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Original article

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.

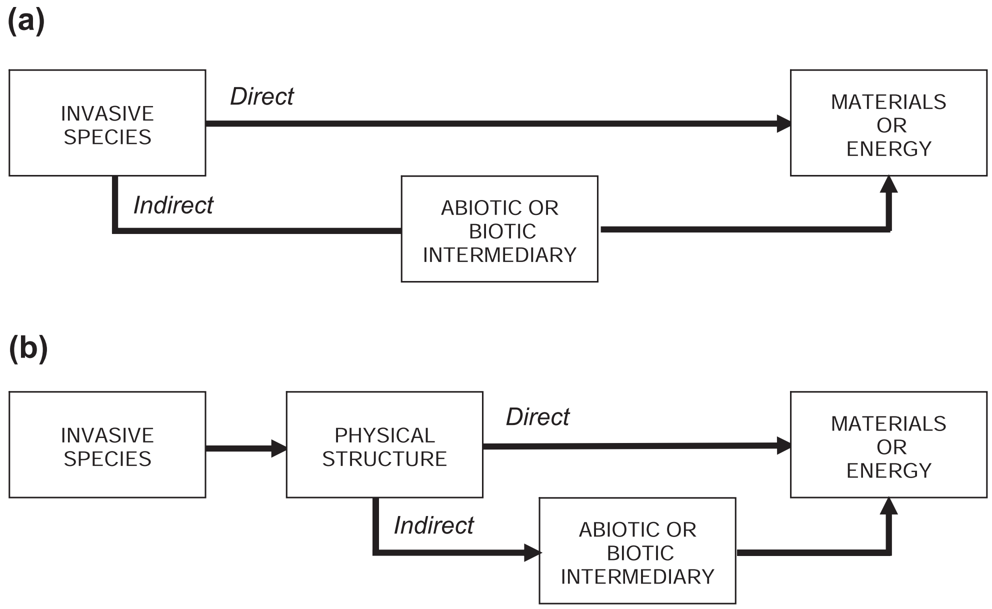

Fig. 1. Pathways of direct and indirect impacts of invasive species on ecosystem functioning involving (a) assimilation–dissimilation, and (b) physical ecosystem engineering mechanisms. While effects of abiotic intermediaries on the stocks and transformations of materials and energy can also be indirect (see Section 4.5.), possible additional intermediaries are not shown here for simplicity.

uptake and litter production; herbivory, predation, detritivory, parasitism, microbial uptake and release). Assimilation–dissimilation by invasive species can alter the rates of material and energy transformation as well as the abundance of other organisms via consumption or the provision of energy and materials in the form of living or dead tissues and metabolic end-products.

Physical ecosystem engineering arises from structural modification of the physical environment caused by the presence and/or activities of organisms (e.g., tree growth and wind attenuation, coral reef wave protection, invertebrate burrowing, dam-building by beaver, soil compaction by large mammals; see Jones et al., 1994, 1997; Jones and Gutiérrez, 2007). Changes to the physical structure of the environment can then affect the inputs and outputs of energy and materials to ecosystems, as well as the abiotic resources and conditions that influence the abundance and activity rates of other resident organisms. While such structure-mediated effects are often but not invariably associated with assimilatory and dissimilatory transfers to varying degrees (e.g., pits made while digging for food, wind attenuation as a consequence of canopy light harvesting), their impact on the abiotic environment occurs regardless of any influence of these transfers (e.g., the magnitude of effects of insect defoliation on understory light, wind and temperature depend upon consumption, but occur irrespective of herbivore effects on trees or *vice versa*; see Jones and Gutiérrez, 2007).

Since assimilation–dissimilation and physical ecosystem engineering by invasive species can alter both the magnitude of material and energy fluxes and the abundance of other organisms, direct and indirect impacts of invasive species on ecosystem process rates can occur via either or both mechanisms (see Sections 4.3 and 4.5).

3.1. *Difficult cases*

The two above general mechanistic categories can encompass a great many of invasive species impacts on biotic intermediaries and/or ecosystem functioning, but not all. Nevertheless, as one would expect given the diversity of kinds of interactions in nature, some do not conveniently fit into the above two categories. For example: (a) the effects of invasive pollinators on plant populations (e.g., Aizen et al., 2008) are associated with assimilatory transfers (nectar consumption), but involve pollen transfer; (b) cross-ecosystem consumption and release of energy and materials by moving animals (e.g., invasive anadromous fish; Cucherousset and Olden, 2011), involve assimilation and dissimilation in different ecosystems driven by migration; and (c) non-lethal effects of invasive predators on prey (e.g., deeper depth distribution and decreased birth rate in planktonic prey due to vertical migration induced by an invertebrate predator; Pangle et al., 2007) obviously do not involve actual assimilation. Such hard to categorize mechanisms clearly can have important consequences for ecosystem functioning, but are beyond the scope of this paper.

4. Integrating biotic mediation and mechanisms

Table 1 summarizes the four general situations (Cases 1–4) where the combination of assimilation–dissimilation and physical ecosystem engineering can have direct and indirect effects on ecosystem process rates, and helps organize the variety of ways in which the stocks and fluxes of material and energy in ecosystems can be affected by invasive species. The four cases and their combination are discussed in detail below, and are illustrated with examples from this Special Issue and the ecological literature.

4.1. *Direct assimilatory–dissimilatory impacts on material and energy transformation rates (Case 1)*

Impacts of this kind occur when assimilation or dissimilation of energy and materials by the invasive species substantially contributes to a pathway of chemical transformation in the ecosystem (e.g., altered photosynthetic rates, altered conversion of plant biomass into herbivore biomass), or when the products of assimilation or dissimilation by the invasive species (e.g., living and dead tissues, waste products) are relatively abundant and/or differ in quality from those already present in the ecosystem. Classic examples of direct, assimilatory–dissimilatory impacts of invasive species include increased soil nitrogen due to fixation of atmospheric nitrogen by diazotrophs symbiotic to invasive plants (Vitousek et al., 1987), and changes in the flammability of an invasive plant (Brooks et al., 2004). Other examples include increased photosynthetic rates after the conversion of subtropical forests into bamboo-invaded areas (bamboos have twice the photosynthetic capacity of native trees; see Montti et al., 2013), altered decomposition rates due to altered litter quantity and/or quality (see Aragón et al., 2013; Furey et al., 2013; Mincheva et al., 2013; and Spirito et al., 2013), and increased secondary production due to higher biomass and growth rates of invasive consumers (Hall et al., 2006; Sousa et al., 2008).

4.2. Direct physical ecosystem engineering impacts on inputs and outputs of materials and energy (Case 2)

Physical structures made or modified by invasive species interact with different forms of kinetic energy – such as light, heat, or energized fluids containing dissolved or suspended materials – causing dissipation, reflection, and conversion along with material redistribution (see Jones et al., 2010 for detailed discussion). Interactions between kinetic energy and these structures can have direct impacts on ecosystem process rates by altering inputs and outputs of assimilable energy and materials (e.g., light, nutrients, carbon, water). Invasive plants intercept light often causing irradiance levels in the understory to differ from those that characterize the un-invaded habitat (e.g., Abreu et al., 2013; Montti et al., 2013; Muñoz-Vallés et al., 2013; see also Reinhart et al., 2006). Effects occur because the invasive species is assimilating light (photosynthesis) and because the plant canopy, as with any physical structure, also absorbs and reflects light (physical ecosystem engineering). Invasive plant canopies can also alter heat transfer to and from the understory with consequences for soil moisture (e.g., Muñoz-Vallés et al. 2013; see also Yelenik et al., 2004), and dissipate/reflect/convert the energy of fluid flows (wind, water) increasing the deposition of particulate or dissolved carbon and nutrients (see Neira et al., 2006; Muñoz-Vallés et al., 2013). Such physical influences of invasive plant canopies can significantly contribute to changes in the overall energy and mass balances of ecosystems (see Ehrenfeld, 2003). Similarly, physical structures made or modified by invasive animals can have substantial direct impacts on ecosystem process rates by altering inputs and outputs of assimilable materials and energy. For example, dams built by invasive beaver in Tierra del Fuego attenuate stream flow and increase the deposition of suspended particles leading to 20+-fold increases in benthic organic matter availability (Anderson and Rosemond, 2007; Valenzuela et al., 2013), while burrowing by invasive isopods weakens mud and clay banks of salt marsh edges increasing wave-driven erosion (Talley and Crooks, 2007).

4.3. Assimilatory–dissimilatory impacts on biotic intermediaries (Case 3)

Assimilation–dissimilation by invasive species can affect the abundance of other species and, in so doing, the magnitude of the effects of such species on ecosystem process rates. These effects may occur when the invasive species reduces the abundance of native biotic intermediaries via consumption. For example, invasive apple snails in some Asian wetlands decrease macrophyte density and biomass via grazing, which then results in increased nutrient availability in the water column and increased phytoplankton production (see Horgan et al., 2013; and cites therein). Selective grazing by ungulates often alters plant composition as well as litter quantity and quality with consequences for soil nutrient cycling (e.g., Stritar et al., 2010; but see Relva et al., 2013). The aforementioned positive impacts of zebra mussels on submersed macrophyte production via phytoplankton consumption and concomitant increases in light penetration (Strayer et al., 1999; Zhu et al., 2006) also serve to illustrate this case.

Alternatively, the living or dead tissues of invasive species, as well as their metabolic end-products, can alter the overall supply of assimilable energy and nutrients (quantity, quality, or both) to biotic intermediaries, with consequences for their abundance and activity rates. Examples include species that increase availability of nitrogen to microbes and plants via fixation by diazotrophs symbiotic to invasive plants (Vitousek et al., 1987); changes in decomposer communities and activity rates associated with altered litter inputs after plant invasions or massive die-offs of invasive species after extreme climatic events (Mincheva et al., 2013; van der Putten et al., 2007; Bódis et al., 2013); and increased abundance of frugivorous birds after establishment and spread of invasive fruiting trees in forests (see Ayup et al., 2013).

4.4. Physical ecosystem engineering impacts on biotic intermediaries (Case 4)

By structurally modifying the environment, physical ecosystem engineers can also affect the abundance of other species and, in turn, the rates of the ecosystem processes they mediate (Jones et al., 1994, 1997; Gutiérrez and Jones, 2006). Effects on other species occur when structure alters consumable resources (e.g., nutrient subsidies), non-trophic resources (e.g., enemy-free space) and abiotic conditions (e.g., temperature); all of which can influence establishment, survival, and reproduction of other species and interactions among species (e.g., increased refugia from predators). Changes in resources and conditions can be simply due to the presence of the structure itself (e.g., structure as living space), or due to the interaction of structure and kinetic energy and materials (see 4.2 above). Engineering impacts of invasive species on biotic intermediaries often occur as knock-on consequences of direct physical ecosystem engineering impacts on resource inputs or outputs, hence storage (Case 2, see Section 4.2.). For example, enhanced organic matter retention upstream from dams built by invasive beaver in streams of Tierra del Fuego Archipelago (i.e., a direct, physical ecosystem engineering effect on material availability; see above) then increases the abundance of benthic invertebrates with a concomitant increase in benthic secondary production (Anderson and Rosemond, 2007). In other situations, engineered structures made by invasive species have impacts on biotic intermediaries by altering abiotic environmental conditions. For example, the canopy of some invasive dune plants attenuates wind, reducing sand transport, which then facilitates the occurrence of other species intolerant to sand burial that would otherwise occur at low abundance or not at all (Alberio and Comparatore, 2013; Muñoz-Vallés et al., 2013), and invasive burrowing isopods enhance salt marsh erosion transforming vegetated areas into unvegetated tidal flats (Talley and Crooks, 2007).

4.5. Biotic intermediaries and ecosystem impact (Cases 3 and 4)

Indirect pathways of invasive species impact on ecosystem process include the effects of invasive species on other species (see Sections 4.3 and 4.4 above) but also the effects of the latter species – or biotic intermediaries – on the stocks and transformations of energy and materials. General mechanisms and pathways mediating the impacts of biotic intermediaries on ecosystem process rates are analogous to Cases 1–4 above. In other words, the effects of biotic intermediaries on ecosystem process rates can be due to the presence or activity of the biotic intermediary *per se* (analogous to Cases 1–2 above) or its effects on other organisms (i.e., second to *n*th order biotic mediation; analogous to Cases 3–4 above). Biotic intermediary impacts on ecosystem process rates or other organisms can also proceed via assimilatory–dissimilatory mechanisms (e.g., increased nutrient availability in wetlands after macrophyte declines caused by invasive golden apple snail grazing; see Horgan et al., 2013), or physical ecosystem engineering (e.g., decreased water retention by tank bromeliads after bromeliad-eating weevil invasions; see Cooper et al., 2013).

5. Concurrent impacts on one or more ecosystem functions

The net effect of invasive species on a particular ecosystem function may result from the combination of distinct, concurrent mechanisms. This is well illustrated by studies in this Special Issue addressing the impacts of invasive plants on litter stocks and decomposition rates. Invasive plants can affect litter accumulation and decomposition *per se* by altering the amount and quality of litter that reaches the soil and, thus, the quantity and nutritional value of litter as food to decomposers (i.e., a direct impact; e.g., Aragón et al., 2013; Furey et al., 2013; Mincheva et al., 2013; Spirito et al., 2013). Concurrently, invasive plants can affect litter decomposition rates by affecting soil microclimate (e.g., effects on soil moisture and temperature via shading or water consumption; Muñoz-Vallés et al., 2013; Spirito et al., 2013), with concomitant effects on the abundance, identity and activity rates of decomposers (i.e., an indirect impact; e.g., Mincheva et al., 2013). Since the relative contribution of different impact pathways to particular ecosystem processes will vary from place to place and time to time, analyzing them separately and then integrating them is important if we seek to identify and predict the contingent circumstances affecting the magnitude of net invasive species impacts (see Gutiérrez and Jones, 2006).

Concurrent mechanisms can also lead to invasive species having simultaneous impacts on different ecosystem processes. Several papers in this Special Issue illustrate such simultaneous impacts (Horgan et al., 2013; McLaughlan et al., 2013; Muñoz-Vallés et al., 2013; Reid and Torres, 2013; Valenzuela et al., 2013). Impacts on two distinct processes can be mutually interdependent (e.g., impacts of golden apple snails on macrophyte and phytoplankton production; see Horgan et al., 2013), or bear no apparent relationship to each other (e.g., beaver impacts on stream invertebrate production and riparian plant composition, see Valenzuela et al., 2013). Since the magnitude of individual impacts is generally context-dependent, the number of detectable impacts and their relative importance is expected to vary in space and time (see Eviner and Chapin, 2003).

Appreciating that invasive species often cause distinct, but co-occurring impacts on other biota and ecosystem process rates is particularly important in the light of management of ecosystem services. As McLaughlan et al. (2013) illustrate, a single invasive species can concurrently affect a diverse array of resources and processes that support humanity. While some of these impacts may be desirable, it is worth noting that they may co-occur with undesirable effects. The degree to which one or more impacts are desirable will depend on the specific management goals and priorities proposed for the invaded ecosystem. For example, management goals are unlikely the same for a polluted urban lake and a lake in a national park or ecotourism area. In the first case, water purification – a regulating ecosystem service – should be a priority. In the second case, cultural services (e.g., aesthetic, spiritual, and educational rewards from the preservation of biodiversity or endangered species) might be more important. Thus, zebra mussel invasions of these lakes would respectively have desirable and undesirable consequences for prioritized ecosystem services (e.g., desirable effects of filtration on water quality for the urban lake; undesirable effects of fouling of native unionids in a conservation area; see Reeders and de Vaate, 1992; Sousa et al., 2011).

An invasive species with concurrent beneficial and detrimental effects on ecosystem services presents a management dilemma. The species may be considered beneficial in one ecosystem and detrimental in another, invoking different management strategies in different ecosystems; or beneficial and detrimental in the same ecosystem requiring consensus on the most important service(s) in that ecosystem in order to implement management strategies.

6. Integrating impacts on multiple functions

As illustrated above, invasive species impacts on ecosystem processes often involve one or more biotic intermediaries, interactions between engineered structure and varied sources of kinetic energy and materials, and/or multiple concurrent drivers and mechanisms that synergistically or antagonistically affect the magnitude of particular process rates. Formulating testable predictions about such complex causal networks requires an appreciation of the drivers and mechanisms of invasive species impact, as well as the possible ways in which distinct impact drivers and mechanisms relate to each other. Ecological Flow Chains (EFC) and Ecological Systems (ES) (Shachak and Jones, 1995) can provide useful representations of such complex causal networks. An EFC is a functional description of the flow of one currency of interest (e.g., organisms, nutrients, light, hydraulic energy) as a connected series of *organizational state changes*, where “organizational state” is a particular biotic and abiotic condition occurring at a specific time and place that can be described, for example, in terms of structure, amount, composition, or process rates; and where “change” refers to a shift in that state over time or space (e.g., from propagule supply to subsequent species establishment, from particulate to dissolved nutrients, from transmitted to reflected light, from potential to kinetic hydraulic energy). An ES is a collection of interconnected EFCs of different flow currencies that suffice to functionally describe and explain a particular set of relationships between organisms, energy, and materials. An ES includes the interconnections among EFCs, which represent the control by an organizational state in one flow chain on an organizational state in another flow chain.

Fig. 2 illustrates how EFCs and ESs can be used to represent pathways of invasive species impact and formulate testable predictions. The ES in Fig. 2 represents the relationships between the invasive bromeliad-eating weevil, *Metamasius callizona*, the epiphytic tank bromeliad *Tillandsia utriculata*, and water fluxes at the Enchanted Forest Sanctuary, Florida, USA, as depicted by Cooper et al. (2013). Invasive weevils caused an 87% decrease in the abundance of *T. utriculata* in just 6 months. This translated into dramatic reductions in water contained in phytotelmata (from 16,000 to 3000 L during the same period), with concomitant changes to the local hydrological cycle (see Cooper et al., 2013). In Fig. 2, weevil establishment and spread, *T. utriculata* mortality, and water distribution are each represented as EFCs consisting of organizational state changes (e.g., rainfall to soil moisture; high to low *T. utriculata* abundance); while the effects of weevils on *T. utriculata* abundance as well as those of *T. utriculata* on water fluxes are shown as interconnections among EFCs. Explicitness about organizational state changes within each EFC expose some possible though not yet evaluated interconnections within the ES, such as negative feedback effects of low *T. utriculata* abundance on weevil abundance (Fig. 2, see also Cooper et al., 2013). In addition, this relatively simple representation can be further expanded with the addition of EFCs relevant to known or potential impacts of weevils on other ecosystem functions. For example, a nutrient

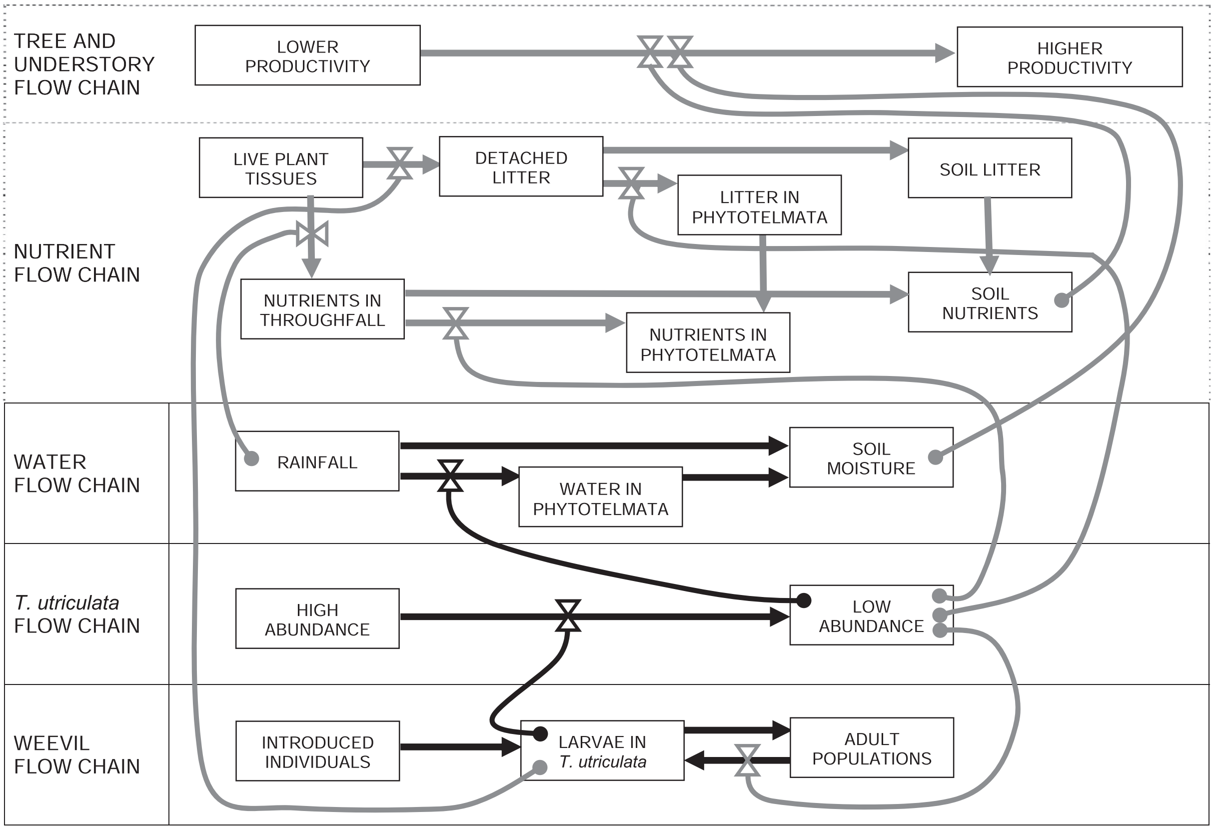

Fig. 2. Ecological System representing the relationships between bromeliad-eating weevils (*Metamasius callizona*), epiphytic tank bromeliads (*Tillandsia utriculata*), and water fluxes at the Enchanted Forest Sanctuary, Florida, USA (see Cooper et al., 2013). Weevil invasion, bromeliad abundance, and water fluxes, are represented as 3 Ecological Flow Chains (EFCs) consisting of organizational state changes (Straight Solid Arrows). Organizational state changes within an EFC can be controlled by organizational states in a different EFC (see Curved Solid Arrows with initiating control states and regulatory control points; i.e., ● and ⧖, respectively). Hypothetical interconnections with 2 additional EFCs representing nutrient fluxes and plant productivity are also shown (see Straight Gray Arrows and Curved Gray Arrows with gray initiating control states and regulatory control points, respectively). See text (Section 6) for explanation of processes underlying organizational state changes within and between EFCs.

flow chain can be added to represent potential decreases in throughfall and litterfall interception by *T. utriculata* phytotelmata and consequent increases in soil litter and nutrient content (Cooper et al., 2013; see Fig. 2). Again, by making explicit a nutrient flow chain and the different nutrient organizational states, connections to a tree and understory flow chain become apparent (i.e., increased tree and understory productivity due to increased soil nutrient availability; see Fig. 2 and Cooper et al., 2013).

A number of expectations for dynamics emerge from the analysis of known and potential linkages between EFCs in Fig. 2. For example, soil moisture will significantly increase after phytotelmata loss only if rainfall is relatively low. Plant productivity will positively respond to increased soil moisture as long as it is not nutrient limited. Nutrient limitation will be attenuated if a high volume of throughfall water relatively rich in labile nutrients is released after phytotelmata loss. From this analysis, we can deduce that the magnitude of the impacts of weevil invasion on forest production will, at least, be a function of water and nutrients release following phytotelmata loss; water and nutrient inputs from rainfall and throughfall; and baseline soil moisture and nutrient content.

Clearly, further interconnections can be postulated and investigated for the ES in Fig. 2 (e.g., connections between forest productivity and the amount of nutrients transported as throughfall) and more EFCs could be incorporated (e.g., a flow chain for bromeliads other than *T. utriculata*, which may serve as weevil reservoirs; see Cooper et al., 2013). The number of EFCs and organizational states to include in an ES will depend on the ecosystem process(es) of interest and the degree of manageable complexity that also affords sufficient explanation. When dealing with concurrent impacts of invasive species on distinct ecosystem functions (water and nutrient fluxes in the above example), integrating them into a single ES can help expose interconnections and mutual dependencies that may not be apparent beforehand. If not overwhelmingly complex, ESs and EFCs can facilitate the joint understanding of varied ecosystem functions by exposing their dynamic interdependencies with invasive species, other biota, and abiotic factors. These relationships among ecosystem components are amenable to mathematical formalization and system dynamic modeling, although this is beyond the purview of this paper.

7. Summary and prospects

Despite the fact that causal links between invasive species and ecosystem functioning are often diverse and intricate, the above discussion illustrates that they are amenable to conceptual generalization. Four general kinds of invasive species impact that encompass a great many influences on ecosystem functions (Section 4, Table 1) can be revealed by focusing on whether such impacts are directly or indirectly mediated by the invasive species (Section 2) and whether they occur via assimilation–dissimilation of energy and materials or physical ecosystem engineering mechanisms (Section 3). By characterizing impacts in this way, biotic and abiotic factors relevant to changes in ecosystem functioning become exposed (participation of biotic intermediaries, structural-abiotic mediation in the case of physical ecosystem engineering). The interrelations between the multiple, concurrent impacts of invasive species on one or more ecosystem functions (Section 5) and other drivers of ecosystem change can then be conceptually modeled by representing the functions of interest and relevant biotic and abiotic factors as a series of causally connected state changes (Section 6). Such a mechanistic perspective is, in our view, an effective means of integrating the biotic and the abiotic into an overall ecosystem analysis of invasive species impacts. We very much hope that the above generalizations and approaches can help guide scientists generate testable predictions about ecosystem change following species invasions. While this perspective was introduced and exemplified here with invasive species in mind, it can certainly be applied to analyze the mechanistic links between species and ecosystems in general (see Shachak and Jones, 1995).

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