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Toward an integrated ecosystem perspective of invasive species impacts

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ABSTRACT

Progress in the study of ecosystem impacts of invasive species can be facilitated by moving from the evaluation of invasive species impacts on particular processes to the analysis of their overall effects on ecosystem functioning. Here we propose an integrative ecosystem-based approach to the analysis of invasive species impacts that is based on an understanding of the general mechanistic links between biotic factors, abiotic factors, and processes in ecosystems. Two general kinds of biotic mediation – direct and indirect – and two general mechanisms of invasive species impact – assimilatory–dissimilatory (uptake and release of energy and materials) and physical ecosystem engineering (physical environmental modification by organisms) – are most relevant. By combining the biotic mediation pathways and the general mechanisms, four general situations emerge that characterize a great many of the impacts invasive species can have on ecosystem processes. We propose ways to integrate these distinctive impacts into general mechanistic representations that link ecosystem processes with changes in biotic and abiotic states (changes in structure, composition, amount, process rates, etc.). In turn, these help generate predictions about the interplay of invasive species and other drivers of ecosystem processes that are of particular relevance to ecosystems where invasive species co-occur with other anthropogenic impacts.

1. Introduction

A great deal of research on the impacts of invasive species on ecosystem functioning (i.e., the stocks and fluxes of energy and materials and their stability over time; sensu Pacala and Kinzig, 2002) evaluates changes in particular ecosystem functions (i.e., changes in stocks or transformation rates of particular kinds of materials and energy; see Crooks, 2002; Ehrenfeld, 2003, 2011 for reviews, and papers in this Special Issue). Establishing causal connections between these impacts and other drivers of ecosystem change is, however, emerging as an important challenge for progress in this field (Simberloff et al., 2013). Clearly, changes in overall ecosystem functioning after biological invasions can result from the interplay between invasive species effects and other biotic and abiotic drivers of ecosystem processes (Crowl et al., 2008; Strayer, 2010, 2012). We are also becoming increasingly aware that interactions between invasive species impacts and other anthropogenic influences can co-occur (e.g., habitat degradation; other invasive species, pollution, altered climate, hydrology, or fire regimes; Smith et al., 2000; Richardson et al., 2007; Strayer, 2010). To understand and manage ecosystems in the Anthropocene (Crutzen and Stoermer, 2000) it is becoming increasingly necessary to shift research emphases from how an invasive species affects a particular function to how it interacts with other drivers to determine overall ecosystem functioning (see Strayer, 2012). Analyzing invasive species impacts from such an integrative ecosystem perspective requires understanding how distinct functions as well as biotic and abiotic factors in ecosystems are mechanistically interrelated.

Here we summarize and exemplify some general relationships between biotic factors, abiotic factors, and functions in ecosystems and illustrate how they can be mechanistically integrated to understand changes in overall ecosystem functioning after invasions. We first illustrate two general ways in which biotic change after invasions mediate ecosystem impacts (i.e., direct and indirect mediation; see Section 2), and two general mechanisms by which

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invasive species often affect other organisms and the stocks and fluxes of energy and materials in ecosystems (as assimilatory–dissimilatory and physical ecosystem engineering impacts, sensu Jones and Gutiérrez, 2007; see Section 3). We then combine biotic mediation and the general mechanisms into four general situations (see Cases in Table 1 and Section 4) that characterize a great many kinds of impacts that invasive species can have on other species and the stocks and fluxes of energy and materials. Last, we illustrate multiple concurrent impacts of invasive species on one or more functions (see Section 5), and integrate distinct impacts into general mechanistic ecosystem representations (i.e., Ecological Flow Chains and Ecological Systems; Shachak and Jones, 1995) that help expose the known and potential links among them (see Section 6).

2. Direct and indirect biotic mediation

Given the presence of invasive species, their impacts on ecosystem functioning can be classified *direct* or *indirect* (Fig. 1). Direct effects occur when the presence and/or activities of the invasive species *per se* alters ecosystem process rates. Indirect effects occur because the invasive species impacts biotic and abiotic intermediaries that, in turn, affect ecosystem process rates. The construal of indirect effects as biotically-mediated is in agreement with traditional definitions of indirect effects in ecology (e.g., Strauss, 1991; Wooton, 1994) in that it denotes ecosystem-level effects that arise via influence of the invasive species on third to *n*th biotic parties. Abiotically-mediated indirect effects are a logical extension that explicitly recognizes that invasive species can affect abiotic intermediary parties that affect biota (Jones and Callaway, 2007).

Direct ecosystem impacts can be further defined as changes in the stocks and transformations of energy and materials resulting solely from the presence and/or activities of the invasive species. Decreased phytoplankton biomass and production due to zebra mussel filter feeding (Caraco et al., 1997; MacIsaac et al., 1999) – a direct biotic effect – and altered fire frequency and intensity due to the establishment of a flammable invasive (Brooks et al., 2004) – a direct abiotic effect – are classical examples of direct impacts of invasive species on ecosystem processes.

Indirect impacts can be further defined as occurring when the invasive species alters the abundance and/or activity rates of one or more other species and, in so doing, modulates their impacts on the stocks and transformations of energy and materials. Positive effects of zebra mussels on submersed macrophyte production, via increased water clarity resulting from mussel filter feeding on phytoplankton (Strayer et al., 1999; Zhu et al., 2006) is a good example of such indirect impacts. In this example, the presence or activities of zebra mussels *per se* do not explain increased light availability for macrophytes. Rather, it is the effects of zebra mussels on biotic intermediaries – i.e., phytoplankton that occlude light – which ultimately determines light incidence at the lake or river bottom. At the same time, zebra mussel filter feeding removes suspended sediments, also increasing light availability to macrophytes (Strayer et al., 1999); in this situation, sediments are a necessary abiotic intermediary for a macrophyte effect.

The net effects of invasive species on ecosystem processes rates may result from a combination of direct and indirect species impacts. Nevertheless, and as addressed later (see Section 5), distinguishing direct and indirect pathways of biotic interaction and their underlying mechanisms helps identify and predict the context dependencies of the net effect of invasive species.

3. General mechanisms

A great many of the mechanisms underlying the direct and indirect effects of invasive species on ecosystem process rates can be grouped into two broad categories, namely assimilation–dissimilation and physical ecosystem engineering (*sensu* Jones and Gutiérrez, 2007; see Fig. 1).

Assimilation–dissimilation involves the uptake (assimilation) of energy and materials (light, water, nutrients, other minerals, O_2, CO_2, trace gases, organic compounds) and their release (dissimilation) in the form of dead tissues and waste products (carbon and nutrients in litter, woody debris, feces, urine, and carcasses; water, O_2, CO_2, trace gases, H^+, other organic and inorganic chemicals). Assimilatory–dissimilatory transfers encompass all kinds of autotrophic, mixotrophic and heterotrophic interactions (e.g., plant

Table 1
General mechanisms and biotic mediation of invasive species impacts on the stocks and transformations of energy and materials in ecosystems. Cases 1–4 define the general circumstances where these impacts occur.

		General mechanism *Assimilatory–Dissimilatory* Uptake of energy and materials and their release in the form of dead tissues and waste products.	 *Physical Ecosystem Engineering* Structural modification of the environment caused by the presence or activities of organisms.
Biotic mediation	*Direct* Stocks and transformations of energy and materials are altered solely by the invasive species (i.e., there are no intermediary species).	Case 1 The invasive species assimilates or dissimilates energy and materials at rates that substantially contribute to a chemical transformation pathway in the ecosystem; *and/or* the products of assimilation or dissimilation by the invasive species (e.g., living and dead tissues) are relatively abundant and differ in "reactivity" from those already present in the ecosystem.	Case 2 Physical structures made by the invasive species interact with different forms of kinetic energy (light, heat, or energized fluids along with suspended or dissolved materials) causing dissipation, reflection, or conversion (e.g., mechanical or potential energy) and material redistribution. This alters ecosystem inputs or outputs of assimilable energy and materials and storage in the ecosystem.
	Indirect Stocks and transformations of energy and materials are altered because of the impacts of the invasive species on other species (i.e., biotic intermediaries).	Case 3 Assimilation–dissimilation by the invasive species first affects the abundance of other species (e.g., predation, disease), and then these biotic intermediaries affect the stocks and transformations of energy and materials via successive, direct or indirect pathways.	Case 4 Structural modification of the environment by the invasive species changes the abundance of other species via alteration of abiotic conditions and resources. The affected biotic intermediaries then alter the stocks and transformations of energy and materials via successive, direct or indirect pathways.