

Ecosystem-level consequences of invasions by native species as a way to investigate relationships between evenness and ecosystem function

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Abstract Biodiversity is currently undermined worldwide principally as a result of human activities. The irreversibility of species extinction has encouraged the research community to investigate the potential effect of declining species or functional group diversity and/or composition on ecosystem function since the beginning of the 1990s. However,

while changes in relative abundance among species (i.e., evenness) are more frequent than extinction of species and are able to cause important changes in ecosystem function, most studies have curiously not examined thoroughly the potential role of that diversity component. The few small-scale experimental manipulations that have so far examined the relationship between evenness and ecosystem function have produced ambiguous results, sometimes indicating an effect on selected functions, and sometimes not. Because one reason for the inconsistency of the previous results may be scale-dependency issues, we propose here an alternative approach, investigation of this relationship directly at the system-level through the opportunity offered by field studies of ecosystem-level consequences of invasions by native species. Indeed, the specificities of changes in ecosystem structure induced by native invaders compared to exotic ones could constitute a useful tool to improve our understanding of the relationship between evenness and ecosystem function as well as to evaluate the importance of the spatial arrangement of species in the stability of ecosystems.

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Introduction

As human activities cause widespread threats to Earth's biodiversity—notably through land use changes, habitat fragmentation and nutrient enrichment (Chapin et al. 1997; Vitousek et al. 1997; Sala et al. 2000), investigation of the potential effect of declining species diversity on ecosystem function has emerged as an important scientific question (Loreau et al. 2001; Hooper et al. 2005). As a result, for the last decade, a growing number of experimental studies (conducted in the field—mostly in managed grassland communities—or in the laboratory, in both cases by means of mesocosms or controlled-chambers like the Ecotron) have manipulated the number (i.e., richness) and/or composition of species or functional groups and have often demonstrated that productivity or stability is reduced when plant species diversity declines (Naeem et al. 1994; Tilman and Downing 1994; Johnson et al. 1996; Lawton 1996; Tilman et al. 1996, 1997, 2001; Hooper and Vitousek 1997; Hector et al. 1999; Schwartz et al. 2000; Fukami et al. 2001; Hooper and Dukes 2004; Hooper et al. 2005; Roscher et al. 2005). Nonetheless, the interpretation of these results is still controversial because the experimental design could yield spurious relationships directly linked to “hidden treatments”, such as a sampling effect (Givnish 1994; Huston 1997; Hodgson et al. 1998; Wardle 1999).

Although the relationship of species richness and/or composition to ecosystem functioning has attracted considerable theoretical and experimental attention because of the irreversibility of species extinction, human activities influence the relative abundances or biomasses among species (i.e., evenness) more frequently than the presence or absence of species (Chapin et al. 2000). Changes in species evenness deserve increased attention, because evenness usually changes more rapidly in response to human activities than does species richness and because evenness changes have important consequences for ecosystems long before a species is threatened by extinction (Chapin et al. 2000). This last point could be due to the way each of these two diversity components is linked to ecosystem function: linearly in the case of evenness compared to a saturated-type relationship for species richness (Nijs and Roy 2000; Schwartz et al. 2000). Lastly, relative abundances of species

can account for substantially more of the variance in diversity than does species richness, leading to the conclusion that evenness is necessary to capture the full complexity of diversity in conservation studies and in experiments dealing with biodiversity and ecosystem function relationships (Stirling and Wilsey 2001; Wilsey et al. 2005).

Paradoxically, to date, only a handful of studies, all using experimental manipulation of relative species abundance through controlled field- or greenhouse-experiments, have explicitly examined the relationship between evenness and ecosystem function (namely, primary production and resistance to invasion). Although some of them showed that evenness can be an important determinant of diversity–function relationships (Wilsey and Potvin 2000; Foster et al. 2002; Kirwan et al. 2007) matching expected results of models (Nijs and Roy 2000; Schwartz et al. 2000), others yielded more nuanced results concerning the importance of evenness (Wilsey and Polley 2002, 2004; Mattingly et al. 2007), while yet others found no effect of evenness on function (Polley et al. 2003; Emery and Gross 2007). Thus, as noted by Mattingly et al. (2007), one must admit that presently too few evenness studies exist to draw firm conclusions about the importance of relative species abundance as a driver of ecosystem function. One of the reasons why no clear pattern has been found could be that, to our knowledge, all evenness studies have so far been based on similar approaches through the use of relatively small-scale experiments. It is thus difficult to draw strong inferences about the importance of evenness at the system-level (Schindler 1998), particularly about its role on some emergent functions such as stability—of which resistance to invasion is a component (Ives and Carpenter 2007).

Here, we propose a new, complementary approach to examine relationships between ecosystem structure (mostly, evenness) and function directly at the system-level, using the opportunity afforded by field studies of ecosystem-level consequences of native invasive species. Based on a systems theory approach, we first define what system structure actually is in order to show clearly what an invasion consists of and, above all, what are the particular structural changes caused by the invasion of native species compared to exotic invaders. We then suggest how these changes could be used as a tool to study

structure–function relationships, focusing particularly on the evenness–stability relationship. Finally, a concrete example of a potential application complements the conceptual approach developed in the previous parts of the study.

Conceptual approach

Structure–function relationships from a systems theory viewpoint

From systems theory postulates (Delattre 1971; Bonsack 1979), an ecosystem is defined as a group of interacting elements (i.e., species). Ecosystem structure is then considered as the arrangement of those elements (i.e., species) according to the conceptual framework chosen to study the system. One simple conceptual framework may be, for example, that of the food web. The structure can be decomposed into two parts: (i) from a qualitative viewpoint, the structure corresponds to the role of each element in the system, which commonly refers to species composition (i.e., functional diversity) and redundancy. In the case of a trophic network, it covers the food web topology (*sensu* Ives and Carpenter 2007), that is, the trophic role of species in the system (e.g., primary producer, herbivore, predator), the strength of their interactions and the number of species by type of trophic role (i.e., functional group) including their internal (i.e., within each group) interactions (e.g., competition, mutualism). (ii) From a quantitative viewpoint, the structure refers to the absolute number of elements as well as to the relative numerical importance and biomass of each of them within the system, that is, species richness and evenness, respectively. From trophic considerations, ecological pyramids of numbers or biomass constitute a good representation of such a quantitative view of the structure. According to systems theory, ecosystem function could finally be regarded as the expression of the system's structure, integrating simultaneously qualitative and quantitative aspects of the latter. In that way, functions can be classified in two categories: (i) elementary functions resulting from the expression of one or several elements, and (ii) emergent functions resulting from at least one non-trivial interaction between some system elements.

Limitation on the use of exotic invaders for studying structure–function relationships

In accordance with this theoretical approach, biological invasions can then be considered as a quantitative variation of only one system element (i.e., invader) whose rapid increase modifies the ecosystem structure (e.g., species richness and composition, evenness) and, as a consequence, could sometimes cause variation in elementary and/or emergent functions of the recipient ecosystem. In this respect, numerous studies have underlined the ability of exotic invasive species to change many basic processes of ecosystems such as energy and matter fluxes (including primary productivity, nutrient cycles, hydrology), disturbance regimes (i.e., frequency and/or intensity), as well as the nature and intensity of exchanges between systems (Vitousek et al. 1987; Vitousek 1990; D'Antonio and Vitousek 1992; Gordon 1998; Mack and D'Antonio 1998; Cicchetti and Diaz 2000; Mack et al. 2000; Meyerson et al. 2000; Ehrenfeld 2003; Kourtev et al. 2003; Levine et al. 2003; Dukes and Mooney 2004). However, when we investigate basic underlying mechanism(s) behind ecosystem-level consequences of biological invasions, one major limitation persists: changes in ecosystem function are often difficult to relate to the exact nature of change in ecosystem structure, because invasion of one allochthonous element causes, by definition, both qualitative and quantitative changes in the structure. In ecological terms, invasions of introduced species necessarily produce a simultaneous change in evenness on the one hand (because of the demographic explosion) and specific diversity and composition on the other hand (because of specific traits of the introduced invader).

Native invasive species as a new complementary approach

To circumvent this difficulty, it seems possible to take advantage of a property of native invasive species that is not shared by exotic invaders, namely the obvious fact that the former component is already present in the system before its spatial expansion. Indeed, the expression “native invasive species” corresponds to a species already native to (i.e., already an integral part of) the region or the ecosystem it is going to invade, but whose distribution changes owing to a change in its environment (e.g., fire/change in fire regime,

eutrophication). We believe that any species, whether native or exotic, that spreads in a region may be termed “invasive” because in either case it is the same basic mechanism at work, namely interspecific competition *sensu lato* (Valéry et al. 2008). Examples include invasions of hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore) in the understories of pine and hardwood forests throughout eastern North America owing to both increased understory light intensity following overstory thinning and removal of competing plants by intensive browsing of seedlings by white-tailed deer (*Odocoileus virginianus* Zimmermann) (Horsley 1984; De la Cretaz and Kelty 1999), and of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) and western juniper (*Juniperus occidentalis* Hook.) in meadows across western North America owing to domestic livestock grazing and cessation of frequent fire (Miller and Rose 1999; Heyerdahl et al. 2006).

This view of native invasive species entails two major assumptions, which in turn provide new opportunities for investigating diversity–function relationships: (i) an initial state of both structure and function of the ecosystem, including its future invasive component, (ii) because no new element is introduced into the system, changes in ecosystem function are related only to quantitative variation of species as a consequence of the demographic explosion of the native invader. Thus, at least in the first stages of the invasion process, when no species has become extinct yet owing to the invasion, there is only a change in evenness without any modification in species composition and species richness. That constitutes a very important difference from the situation with exotic invasive species in which, as previously mentioned, simultaneous qualitative (owing to introduction of new traits) and quantitative structural changes are likely to add new functions.

Consequently, unlike exotic invasion studies, the isolation of evenness allows us to examine relationships between structure and ecosystem function in a more unambiguous way. Particularly, invasion by native species could give us a better understanding, at the system-level, of the role of evenness in ecosystem stability. Indeed, at least during the first stages of the invasion process, changes in function would be related only to changes in the proportion (in biomass, or number) of different pre-existing species of the system including the invader itself (i.e., elements

already present before the invasion). This fact could help us determine accurately some disequilibrium thresholds in the relative numerical importance or biomass of species beyond which the system is likely to reach new alternative stable states (Scheffer et al. 2001). Moreover, comparative studies based on several native species invasions, chosen because of their similar impact on structure (i.e., each of them leading to similar change in evenness), could also inform us, in a new way (i.e., still at the system-level), about the role (i.e., “efficiency”) of invasion patterns (e.g., phalanx or guerilla strategies *sensu* Lovett-Doust and Lovett-Doust 1982) in modifying functions, so that, in turn, it could be possible to draw some conclusions at the system-level on the importance of spatial arrangement of species in the stability of ecosystems.

Finally, without ignoring some insightful results already gained from controlled experiments, the use of ecosystem-level consequences of invasion by native species could constitute a valuable alternative approach to experimental studies conducted in mesocosms whose advantages such as rapidity or replication are often counterbalanced by some limitations directly linked to spatial and temporal scaling considerations (Carpenter 1996; Schindler 1998; Loreau 2008). In particular, three main considerations reinforce the importance of that system-level view in the study of structure–function relationships: (i) ecosystem function can be best assessed quantitatively when the uncertainty or inaccuracy of results from replicated mesocosm studies is likely to be amplified owing to the scaling up of processes (Likens 1985; Carpenter 1996; Schindler 1998); (ii) an evolutionary history of the system is taken into account, whereas mesocosms are systems whose structure is artificial so that species assemblages have no such history (Carpenter 1996; Schindler 1998). Thus, native invaders guarantee us a reliable system from a functional and evolutionary viewpoint, which constitutes a relevant—maybe, essential—characteristic, particularly for studying the effect of structure on ecosystem stability comprehensively including diversity as only one of the possible factors that affect ecosystem responses to environmental change (cf. below; Ives and Carpenter 2007); (iii) last, and not least, from a system theory viewpoint (Delattre 1971; Bonsack 1979), stability (i.e., homeostasis) is by definition an emergent function that seems out of

reach in experimental approaches (notably, because of its scale-dependency). Thus, in the particular case of a structure–stability relationship, system-level studies like the one proposed here seem to be highly recommended.

Co-varying environmental factors as a limit of the approach?

Based on some previous studies (Gurevitch and Padilla 2004; MacDougall and Turkington 2005), it may be reasonably argued that the opportunity afforded by native invaders is invalid because of direct confounding effects on ecosystem functions owing to the environmental change itself, since the latter is supposed to be at the origin of the demographic explosion of the native invader. Thus, to use the expression of MacDougall and Turkington (2005), native invaders would not be the driver of changes in ecosystem functions but rather a passenger of the environmental change. This view bears discussion. As Didham et al. (2005) have already observed, it seems more realistic to consider the driver and passenger models as extreme cases of a general model incorporating additive or synergistic effects of the two factors (i.e., “interacting drivers” explanation), with the relative importance of invasive species and environmental factors varying between species and between ecosystems. Thus, even though invasion by native species is always triggered by a change in the environment, this environmental factor need not be the main driver of functional changes. In particular, it is highly conceivable that beyond a threshold value of the environmental factor, native invaders could continue their spread even when that factor has stabilized. Then, in such a simple case, subsequent changes in ecosystem function that may occur would be linked only to changes in structure (i.e., evenness) caused by native invaders.

As a consequence, in all cases, the respective roles of both native invaders and environmental changes as drivers of fluctuations in ecosystem function should be quantified during the invasion process in order to eliminate cases where confounding effects actually occur, allowing us to select only appropriate study cases (i.e., those for which the factor “native invader” can be isolated and those for which it is the major driver) for examining structure–function relationships correctly. Thus, one should first collect

simultaneously data on structural changes resulting from the spread of the native invader (i.e., changes in evenness) and data on the environmental factor (e.g., N or P content of water, for eutrophication) potentially involved in the whole invasion process (if the passenger model actually obtains), in addition to results coming from system functions monitoring. Then, discriminating among potential drivers of changes in ecosystem function (i.e., establishing a hierarchy between both causes) will be possible through linear/non-linear structural equation modelling, such as path analysis, which constitutes an extension of multiple linear regression modelling, precisely designed for the decomposition and interpretation of relationships among causal factors (Legendre and Legendre 1998; Grace et al. 2007). Successful studies using path analysis (or related statistical approaches) to disentangle multiple causal factors (e.g., Bach et al. 1992; Wootton 1994), notably those of Light and Marchetti (2007) distinguishing precisely between invasions and habitat changes as drivers of diversity loss and of Grace et al. (2007) controlling for environmental influences to evaluate diversity–productivity relationships, suggest that this approach is feasible.

Lastly, to control for variation in ecosystem function that may be caused by other potentially co-varying factors (i.e., other than the one triggering the invasion), like ecosystem maturation effects or successional effects, one could attempt, as a complementary approach to path analysis, simultaneous comparisons of “identical” ecosystems located in the same biogeographic region, some uninvaded and others invaded by the same native species but at different times. These could inform us about such site-specific co-varying factors. Indeed, as Didham et al. (2005) note, judicious use of comparative quantitative data can allow powerful tests of the degree of inter-correlation among multiple drivers.

A potential methodological application: towards long-term monitoring of oligotrophic systems

Some strategies and applications for research can be derived directly from this conceptual approach. Trivially, it is necessary to set up monitoring programs focusing on ecosystems likely to suffer from native invaders. Owing to the constantly

increasing nutrient enrichment of the environment (Vitousek et al. 1997), oligotrophic ecosystems, or more precisely, systems that are supposed to be oligotrophic but are actually suffering eutrophication, are nowadays often invaded by native fast-growing clonal grasses (Aerts and Berendse 1988; Bakker and Berendse 1999). The most illustrative and well-researched examples are European ones because of the singular hydrologic and atmospheric supply of nitrogen in this region (Ågren 1990; Berendse et al. 1993; Bakker and Berendse 1999). Examples include the demographic explosion of *Brachypodium pinnatum* (L.) Beauv. and *Arrhenaterum elatius* (L.) Beauv. in Dutch and English calcareous meadows (Bobbink and Willems 1987; Soukupova 1992; Hurst and John 1999), the rapid spread of *Molinia caerulea* (L.) Moench. in Dutch, English and Welsh wet heathlands (Berendse and Aerts 1984; Aerts and Berendse 1988; Berendse 1990; Hogg et al. 1995; Kirkham 2001; Tomassen et al. 2003), the increasing dominance of *Deschampsia flexuosa* (L.) Trin. in Dutch and English dry heathlands (Berendse and Aerts 1984; Hogg et al. 1995; Bakker and Berendse 1999), the spread of *Holcus mollis* (L.) and *Calamagrostis villosa* (Chaix) Gmelin in central European understory poor soils and of *Calamagrostis canescens* (Weber) Roth in continental wetlands (Soukupova 1992), the encroachment of *Calamagrostis epigejos* (L.) Roth on dunes or sandy soil communities (Soukupova 1992; Bakker and Berendse 1999), and the recent invasion of European salt marshes by *Elymus athericus* (Link) Kerguelen along the coasts of the North Sea, English Channel and Atlantic Ocean (Van Wijnen et al. 1997; Bockelmann and Neuhaus 1999; Valéry et al. 2004).

This long list of examples unfortunately shows how frequent native invasions are. Nevertheless, these invasions constitute potential study cases, providing us with the opportunity to relate ecosystem structure (i.e., both evenness and spatial arrangement of species) and function statistically (i.e., many replicates for each native invader) and operationally (i.e., optimal choice of study sites according to accessibility, size, etc.). Monitoring should be undertaken for long enough (i) to establish the initial state regarding structure and function of the ecosystem before its invasion, and (ii) to measure potential changes in ecosystem function in relation to structural modifications, which will depend on the density of the native invader. To achieve this last goal, as many functions as possible (including

emergent functions) should be monitored through a multidisciplinary approach in order to characterize invasion consequences most accurately and, above all, to increase probabilities of taking into account functions that are likely to be modified as a result of invasion. This approach resembles the Long-Term Ecological Research program (LTER), but it would be more narrowly focused on oligotrophic ecosystems. Then, with sufficiently continuous and contrasted data (and provided that the aforementioned precautions about co-varying environmental factors have been taken), slight variations in function or appearance/disappearance of major functions leading to a new stable state of the system could be related to changes in evenness in the course of invasion, allowing us to draw strong inferences, directly at the system level, about the role of evenness and/or spatial arrangement of species on ecosystem function.

To conclude, the advantages of the approach proposed here are still hypothetical and must be proven. However, we think it should be considered for research on relationships between evenness (and/or spatial arrangement of species) and ecosystem function, particularly for the evenness-stability relationship which is a priori out of reach through mesocosm-type approaches. Even if experimental studies have the advantage of being fast and replicable, they also have scale-dependent limitations that often prevent us from drawing firm conclusions at the ecosystem level. That is why it seems unwise to consider controlled experiments as the only way to examine these relationships, as seems to be the trend nowadays. As recently noted by Loreau (2008), it is from the confrontation of results from multiple approaches (i.e., small-scale experiments, controlled field experiments, comparative studies between ecosystems) that we may respond to the challenge raised by structure–function relationships. Thus, we encourage the research community to develop new alternative and complementary approaches in this field.

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