Diversity and Distributions, (Diversity Distrib.) (2004) **10**, 371–375

BIODIVERSITY VIEWPOINT

Comparing alien plant invasions among regions with similar climates: where to from here?

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ABSTRACT

Comparisons between regions with similar climates have traditionally helped to tackle big questions in evolutionary ecology and historical biogeography. We claim that plant invasion ecology can benefit greatly from further and better comparisons at regional and global scales. In this note we discuss the potentials and limitations of comparing climatically analogous regions to provide novel insights into the mechanisms of alien plant invasions. Comparisons among areas with similar climates have the advantage that some features of the abiotic environment are within a narrower range of variation, enabling the researcher to focus on the effects of propagule pressure, microenvironmental differences and, more importantly, the biotic environment in the invasion process. However, there are two major issues that limit the strengths of such comparisons: (1) non-standardized databases of alien species, especially in less developed countries; and (2) deficient sampling designs. We argue that we should take advantage of comparative studies of alien plant invasions across regions with similar climates not only to obtain useful insights about invasions, but to search for generalities beyond invasion ecology that contribute to our knowledge of natural systems.

Keywords

Biological invasions, California, Chile, climatically analogous regions, comparative ecology, exotic floras.

INTRODUCTION

Alien plant invasions are of interest to ecologists not only because of their ecological and economical impacts on the native biota, but also because they represent useful models for studying the ecological functioning of natural systems. The study of alien plant invasions has used two basic approaches: manipulative experiments and natural experiments (*sensu* Richardson *et al*., 2004). The growing trend to study plant invasions at larger spatial and temporal scales, where manipulative experiments are not feasible, has made natural experiments one of the most appealing approach to find generalities in invasion ecology (Richardson *et al*., 2004).

Comparative studies between different regions of the world are a particularly interesting approach for studying alien plant invasions. Some comparative studies of invasions have focused on specific alien species and their capacity to invade different environments (e.g. Rejmánek & Richardson, 1996; Grotkopp *et al*., 2001; Richardson & Rejmánek, 2004). Others have focused on comparing the alien flora of a set of regions, with special interest to the taxonomic or phylogenetic relationships among successful invaders (e.g. Pyšek, 1998). In addition, comparative approaches using climatic matching have been applied to determining potential ranges of distribution for invasive species (Curnutt, 2000; Weber, 2001; see review in Rejmánek, 2000).

Several studies and reviews have addressed the importance of comparing alien plant invasions in climatically analogous regions (Kruger *et al*., 1989; Di Castri, 1991; Groves, 1991; Sax, 2002). Most such studies have focused on regions with similar seasonal patterns in temperatures, and the distribution and amount of precipitation throughout the year. Although no perfect climatic matching exists, some regions are climatically more similar than others (e.g. Mediterranean-type climate zones). Comparisons among climatically analogous regions may help to improve our understanding of the drivers of invasions by taking advantage of global scale 'natural experiments' where the overall climatic factor is within a narrower range of variation. However, most comparative studies have based their analyses on existing datasets, which are usually incomplete or differ significantly in their scope and methods. This methodological shortcoming reduces the power of inference of comparative analyses, especially in developing countries where alien species invasions are generally less well documented.

In this note, we discuss how the comparative approach between climatically analogous regions has been used and how it could be improved to provide further insights into the mechanisms of alien plant invasions. First, we focus on the conceptual framework behind such ecological comparisons. Second, we discuss the type of questions that can be answered by comparing the alien floras, and their interaction with the native biota, of regions that share similar climates. Third, we discuss the limitations of the methods available for undertaking such comparisons. Finally, we call for better cooperation among researchers to advance the field of comparative ecology of alien plant invasions.

The world as a natural experiment: the advantages of comparing invasions in climatically analogous regions

Comparative ecology in regions with similar climates has traditionally helped to tackle big questions in evolutionary ecology and historical biogeography such as the extent to which similar climatic conditions promote evolutionary convergence on biotas with completely different phylogenetic histories (Cody & Mooney, 1978). This general assertion, derived as a corollary of the Theory of Natural Selection, has been particularly fruitful for understanding evolutionary responses of native biota. It has been argued that although convergence was proposed to occur in individual traits of species, convergence at the community level is also theoretically possible. Nevertheless, comparisons between central Chile and California, two areas with Mediterranean-type climate, have shown that although convergence can be found at physiognomic and morphological levels, strong differences exist in plant life-form distribution and fire-responsive life-history traits (Mooney, 1977; Arroyo *et al.*, 1995). In other words, despite the different phylogenetic histories of the biotas, similar climatic conditions promote evolutionary convergence in some, but not all, ecological attributes.

The study of alien plant invasions can benefit greatly from the consideration of regional or global perspectives (A. Pauchard & K. Shea, unpublished data). The conceptual framework provided by comparative ecology among climatically analogous regions is one of the most promising at these larger scales. Although comparisons among climatically similar regions have been used primarily to study natural systems, in the case of alien species these comparisons may help to study both alien species that successfully establish in a new environment, and their interaction with the native biota (Kruger *et al.*, 1989).

Comparing the alien floras and their interaction with new environments between regions with similar climates may help to isolate the effects of limiting factors of invasions. For the purpose of this paper, we have grouped these factors as follows: (1) propagule pressure: the diversity and abundance of the pool of alien propagules; (2) physical conditions and resources in the new environment: determined both by climate and by microenvironmental phenomena (e.g. soil, disturbances, microclimate); and (3) the invaded biota: the invaded plant and animal communities. The outcome of an invasion process will be determined by the interaction of these barriers with the invader and its life history traits (e.g. physiology, competitiveness, reproductive strategy).

Comparisons among areas with similar climates have the advantage that some environmental barriers are somewhat constant among regions, enabling us to address the differential effects of propagule pressure, microenvironmental differences and more importantly the biotic environment on the invasion process (*sensu* Richardson *et al.*, 2000). To specifically isolate the effects of propagule pressure, we should search for areas with similar land use and transportation of new species (e.g. ports, airports, etc.). This should not be a difficult task, considering increasing globalization which has intensified propagule movement and introductions of new species. Thus, differences in invasion patterns between regions should be the product of how the local biota and microenvironmental variables (e.g. disturbance regimes, microclimate) interact with the alien species.

What can we learn from comparing invasions in climatically analogous regions?

Comparisons of alien floras among climatically convergent zones can be particularly useful for assessing the importance of disturbance on invasion processes. For example, Mediterranean-type ecosystems (MTEs) are commonly cited examples of convergent evolution in vegetation structure and function (Mooney, 1977; Arroyo *et al.*, 1995). Among MTEs, California and Central Chile are probably the most similar two regions of the world's five regions with Mediterranean-type climate. However, the MTEs of Central Chile stand out among all Mediterranean-type climate areas because natural fires are extremely rare due to lack of lightning-caused fires (Armesto & Gutiérrez, 1978). Thus, fire represents a 'novel', human-induced disturbance for central-Chilean plant communities. Fire dynamics in central Chile provides an interesting situation for evaluating the importance of fire on plant invasions. Recent studies show that while fire restricts the spread of some invasive species in California (Keeley *et al.*, 2003), in central Chile manmade fires are one of the most important drivers for the successful establishment of alien species, especially for annual herbs (Holmgren *et al.*, 2000; Sax, 2002).

Useful insights on the effects of anthropogenic disturbance may also be drawn from these comparative analyses. By narrowing comparisons to climatically analogous regions, it is possible to isolate more precisely the effects of differential anthropogenic activity. For example, Arroyo *et al.* (2000) found when comparing Chile and California that human activity (e.g. road density, agricultural land) explained differences in alien plant species richness in both between and within regions. When contrasting the two regions, differences in land use may help to explain the divergences in their alien floras. While until the 19th century Spaniards where responsible for changes in land uses in both regions (Kruger *et al.*, 1989), California had a much more intense development and 'internationalization' during the 20th century than central Chile (Figueroa *et al.* in press). This probably accounts, at least partially, for California's more diverse alien flora.

The differences observed in invasion patterns across regions with similar climates open an exciting avenue to address questions about the invader and its interaction with the new environment such as: What are the mechanisms behind a species differential invasiveness? Is there genotypic variation associated to these isolated populations of the invader? Alternatively, are the invaded systems so differentiated in their native biota and microenvironmental conditions to generate contradictory patterns? In addition, comparisons of alien floras among regions with similar climates may help to rank alien species invasiveness and predict their behaviour in areas with similar characteristics (e.g. for *Pinus* species; Richardson *et al*., 1994). By comparing the noxious invaders of California and Chile it is possible to find similarities and differences among species invasiveness (Kruger *et al*., 1989). Although we recognize the limitations of comparing two independent datasets (as we will discuss later), we have compared the alien flora listed in Calflora (California) and in the Herbarium of Concepción (Central Chile). We found that of the 600 alien species of central Chile and the 1191 of California, approximately 386 (64% and 32%, respectively) are shared between the two regions (A. Pauchard *et al.* unpublished data). Several shared species behave aggressively in both regions (e.g. species in the genera *Cytisus*, *Rubus* and *Ulex*; Matthei, 1995; Bossard *et al*., 2000). However, other species are only aggressive in one of the regions. *Acacia dealbata*, introduced from Australia, is naturalized in California and Chile, but it is much more invasive in south-central Chile where it invades riparian habitats and eroded soils (E. Peña, unpublished data). In contrast, the noxious *Centaurea solstitialis* that has invaded most of the grasslands of California (review in Bossard *et al*., 2000) appears only as isolated populations in Central Chile.

Comparisons of alien floras among climatically similar regions may also help us to better understand the process of global homogenization (*sensu* Olden *et al*., 2004) by answering questions such as: Is one biota more resistant to the invasion? What are the characteristics that make them more resistant or more prone to invasions? First, given unlimited propagule movement, climatically analogous regions should, more so than dissimilar areas, become invaded by a similar set of alien species. Deviations from this scenario may help us to identify the mechanisms that limit the process of homogenization. Second, the extent to which within-region variation (i.e. native biota, disturbance regimes, land use) relates to biotic homogenization may help us identify critical factors that favour or slow down this process. Generalities and differences should emerge by comparing two biotas with unique evolutionary history and their response to a common set of alien species.

Limitations and pitfalls

Even though comparative studies of alien floras have tremendous potential, they are bedevilled by the lack of standardization in datasets. Several studies that have compared alien species records from two or more regions have mentioned the uncertainty about the exploratory power of comparing data that has been recorded using different criteria (Pyšek *et al*., 2004a,b). For example, botanists have traditionally undersampled (or even totally ignored) alien species (Pauchard *et al*., 2004). The increase in the number of alien species recorded for most areas is thus at least partly due to the increased awareness among botanists of the importance of alien species. The historic bias against the recording alien species varied among regions (often due to differences in traditional approaches to ecology), which weakens the possibility of useful comparisons.

In addition, classification of alien species into arbitrary and sometime ambiguous categories (e.g. naturalized, weedy, noxious, invasive) makes datasets from different regions difficult to compare. Advances in this topic are being made by agreeing on a common set of definitions (e.g. Richardson *et al*., 2000; Pyšek *et al*., 2004a). In some cases, records of 'occasional' (escaped) alien species may artificially inflate databases, misleading our understanding of alien invasions. Of course, differences in the development of technical and scientific institutions among countries also jeopardize the possibility of meaningful comparisons among datasets. For developing countries, recording alien species is generally a low priority compared to countries like the United States or some countries in Europe where complete datasets have been developed over decades (Pyšek, 2003; Kuhn *et al*., 2004).

Besides the difficulties regarding the quality and concordance of databases, other shortcomings may emerge from the fact that, in most cases, serious problems occur when trying to statistically compare datasets. These kinds of difficulties have been detected in regional comparisons testing ecological convergence (see Schluter & Ricklefs, 1993). In order to compare ecological attributes of regions, it is necessary to consider the within-region variation, that is, variation between localities of one region. Even in regions with similar macroclimatic parallels (e.g. Chile vs. California), subtle differences in topography, microclimate or in land-use history, may create specific habitats which may account for most of the observed community structure and therefore obscure any between-region effect. Statistical tools for regional comparison should evaluate differences on invasion patterns (a) between-regions; (b) within-regions; and (c) their interactions. Curiously, most comparative studies of alien plant invasions have lacked the information or the sampling design to evaluate within-region effects. Sampling in multiple localities of a region would improve our estimation of within-region variation of the studied phenomena and would consequently improve the validity of inter-region comparisons.

The underlying methodological shortcoming in most comparative studies of alien floras resides in how samples or censuses are designed. In many cases, the data represent censuses of populations, but the scale at which they were recorded varies, obscuring the ecological meaning of such comparisons (e.g. comparing countries with state or county data). Furthermore, the lack of replicates to assess within-region variation (more than one locality for each region) restricts the possibility for generalization of the findings. Statistical tools for regional comparisons should evaluate differences on invasion patterns (a) between-regions; (b) within-regions; and (c) their interactions. To strengthening comparative analyses of alien plant invasions methodological approaches should include (1) using standard or comparable sampling methods; (2) developing a stochastic sampling design; and (3) considering within-region variation.

Comparisons of invasibility between regions should account for the most influential variables that control the invasion process within regions. Multiple-variable analysis is the most obvious statistical tool for comparative studies. However, some statistical problems may emerge from this kind of analysis. Firstly, as more independent variables are selected, it leads to overparameterization of the model, which reduces its predictive power (Crawley, 2002). In this context, biological criteria and personal experience in selecting those variables that are most influential in the invasive processes are critical. Secondly, confounding factors may affect the relationship between a variable x and the response variable y (for instance species richness) because of the existence of unexpected correlations among factors. This problem may be solved using residual values to conduct the best multiple regression analysis (Lonsdale, 1999). However, this method has been controversial because (i) the best model depends on the order in which variables are included (forward selection) or excluded (backward selection) in a model (MacNally, 1996; MacNally, 2000; Dalgaard, 2002); and (ii) it leads to biased parameter estimates (Freckleton, 2002). Alternatively, standard multiple regression provides an unbiased estimation of parameters, and by hierarchical methods the variance associated with each variable can be estimated (Freckleton, 2002).

Ordination and cluster analysis provide, probably, the most powerful and flexible tools for comparative analysis of alien flora (for technical details see Jongman *et al*., 1995). Ordination techniques are useful for recognizing major gradients in the structure of alien communities, both within a region and when comparing multiple regions. They are important exploratory tools for pinpointing specific patterns that may be later analysed with, for example, general linear models. On the other hand, cluster analysis helps determine the degree of similarity between alien communities or floras, directly assessing the intensity of the homogenization process.

An additional issue in invasion ecology is that alien plants are explicitly spaced and therefore data shows spatial autocorrelation. This issue is particularly important in invasion biology as the abundance and diversity of alien plants observed in one point (x, y), is negatively correlated with the distance from the points of first introductions or propagule sources (Elton, 1958). The existence of spatial autocorrelation of data will tend to 'inflate' the degree of freedom and therefore statistical differences observed either within or between regions may be simply 'artefacts'. Faced with spatial autocorrelation, ecologists have adopted two attitudes: (a) try to minimize spatial effects, thus designing randomization procedures to gather data in the field; or (b) to include spatial autocorrelation in statistical models (for instance GLS Variograms, Mantel test, see Fortin & Gurevitch, 1993; Ver Hoef & Cressie, 1993). In this way, spatial heterogeneity and its effects on invasion patterns may be evaluated in local and regional comparisons.

Contribution to management and future directions

The use of comparative ecology for the study of alien species may help to improve management of alien species in at least three ways. (1) A comparative approach is useful to develop priority lists for alien invaders (those that have been harmful in other regions may have similar behaviour in the new location); (2) it may also help to evaluate the risk of homogenization of invaded communities; and (3) probably most importantly, it may help to develop guidelines for a sustainable land management directed at avoiding the expansion of alien invaders by targeting dispersal pathways and limiting anthropogenic disturbances associated with increasing risk of alien plant invasions.

We should take advantage of comparative studies of alien plant invasions across regions with climatic similarities not only to gain useful insights about invasions, but to search for generalities beyond invasion ecology that contribute to our knowledge of natural systems (Richardson *et al*., 2004). To properly develop these comparisons, much hard work is needed to refine checklists and systematizing records of alien floras, including the classification of invaders by their ecological and economical effects. In addition, sampling should consider the most appropriate statistical methods. These tasks will only be possible through increased cooperation among researchers and standardization of data collection and analysis. Special attention should be paid to the improvement and systematization of records of alien plant invasions in less-developed countries, to broaden the possibilities of global-scale ecological comparisons.

ACKNOWLEDGEMENTS

We thank David Richardson for inviting us to write this contribution and for his helpful comments. Dov Sax and two anonymous reviewers are also thanked for their constructive comments. We are grateful to Alicia Marticorena who helped with the comparison of the alien floras of Chile and California. This work was partly funded through the research project FONDECYT 1040528.

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