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Review

Expanding the conceptual frameworks of plant invasion ecology

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ABSTRACT

Numerous mechanisms driving alien plant invasions have been described in a rapidly growing body of literature. However these are frequently case specific, making generalizations across species and systems difficult. A number of conceptual approaches have been proposed to help synthesize the literature, stimulating healthy debate among scientists. We build on these syntheses, presenting an expanded framework that incorporates the processes contributing to invasions, and the context within which they must interact. We also provide a model template into which the framework we develop is incorporated, illustrating both with examples. Our general framework includes three contributing processes: these are (1) the characteristics of the introduced species, (2) system context, within which the invasion takes place, and (3) the features of the receiving habitat. System context refers to the influences arising outside of the receiving environment, both spatially and temporally. Each contributing process is comprised of specific mechanisms, drawn from literature on invasion ecology and other related fields. The framework invokes relevant mechanisms for a specific species or situation. Although, a number of frameworks already consider the characteristics of the invading species or those of the receiving habitat, they seldom include all possible characteristics of both. We propose that these approaches alone are inadequate to provide a comprehensive understanding of the invasion process, without explicitly examining the context within which the invasion takes place. The model template we present relates the contributing processes described for a particular invasion, to the change in habitat from one state to another. Each of the contributing processes defined in the framework modulates the degree to which the habitat is changed. We suggest that these additional tools and the explicit inclusion of all three contributing processes, provide for further synthesis and improved understanding of invasions by alien plants.

Contents

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Introduction

The SCOPE program of the 1980s (Drake et al., 1989) established an important milestone in the study of biological invasions by identifying two key features in the invasion process: (1) the attributes that allow organisms to invade, and (2) the features that make some environments more invasible than others. This spurred great progress in guiding and advancing the general understanding of invasion ecology (Richardson and Pyšek, 2006). However, attempts to link the characteristics of invaders and the receiving environment to provide generalizations about alien species invasions have been judged to have limited success (e.g. Vermeij, 1996; Davis et al., 2000; Barney and Whitlow, 2008). Further, the world view taken by biologists to explain ecological phenomena is biased by personal and professional backgrounds (Roux et al., 2005). This leads to tension and competition between scientists and the subdisciplines of science. Many generations of synthesis are probably needed before various mechanisms can be generalized for any specific discipline. We suggest that the framework we present furthers this attempt to reconcile the many and varied syntheses to date.

The field of invasion ecology is mature enough to have gone through several generations of synthesis (for example Drake et al., 1989; Lodge, 1993; Davis et al., 2000; Richardson et al., 2000; Rejmánek et al., 2005; Cadotte et al., 2006; Richardson and Pyšek, 2006; Lockwood et al., 2007; Theoharides and Dukes, 2007; Barney and Whitlow, 2008; Catford et al., 2009). We discuss some of the pertinent aspects highlighted by these syntheses. Lodge (1993) builds on Drake et al. (1989) and reviews a number of widely cited generalizations about biological invasions, stating that the characteristics of a colonist and of the community are both critical to the success and impact of the invader. The theory of fluctuating resource availability (Davis et al., 2000) aimed to integrate most existing hypotheses regarding community invasibility, and builds substantially on our understanding of dynamics in the receiving environment. The assumption is made that an invading species must have access to available resources, and will enjoy greater success in a community where it does not encounter intense competition for these resources. Richardson et al. (2000) present a conceptual model of the barriers that need to be overcome in order for a species to become invasive. This model further ordered and clarified the terminology and concepts that had arisen in the field of invasion ecology. This paper (Richardson et al., 2000), and a follow-up paper by Pyšek et al. (2004), are still widely used as a basis for assigning labels to different types and categories of alien plants. Rejmánek et al. (2005) provide a synthesis of the current state of knowledge of invasion ecology. In particular they address five questions that underpin the field, namely, what are the taxa that invade; how fast do they do so; what makes ecosystems invasible; what is the impact; and how can we control or eradicate harmful invaders? They make a further comment that one of the overriding frustrations in invasion ecology is that generalizing is extremely difficult. The volume edited by Cadotte et al. (2006) aimed to discuss the reciprocal relationship between ecological theory and invasions. Using various conceptual and other tools, they discuss how studies on invasions can advance the general field of ecology and conversely, how conceptual ecology can explain and further the challenges posed by invasive species. Richardson and Pyšek (2006) provide a substantial review of key issues that have arisen in invasion ecology. They discuss a number of issues related to the invasiveness of species (for example, the concept of residence time), the invasibility of habitats (for example, the biotic resistance hypothesis) and overarching concepts (for example, a theory of seed plant invasiveness). The volume by Lockwood et al. (2007) provides an overview of the field of biological invasions, from vector science to evolutionary responses of invasive species. In doing so a number of key hypotheses and concepts are discussed. Theoharides and Dukes (2007) suggest that the invasion process needs to be studied at four separate phases, namely transport, colonization, establishment, and landscape spread. Barney and Whitlow (2008) attempt to provide a unifying framework for biological invasions. They do this using a state factor model that relates a quantifiable property of an invasion (i) as a function of propagule pressure (p), introduced habitat (h), invader autecology (a), source environment (s), and time since introduction (t). This model aims to incorporate all variables that may contribute to an invasion, not only those of the receiving environment or invading species. Catford et al. (2009) synthesize the various hypotheses into a single framework. Assessing the effects of the leading 29 hypotheses currently considered in invasion ecology, Catford et al. (2009) discuss whether a specific hypothesis leads to a positive or negative impact, and the degree to which it is similar to other suggested hypotheses. From this assessment, they present a unifying framework which is a function of propagule pressure (P), abiotic characteristics of the invaded ecosystem (A), and biotic characteristics of both the recipient community and invading species (B).

Notwithstanding the above, the synthesis of Drake et al. (1989) remains a core conceptual framework for invasion ecology, with many of the hypotheses in the literature rearranging the various components already suggested. We expand on this framework by explicitly adding the system context. Further, we sort the various rules suggested as key drivers or mechanisms for invasion into three specific and contributing processes. In doing so we highlight the critical differences between those frameworks already presented and the resulting expanded mechanistic framework for the invasion process we present, and show how it may provide additional insights.

We present three conceptual tools to expose the mechanisms of invasions and to integrate across species, systems and scales: (1) the expanded framework to articulate and organize the causes of invasion, (2) a model template for general relationships among the causal factors, and (3) working models to apply the framework to specific cases. We begin by briefly reviewing the nature of frameworks. Thereafter we describe the components of the framework and then illustrate how to apply the framework for structuring models of particular invasions, using *Opuntia stricta* (Haw.) Haw. var. *dillenii* (Ker Gawl.) L.D. Benson (sour prickly pear or Australian pest pear), in the Kruger National Park, South Africa.

Frameworks as an ecological tool

All sciences have a background set of underlying assumptions which, although often poorly understood, direct the way we approach problems, what things we observe, and how we interpret these (Pickett and Rogers, 1997). Therefore, conceptual frameworks are tools to organize research and evaluate the state of a subject area (Pickett et al., 2007). The strength of the framework approach lies in providing an inclusive, common understanding by articulating the causes that can act in a process or system of interest.