult to study in uninvaded systems. Many ecosystems are close to equilibrium or are following a moving equilibrium from seasonal or longer changes which makes detecting significant changes a long-term prospect and out of sync with two to four year funding cycles. Invasions supply ample examples of unintended experiments with systems well away from equilibrium, often over relatively short time periods. The resultant changes are informative both for the population dynamics of individual species and for the coevolution of communities.

In population dynamics, the growth and spread of populations are natural aspects to study in invaded systems. We will just mention two aspects, lag and the pattern of spread.

There is much misunderstanding of lag. It occurs when a population is not growing in numbers at all. When there are, as so often, casuals, i.e. individuals not producing population growth, it can be difficult to be sure whether the population is growing or not. A common problem is to mistake the early stages of logarithmic or quadratic growth with lag. The quickest solution is usually to plot transformations, e.g. log or square root, of the species counts. Too many statisticians want arithmetic plots which frequently conceal the behaviour of a population. Lags are important for management as they result in invasive species that appear to be harmless, sleeper weeds and such, leading to a lack of action when it would still be relatively cheap and easy to control or even eradicate a population. The lengths of lags are surprisingly variable and some can be quite long. Williamson (2010) found lags from 7 to 154 years in some beautiful Czech plant data, though 22 of 50 species showed no lag. The median lag was 41 years, a period long enough to make a serious management problem. We would emphasize though that lag is an important and little understood aspect of population growth in every sort of species.

It is easy to suggest causes for lag, such as the wrong habitat at introduction, the wrong genotype first introduced or Allee effects, but we know of very few cases when the cause can even be guessed let alone demonstrated. One such is in *Epilobium ciliatum*, a willow herb native to North America, first established in England in the midlands before 1891 but which didn't spread though it did establish. Another introduction into south-east England in the 1920s spread rapidly throughout Britain, overrunning the midlands. It is the plant species with the fastest known spread in Britain so far (Williamson 2011). In that case, the failure of the 19th century introduction to spread can be ascribed with some confidence to genotype. Not that that helps much without knowing the genes and what characters they affect and why those characters prevent spread in England. Lags, though important, are difficult to study and much neglected by ecologists.

Conversely, spread is often quite easy to study though here again some biologists have made an elementary mistake, namely regarding the increase in records as an increase in population size, while nearly always it is only a measure of population range. Possibly this comes from models of spread involving population parameters such as the intrinsic rate of natural increase. Long term records of the ranges of invading species show much variation in the rate and pattern of spread, phenomena complicated by the heterogeneity of natural systems (Williamson 2010). Again, practically nothing is known of the causes of such variation. Yet such knowledge would be most useful in predicting the behaviour of new invaders. It would also, importantly, advance our understanding of basic ecology, and perhaps also provide insights into range expansions and spread under global climate change. The quantitative study of both lag and spread depends on long term, good quality and consistent data. So invasions can be of benefit to ecological science by strengthening the case for long term studies.

The other ecological topic we would like to mention is that species invasions may help us to better understand the mechanisms which generally govern ecosystems. How does co-evolutionary history among species shape the diversity, functioning and stability of ecosystems? Although this topic is somewhat related to the bullet point "Eco-evolutionary feedback between invasive traits and ecosystem function" in the original list, it focuses on different processes.

Interactions among plants, herbivores and microbes influence ecosystem functions (Stein et al. 2009, 2010) and are commonly thought to be shaped by joint evolutionary history (Thompson 1994); exotic species are disconnected from such coevolved relationships and may encounter evolutionarily naïve communities. This in turn may affect competitive outcomes among species (Thorpe et al. 2011) and lead to the disruption of species interactions in the invaded ecosystem (Stinson et al. 2006). It is therefore reasonable to suggest that ecosystem properties are shaped by the coevolutionary history among species, but this hypothesis has been tested only in a very few studies. Recently, Wilsey at al. (2009) set up experimental communities either composed of native plants or composed of exotics which were phylogenetically related to the natives, and revealed that exotic communities declined faster in diversity, but showed higher productivity than the native communities. These findings demonstrate how fine-tuned species interactions within communities are, and suggest that not only the invasive traits of species, but also the novelty of exotic species *per se* may affect ecosystems. In another study, Maron and Marler (2008) showed that the diversity-productivity relationship was even reversed when native plant communities were experimentally invaded by exotics. Perhaps, the dislocation from co-evolved relationships may not only contribute to unifying theories explaining invasions (e.g. Hallett 2006), but also to a predictive framework for the ecosystem impact of invaders.

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