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Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes

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Contents

Summary	615	VI. Invasion syndromes: advancing theoretical integration	627
I. Introduction	615	VII. Conclusions	628
II. A framework for an integrative invasion science	616	Acknowledgements	628
III. Model systems: accounting for the complexity of invasions	618	References	628
IV. Multi-site studies: evaluating context-dependencies	622		
V. Focused meta-analysis: improving prediction through fine-tuning synthesis	625		

Summary

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Invasion science is a very active subdiscipline of ecology. However, some scientists contend that theoretical integration has been limited and that predictive power remains weak. This paper, focusing on plants, proposes a new multi-pronged research strategy that builds on recent advances in invasion science. More intensive studies on particular model organisms and ecosystems are needed to improve our understanding of the full suite of interacting factors that influence invasions ('model system research'). At the same time, comparative studies across many study systems are essential for unravelling the context-dependencies of insights that emerge from particular studies ('multi-site studies'); and quantitative synthesis based on large datasets should be constrained to well-defined theoretical domains ('focused meta-analysis'). We also suggest ways for better integration of information about species biology and ecosystem characteristics ('invasion syndromes'). We expect that a resulting theory of invasions will need to be conceived as a somewhat heterogeneous conglomerate of elements of varying generality and predictive power: laws that apply to well-specified domains, general concepts and theoretical frameworks that can guide thinking in research and management, and in-depth knowledge about the drivers of particular invasions.

I. Introduction

Invasion science is a very active and productive subdiscipline of ecology. It focuses on the fate of species introduced through human activities to new geographic areas and the impact of a subset of those

alien species that became invasive on resident biota and ecosystems (Elton, 1958; Drake *et al.*, 1989; Williamson, 1996; Kolar & Lodge, 2001). Such intensive research activity across many different organisms, ecosystems, and biogeographic regions has led to the accumulation of a large and diverse knowledge base

(Cadotte *et al.*, 2006; Richardson & Pyšek, 2008; Davis, 2009; Richardson, 2011a; Simberloff & Rejmánek, 2011b; Lockwood *et al.*, 2013). Research in invasion science is wide ranging, because it has drawn insights, perspectives and approaches from the fields of genetics, evolutionary biology, population biology, community ecology, ecosystem ecology and landscape ecology, but also from nonbiological fields such as socioeconomics and human history (Kueffer & Hirsch Hadorn, 2008; Richardson, 2011a).

Despite such an integrative approach, some researchers contend that generalisation and theoretical integration are limited and that robust predictions remain elusive (Hulme, 2012; Jeschke *et al.*, 2012a; Moles *et al.*, 2012; Strayer, 2012). Many different hypotheses about mechanisms involved in invasions have been formulated, but meaningful generalizations are difficult, and understanding of the importance of different mechanisms for explaining invasions is rather poor (Dietz & Edwards, 2006; Catford *et al.*, 2009; Jeschke *et al.*, 2012a,b; Richardson & Pyšek, 2012; Strayer, 2012). The accuracy of weed risk-assessment protocols as the basis of preventative action against future invasions remains 'usually insufficient' (Hulme, 2012). This unsatisfactory state of affairs is further aggravated by 'the ghost of invasion past problem' which posits that generalisations accumulated from insights derived from past invasions have limited value for predictions beyond the conditions under which those (past) invasions occurred (Kueffer, 2010b). One of the best predictors of invasiveness is the rule-of-thumb that known invaders will replicate their performance in other places (Kulhanek *et al.*, 2011; Hulme, 2012). However, in an era of rapid and substantial global change it is very likely that taxa not currently known to be invasive and processes not clearly implicated in past and current invasions will interact in new ways to shape invasion trajectories (Walther *et al.*, 2009; Kueffer, 2010b).

We review recent developments in invasion science – focusing on plants – that pave the way for overcoming some inadequacies of past research and show how these different new research activities – that are usually pursued separately – could delineate a productive new approach for studying biological invasions. In particular we argue that building on three new developments could substantially improve predictive power and theoretical integration in the field. Increasingly, (1) comprehensive data are available on particular model systems, either organisms or ecosystems ('model system research'); (2) the same organisms or types of ecosystem are studied at multiple sites ('multi-site studies'); and (3) generalisations across species/ecosystems, or concerning particular invasion mechanisms (e.g. enemy release, novel weapons, phenotypic plasticity), are being enhanced by avoiding biases through constraining meta-analyses to specific invasion contexts ('focused meta-analysis').

Our article is divided into three main parts. We first present a conceptual framework that integrates different emerging research approaches. Then we review promising results emerging from each of the three approaches. Finally we preview the kinds of theoretical insights that could emerge from a more integrative invasion science, including novel syntheses that integrate information about species biology and ecosystem characteristics ('invasion syndromes'). Frequently used terms are defined in a glossary (Table 1). This review focuses on plants because plant invasions are particularly intensively studied (Pyšek *et al.*, 2008; Jeschke *et al.*, 2012b) and

Table 1 Glossary

Alien species: (synonyms: exotic, introduced, nonindigenous, non-native). Species whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (Richardson *et al.*, 2011).

Focused meta-analysis: Analyses of large datasets from different invasive species or invaded ecosystems compiled from the literature or gathered through coordinated efforts such as large multi-taxon experiments that are focused on a well-specified theoretical domain (see separate entry). This can for instance be done by constraining analysis to particular groups of organisms, or to ecosystems characterised by a particular range of environmental and biotic conditions.

Ghost of invasion past: The problem that generalisations accumulated from insights derived from past invasions (as 'natural experiments', see separate entry) might have limited value for predictions beyond the conditions under which those (past) invasions occurred (compare Kueffer, 2010b).

Invasion science: The interdisciplinary study of the causes and consequences of the introduction of organisms to areas outside their native range, and of the management responses for addressing negative outcomes (Richardson *et al.*, 2011).

Invasion syndrome: Typical recurrent associations of species biology and invasion dynamics with particular invasion contexts such as an invasion stage, invaded habitat and/or socioeconomic context.

Invasive species: Alien species that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and have the potential to spread over long distances, possibly leading to adverse effects on invaded habitat ('impacts') (Richardson *et al.*, 2011).

Model system: In-depth research of particular invasions of particular species ('model organisms') or in a particular site ('model ecosystems'); and integration of diverse information on particular species or sites. Place-based long-term ecological research such as at LTER sites represents an example of model ecosystem research.

Multi-site study: Comparative research of the same species or type of ecosystem across multiple sites.

Natural experiment: Studies that interpret observations at different sites (or other observational units) in nature as the outcome of past processes that were influenced by specific differences between observational units ('treatments') (Diamond, 1983; Richardson *et al.*, 2004).

Theoretical domain: The phenomena such as organisms, ecosystems, invasion phases, invasion mechanisms – as well as temporal and spatial scales – for which generalisations are meant to apply (compare Pickett *et al.*, 2007).

have driven most of the theoretical debates in invasion science. The conceptual framework and proposed research approach are, however, transferable to other groups of organisms. Indeed, main messages of our review are that the bias in research efforts in favour of a limited number of organism groups should be minimised, and that more cross-taxonomic studies are needed that compare invasions of plants and animals (Pyšek *et al.*, 2008; Jeschke *et al.*, 2012b).

II. A framework for an integrative invasion science

Invasion science has relied heavily on *post hoc* analyses of the outcomes of past and current invasions as natural experiments. Generalisations about the drivers of invasions have come mostly from observed invasion patterns across many different species and ecosystems. By focusing research on the study of natural experiments, invasion science is probably unique in how it has

comprehensively dealt with the longer-term dynamics of a particular set of ecological processes across many different real-world settings. Nonetheless, we see three key challenges that still need to be addressed to achieve further progress, and we suggest that emerging new research approaches offer exciting opportunities to achieve broad new perspectives on invasions (Fig. 1).

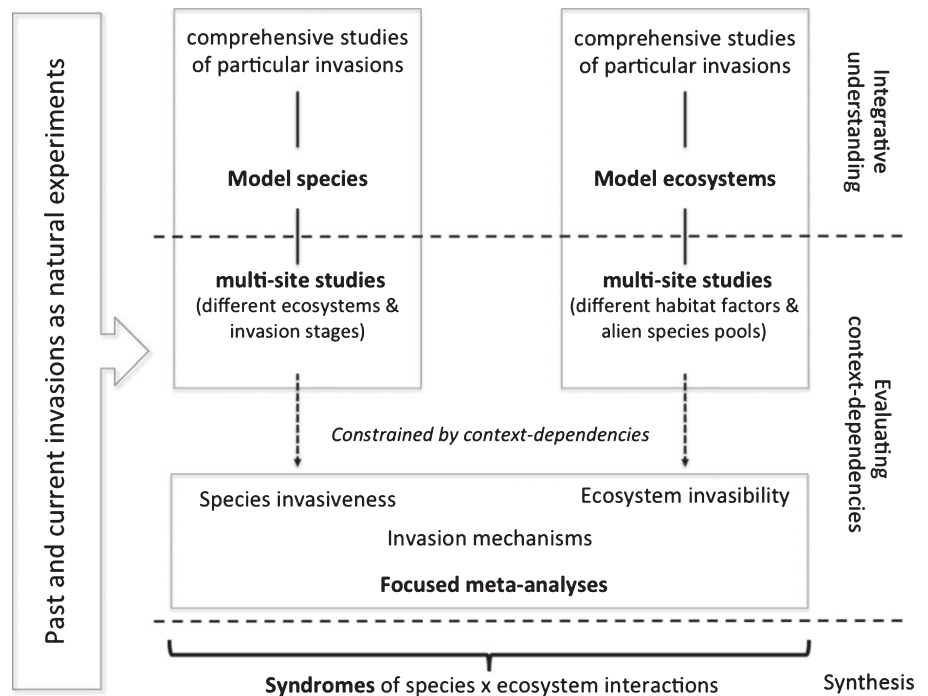
First, ecological systems are complex; invasions are characterised by multi-faceted dynamics involving multiple drivers (Didham *et al.*, 2005, 2007; Foxcroft *et al.*, 2011; Gurevitch *et al.*, 2011; Strayer, 2012). The functioning of such complex systems cannot be fully understood by elucidating the working of its parts. Sciences dealing with complex systems must therefore simultaneously address many interrelated processes. Practically, comprehensive research can only be done with a limited number of study objects. This is why research on selected model systems at different levels of biological organisation is so prominent in biology (Mitchell-Olds, 2001; Hobbie *et al.*, 2003; Travis, 2006; Leonelli, 2007; Grant & Grant, 2008; Bolker, 2012). In the context of invasion science, model system research involves in-depth research of invasions of particular taxa ('model organisms') or at a particular site ('model ecosystems'), and the integration of diverse information on such taxa or sites. The recent accumulation of comprehensive datasets on selected invasive species or invaded ecosystems has created a strong foundation for developing model systems in invasion science. Research focused on particular model systems will help to identify processes relevant for understanding invasions; elucidate the interactions of multiple evolutionary, ecological and social processes implicated in invasions and their underlying mechanisms; and evaluate the relative importance of different mechanisms in shaping particular invasions.

Second, no two ecosystems or species work the same way, making the transfer of insights gained from a particular system to

another tenuous, and potentially misleading. Consequently, comparative studies across multiple study systems are needed to evaluate the context-dependencies of insights gained from in-depth research of particular model systems. We suggest two strategies that could help to account for context dependencies: (1) model system research should involve multiple sites (horizontal integration, Travis, 2006); and (2) meta-analysis should account for context-dependencies by being constrained to appropriate theoretical domains (Pickett *et al.*, 2007). As we will discuss, multi-site studies are rapidly gaining prominence in invasion science, and awareness is growing that data biases or a broad focus can lead to spurious results in meta-analysis (e.g. Daehler, 2003; Colautti *et al.*, 2009; van Kleunen *et al.*, 2010a).

There are different types of context-dependencies that matter for biological invasions, but it is particularly urgent to deal with species × ecosystem interactions and differences among invasion stages (establishment, naturalization, invasion). Indeed, different species traits are advantageous in different ecosystems (Daehler, 2003; Martin *et al.*, 2009; Drenovsky *et al.*, 2012; Kueffer *et al.*, 2013b) or invasion stages (Dietz & Edwards, 2006; Theoharides & Dukes, 2007; Pyšek *et al.*, 2009a; Richardson & Pyšek, 2012). Similarly, impact is also context-dependent and is defined by interactions between traits of invading species and invaded ecosystems (Vilà *et al.*, 2011; Pyšek *et al.*, 2012). Here 'ecosystem' refers broadly to the ecological context of an invasion and not a particular type of ecosystem. Thus, context-dependence can mean the differences in the behaviour of a species at different sites of the same type of ecosystem (e.g. intertidal invasions of *Spartina* at different sites) or in different ecosystem types (e.g. *Fallopia* taxa invading riparian, ruderal, disturbed forest, beach and saltmarsh habitats, see Supporting Information Table S1). Species × ecosystem interactions are also relevant in ecosystem invasibility studies:

Fig. 1 Schematic diagram of the interrelationships among emerging approaches in integrative invasion science. Much research on invasions is based on the evaluation of past invasions as natural experiments. We propose that such research can be improved through the use of model systems that facilitate: integrative studies on particular invasions to gain a multi-level understanding of invasion dynamics; and comparative research across multiple native and invaded sites to evaluate the context-dependencies of insights gained from particular invasions ('multi-site studies'). Based on results from model system research, meta-analyses of large datasets can be better focused to generalise insights across particular subsets of species or ecosystems ('focused meta-analysis'). An important achievement will be to overcome the separation of species-focused and ecosystem-focused research, for instance by studying recurrent patterns of species × ecosystem interactions ('invasion syndromes').



the invasibility of an ecosystem depends on the pool of alien species in an area (e.g. alpine ecosystems might be less invaded because only few alien alpine plants have been introduced to mountains; Kueffer *et al.*, 2013b) and the invasion phases considered (e.g. an ecosystem might be colonized by many casual species but few become invasive; Lonsdale, 1999; Richardson & Pyšek, 2012).

The third challenge is that theoretical syntheses should move beyond the search for broad generalisations that would explain all types of invasions, and must account for interactions among species, ecosystems and invasion stages (e.g. Kueffer & Hirsch Hadorn, 2008; Gurevitch *et al.*, 2011; Richardson & Pyšek, 2012). Invasion science is still largely separated into research on species traits and ecosystem characteristics although it is evident that species \times ecosystem interactions shape invasion patterns, and theoretical generalisations rarely differentiate between invasion stages. We propose that theoretical synthesis should aim for identifying recurring patterns of species \times ecosystem interactions characterising invasion dynamics in different socio-ecological contexts for which we apply the term 'invasion syndromes'.

Figure 1 suggests that the different emerging research approaches are not independent. In-depth research on particular model systems, multi-site studies and focused meta-analysis represent a sequence of approaches that should be interlinked to ensure a mutual sharpening of research questions and interpretation of results. And species-focused (invasiveness) and ecosystem-focused (invasibility) studies should not be performed, and cannot be interpreted, independently. In fact, it is the combination of different approaches that might, synergistically, help invasion science master some of its most pressing challenges.

Clearly, our framework is ambitious, and for practical reasons it may not be possible to implement all of its components simultaneously. However, all research faces the dilemma of what needs to be done and what can be achieved with currently available resources. Our framework and arguments offer a new perspective on how to plan, design, integrate and interpret different research projects in invasion science. The emphasis that should be given to in-depth studies on particular model systems vs comparative studies and meta-analyses across many study systems depends on the questions asked and the state of research. We suggest that emerging theories and generalisations in invasion science will need to be conceived as a somewhat heterogeneous conglomerate of elements of varying generality and predictive power. We see these as comprising 'laws' and generalisations applying to well-specified domains, general concepts and theoretical frameworks for guiding thinking in research and management, and increasing in-depth knowledge about the key mediators of particular invasions.

III. Model systems: accounting for the complexity of invasions

Disproportionate progress in biological laboratory research in recent decades has come from coordinated work on only a few model organisms (<http://www.nih.gov/science/models>, accessed 20 June 2013). Focusing research on particular model organisms (Mitchell-Olds, 2001; Travis, 2006; Grant & Grant, 2008) or model ecosystems through place-based long-term research (Hobbie

et al., 2003; Coleman, 2010; Billick & Price, 2011) has also been a success story in evolutionary biology and ecology. Model system research allows for particular study systems to be studied in great detail and breadth, and paves the way for synergies through the accumulation and sharing of large datasets, tools, infrastructure, standardised research protocols and knowledge from multiple disciplines (Mitchell-Olds, 2001; Hobbie *et al.*, 2003; Travis, 2006; Grant & Grant, 2008; Coleman, 2010; Billick & Price, 2011). However, no model organism or ecosystem is representative of all organisms/ecosystems or is amenable to answering all questions, and therefore combining research on multiple complementary model systems is crucial to avoid biases and ineffective research (Hobbie *et al.*, 2003; Travis, 2006; Bolker, 2012).

Invasion science is well placed to capitalize on model system research. There are well-known 'poster child' examples of problematic invaders that feature prominently in the literature. The international research programme on biological invasions initiated in the 1980s by the Scientific Committee on Problems of the Environment (SCOPE) that was pivotal in moving invasion science to the forefront of international interest, was designed as a global comparative study of invasions in different types of 'model' ecosystems (such as Mediterranean-type ecosystems) (Drake *et al.*, 1989; Simberloff, 2011a). Despite these promising foundations, however, advances in model system research in invasion science have been modest. Most ecosystem-focused research has not moved beyond documenting case examples of impacts of invasive species without developing and testing an integrative understanding of complex interactions among invasive species, ecosystem properties and other factors of global change (Strayer, 2012). Species-focused researchers have been more interested in testing different hypotheses in isolation than in performing comprehensive studies of particular species.

A unique strength of invasion science is that a large and growing group of globally networked scientists work on a particular subset of organisms – invasive species – and compile and share data through large databases and networks. A focus on model systems can further strengthen such collaborative efforts. We expect that the selection of appropriate model systems will be the result of self-organised and bottom-up processes in the research community, but it is useful to consider what makes a good model system. Many of the criteria that define a promising model organism in laboratory research also apply to invasion science (e.g. Leonelli, 2007; Bolker, 2012). First, it is convenient to build a model system on pre-existing research (Tables 2, S1), when data, tools, infrastructure and knowledge are available. Second, a good model system is characterised by high versatility: that is, it is suitable for addressing many research questions, is attractive to funders and collaborators, and lends itself to sharing of tools, infrastructure and data. Third, the species or ecosystems must be amenable to study and use for experiments (e.g. size and growth rate of an organism, accessibility of a site). Finally, different model systems should be selected to represent a broad range of different organisms and ecosystems. We also suggest that a primary focus should be on invasions (including introductions that have failed to result in invasions) that seem to deviate from predictions based on current models and theories (compare Table 2).

Table 2 Different types of model systems appropriate for model-organism research in invasion science (for more information see Supporting Information Table S1)

	Description	Examples
Intensively studied species	Invasive species for which a broad information basis is available	<i>Alliaria petiolata</i> , <i>Bromus tectorum</i> , <i>Centaurea</i> spp., <i>Fallopia</i> spp., <i>Heracleum mantegazzianum</i> , <i>Phragmites australis</i> , <i>Solidago</i> spp.,
Specialised research	Invasive species that have become models for studying particular mechanisms in detail, often involving expensive techniques	<i>Alliaria petiolata</i> , <i>Centaurea</i> spp., <i>Lythrum salicaria</i> , <i>Phalaris arundinacea</i> , <i>Silene</i> spp., <i>Spartina</i> spp.
Understudied species	Important invasive species that are understudied; especially (sub)tropical species: a coldspot of comprehensive studies and a likely hotspot of future invasions	<i>Clidemia hirta</i> , <i>Falcataria moluccana</i> , <i>Hedychium</i> spp., <i>Melinis minutiflora</i> , <i>Miconia calvescens</i> , <i>Morella [Myrica] faya</i> , <i>Pennisetum setaceum</i> , <i>Psidium</i> spp., <i>Pueraria montana</i>
Genera/families	Genera and families with many widely introduced species that range broadly in their invasiveness	<i>Acacia</i> , <i>Bromus</i> , <i>Eucalyptus</i> , <i>Impatiens</i> , <i>Melastomataceae</i> , <i>Myrtaceae</i> , <i>Pinus</i> , <i>Rubus</i> , <i>Senecio</i>
Genera/families/functional groups with an underrepresentation of invasive species	Groups of species with an underrepresentation of invasive species have attracted less research interest. Understanding why these groups have not become invasive may help to advance invasion science significantly, especially in the case of functionally unique groups (e.g. <i>Orchidaceae</i> , <i>Proteaceae</i>) or those adapted to less invaded habitat. This may be important for management since with global change abiotic conditions will change and different species are likely to be targeted for use by humans and it is important to know which could become invasive (Kueffer, 2010b).	<i>Betulaceae</i> , <i>Burseraceae</i> , <i>Dipterocarpaceae</i> , <i>Fagaceae</i> , <i>Moraceae</i> , <i>Orchidaceae</i> , <i>Proteaceae</i> , <i>Rubiaceae</i> , or <i>Sapotaceae</i> . Invaders of less invaded habitat such as undisturbed habitat, shaded forest understoreys, nutrient-poor habitat, habitat of harsh climate (mountains, high/low latitudes, dry habitat), or mainland tropics

1. Model organisms

Many fundamental questions in invasion science can only be answered through integrative studies of selected model organisms. Such model organism research encompasses comprehensive studies of invasions of a particular species at particular sites, comparative studies of invasions of the same species across multiple sites, and integrating diverse information about a particular species to address complex research problems (multi-site studies will be discussed in section IV Multi-site studies: evaluating context-dependencies). To date, detailed databases have been accumulated only for a small number of invasive species; and even in these cases often not very systematically (Tables 2, S1). As we will demonstrate, concentrating research on model species is promising, but will require research efforts to be strengthened and better coordinated and model organisms to be carefully selected. The most problematic invaders and best-studied species (Tables 2, S1) are certainly good candidates for model organisms, but, as argued above, there are also other criteria for good model organisms.

The value of comprehensive studies of particular invasions Studying an individual species at a particular site allows for a thorough assessment of the full range of factors and their interactions affecting the outcome of an invasion. Without a comprehensive understanding of the anthropogenic, ecological and evolutionary processes involved in particular invasions, conclusions about the invasiveness and impacts of alien species can be misleading. Indeed, much recent research shows that invasion dynamics are multifaceted and require a multi-level understanding of interacting genetic, physiological, ecological and socioeconomic factors (Hobbs & Huenneke, 1992; Didham *et al.*, 2005, 2007; Stromberg *et al.*, 2009; Kueffer *et al.*, 2010b; Gurevitch *et al.*, 2011; Richardson, 2011a; Strayer, 2012).

Comprehensive case studies of particular invasions help to clarify the relative importance of general drivers and case-specific factors in determining invasion success and impacts (Mooney & Drake, 1986; Foxcroft *et al.*, 2011; Jarošík *et al.*, 2011; Hulme *et al.*, 2012; Kueffer, 2012), which is necessary information for designing robust meta-analytical studies and effectively applying general knowledge to concrete management cases. In particular, accounting for the socioeconomic context of invasions is crucial. Some of the most dramatic invasions were triggered by massive past habitat destruction and/or large-scale deliberate introduction of the invasive species to the site of invasion (Stromberg *et al.*, 2009; Kueffer *et al.*, 2010b; Kueffer, 2013). Even for dramatic and seemingly undisputable invasions such as that by *Tamarix* species in the United States (Stromberg *et al.*, 2009), or the dominance of large tracts of forest in the Seychelles islands by *Cinnamomum verum* (Kueffer *et al.*, 2010b), idiosyncratic factors such as past land use and introduction efforts played a decisive role in determining invasion success. For a robust understanding of *Tamarix* invasions in western USA it is important to consider that this species was initially introduced at a substantial scale for erosion control (Stromberg *et al.*, 2009). *Cinnamomum* has likely profited from a window of opportunity in the 19th century when the Seychelles islands were largely deforested (Kueffer *et al.*, 2013a). Failure to factor in such key drivers for some invasions can result in spurious results from meta-analyses.

Comprehensive studies of particular invasions can also help to reconcile conflicting views about threats imposed by alien species (Davis *et al.*, 2011; Simberloff *et al.*, 2013). Although the adverse effects of invasive species are often obvious and undisputed, in other situations, especially for plants, the effects of invasive species are less clear (Pyšek *et al.*, 2012). The situation is further complicated in an era of rapid human-mediated global change when options for managing ecosystems are being fiercely debated and range 'from

complete eradication to tolerance and even consideration of the 'new' species as an enrichment of local biodiversity and key elements to maintain ecosystem services' (Walther *et al.*, 2009). In such situations invasion science must seek to elucidate a broad range of potentially relevant dimensions of invasions to gain an understanding of when invasive species are 'drivers' as opposed to 'passengers' of ecological change and how invasions interact with other factors such as habitat modification in affecting biodiversity (Didham *et al.*, 2007; Chytrý *et al.*, 2012). Invasion science relies heavily on case studies of problematic invasions for raising public awareness and gaining political support for management action. However, many poster-child examples of problematic invasions are poorly documented with comprehensive and long-term data (Hager & McCoy, 1998; Blossey, 1999; Stromberg *et al.*, 2009; Lavoie, 2010; Hulme *et al.*, 2012; Strayer, 2012).

Changes over time Current invasions are the result of the interplay of *past* events and processes (Kueffer, 2010b; Pyšek *et al.*, 2010; Essl *et al.*, 2011), and the justification for simply extrapolating into the future is questionable (Strayer *et al.*, 2006; Kueffer, 2010b). Resolving fundamental questions in invasion ecology relies on the accumulation of detailed information on invasions of particular species over many decades. Such insights are indispensable for understanding, for example, why time lags are frequent but differ in length for different species/localities, or how invasion patterns change over longer time periods (Blossey, 1999; Strayer *et al.*, 2006; Lankau *et al.*, 2009).

An exciting research opportunity is, for instance, provided by well-documented chronosequences of *Alliaria petiolata* invasions in North America. Comparisons of invaded sites with different residence times of invading *Alliaria* populations illustrate how evolutionary changes interact with ecological responses of the invaded habitat (Lankau *et al.*, 2009; Lankau, 2011b). The invasion success of *Alliaria* is partly a result of competitive advantage through the release of allelochemical substances. It appears that allelochemical release declines with population age (Lankau *et al.*, 2009) – possibly selected for in response to increased intraspecific competition in monospecific stands of *Alliaria* in the invaded range (Bossdorf *et al.*, 2004; Lankau *et al.*, 2009) – while the invaded communities develop an increased resistance to the released allelochemicals (Lankau, 2011b).

Evaluating and integrating multiple hypotheses Several authors have recently proposed frameworks for synthesising a broad array of different hypotheses in invasion science (Dietz & Edwards, 2006; Facon *et al.*, 2006; Theoharides & Dukes, 2007; Catford *et al.*, 2009; Milbau *et al.*, 2009; Gurevitch *et al.*, 2011). Different invasion mechanisms, for example, enemy release, novel weapons, phenotypic plasticity or unused resources, work together – additively, synergistically, or antagonistically – and these interactions must be better understood (Blumenthal, 2006; Blumenthal *et al.*, 2009; Gurevitch *et al.*, 2011). Large datasets gained from particular model organisms will pave the way for addressing interactions and testing the application of synthetic frameworks more effectively. For instance, research on *Alliaria petiolata* has contributed to a better understanding of many central hypotheses

and issues in invasion biology: enemy release, evolution of increased competitive ability, allelopathy, the role of plant–soil interactions, belowground effects on competing plants (both direct, and indirect via interference with mutualisms), phenotypic plasticity and the empty niche concept (Bossdorf *et al.*, 2004; Callaway *et al.*, 2008; Rodgers *et al.*, 2008; Lankau *et al.*, 2009). However, the relative importance of different factors in explaining the spread and impacts of *Alliaria* in different sites is not well understood (Barney & Whitlow, 2008; Rodgers *et al.*, 2008). Similarly, the relative importance of belowground interactions and release from aboveground herbivory is not well understood for *Centaurea* invasions (Seastedt *et al.*, 2005). Indeed, research on most model organisms has been driven by an interest in one to a few mechanisms or aspects of invasion dynamics (see Table S1), while comprehensive information that allows addressing different mechanisms in combination is lacking for most species. None of the most intensively studied invasive plant species identified by Pyšek *et al.* (2008) is consistently represented in different meta-analyses about important mechanisms and hypotheses (e.g. Daehler, 2003; Liao *et al.*, 2008; Morales & Traveset, 2009; Chun *et al.*, 2010; Davidson *et al.*, 2011; Vilà *et al.*, 2011). One reason for this might be that it is difficult to publish studies that confirm known mechanisms for an additional species or ecosystem (Kueffer *et al.*, 2011).

We see two main ways of evaluating and integrating multiple hypotheses using information from large datasets. Given enough data, population modelling can be used to evaluate the relative importance of factors such as enemy release or differences in life-history strategies in driving invasions (e.g. Maron *et al.*, 2010; and entry on *Cynoglossum officinale* in Table S1). Where data are too heterogeneous or processes are too complex to be integrated into a population modelling framework, invasion theory can be considered as a conceptual framework that helps to structure the understanding of a particular invasion (Pickett *et al.*, 2007; Foxcroft *et al.*, 2011; Kueffer, 2012). Indeed, Foxcroft *et al.* (2011) demonstrated that invasion theory as a general framework can help to structure the factors – and their interactions – that need to be considered to understand a specific problem (the invasion of *Opuntia stricta* in South Africa). Sometimes, comparing the performance of theory-based and species-specific models can clarify the interplay and assess the relative contributions of general drivers and species-specific factors in driving invasions (Jarošík *et al.*, 2011).

Understanding the underlying mechanisms of different drivers In-depth research on particular invasive species has uncovered many evolutionary and ecological processes, some of which have fed directly into general ecology and evolutionary theory; among others related to rapid evolution, range limits, effects of species on ecosystem processes and community assembly (Cadotte *et al.*, 2006; Sax *et al.*, 2007; Richardson, 2011a). For instance, different *Centaurea* species have become model species for understanding the role of coevolution in shaping coexistence patterns in plant communities (Callaway & Aschehoug, 2000; Callaway *et al.*, 2011) or climate niche shifts during invasions (Treier *et al.*, 2009; Hahn *et al.*, 2012; Petitpierre *et al.*, 2012).

The biological mechanisms underlying these processes can often only be thoroughly understood through specialised and costly

research that necessitates focus on a few model species. Research on *Alliaria* and *Centaurea* helped to elucidate the detailed mechanisms involved in allelopathic belowground plant–plant interactions. It has, for example, been shown that allelochemicals of *Alliaria* differ between genotypes, and their impacts on mycorrhiza and native plants are species specific, and shaped by the biotic and abiotic soil environment (Barto *et al.*, 2011; Lankau, 2011a,b). Studying the role of hybridisation and polyploidy in the invasion of *Spartina* species involved sophisticated molecular and genetic techniques (Ainouche *et al.*, 2009; Chelaifa *et al.*, 2010). Indeed, every new development in molecular ecology has exciting implications for uncovering key issues in invasion science, for example, as a means of understanding genetic constraints that hinder rapid evolution by studying the genetic architecture of different native and invasive populations (Lavergne & Molofsky, 2004; Colautti & Barrett, 2011). However, such focused and often expensive studies of underlying mechanisms are most fruitful once comprehensive knowledge about an invasive species and its invasion history is available; in the absence of such information it is difficult if not impossible to assess the relevance of detailed molecular variation for overall invasion dynamics.

Uncovering new processes Finally, those invasions that involve a change in behaviour of an organism following its introduction and are not simply the result of large-scale plantings (massive propagule pressure) or major anthropogenic habitat disturbances (often leading to relaxed inhibition from interactions with resident biota) in the new range, may be particularly useful for elucidating the role of established mechanisms, such as enemy release or rapid evolutionary change, in explaining the unexpected behaviour of invasive species. In-depth research on these invasions may also uncover unknown mechanisms and lead to improved models. However, we do not have good information to identify these cases. For instance, Firn *et al.* (2011) found that abundances of recognised herbaceous invaders in invaded communities were not on average higher than levels they achieve in their native ranges (see also Parker *et al.*, 2013). Information on novel behaviour in the introduced range can also not be inferred from the few existing accounts of particularly problematic invaders (e.g. Weber, 2003). A necessary first step, therefore, is to filter existing data to identify such cases of novel behaviour.

The likelihood that new patterns and processes are detected might also be particularly high when choosing model organisms from a broad range of different taxonomic groups or geographic regions (Pyšek *et al.*, 2008; Hulme *et al.*, 2012; Jeschke *et al.*, 2012b) and from different types of invasion dynamics including rare invasions in habitats relatively unaffected by plant invasions such as undisturbed forest (Martin *et al.*, 2009), or failed invasions (Zenni & Nuñez, 2013). A diversity of model systems will also minimise the risk of biases introduced through an unrepresentative sample of model organisms (Travis, 2006; Bolker, 2012; Strayer, 2012).

2. Model ecosystems

The ecosystem equivalent of model organism research is place-based long-term ecological research (Hobbie *et al.*, 2003; Billick &

Price, 2011). Thus, ‘model ecosystem’ refers to the ecological context of invasions at a particular site that is studied in detail. Most long-term ecological research sites are situated in (relatively) undisturbed and often uninvaded sites (see <http://www.ilternet.edu>, accessed 20 June 2013). In invasion science, in-depth studies of invaded ecosystems focus mostly on sites dominated by a single dominant invader – we have discussed examples of such studies in the section on model organisms above. Therefore, in-depth place-based studies of the multifarious and longer term dynamics of ecosystems affected by multiple invaders are mostly lacking. Such studies are, however, important to understand shifts in dominance of alien species, possibly leading to alternative stable states (Fike & Niering, 1999; Simberloff & Gibbons, 2004; Simberloff, 2006; Strayer *et al.*, 2006; Hobbs *et al.*, 2007; D’Antonio *et al.*, 2011; Weller *et al.*, 2011; Strayer, 2012), and interactions among multiple invaders and resident biota, including indirect effects and effects of less abundant alien species (Meiners *et al.*, 2002; Strayer *et al.*, 2006; White *et al.*, 2006; Kueffer & Daehler, 2009; Peltzer *et al.*, 2009; Hulme *et al.*, 2012; Strayer, 2012; Hobbs *et al.*, 2013).

Most studies of long-term invasion dynamics either compare patterns between only a few sampling periods in time or are chronosequence studies that compare invasions of different age across sites (Strayer *et al.*, 2006). While such studies are useful, they have important limitations. They do not yield continuous time series and may therefore miss the importance of land-use legacies (Stromberg *et al.*, 2009), inter-annual variability (Cleland *et al.*, 2004), population fluctuations (Fike & Niering, 1999; Carlsson *et al.*, 2010), or events such as fires (D’Antonio *et al.*, 2011), floods (Parendes & Jones, 2000), anthropogenic disturbances (Hobbs & Humphries, 1995; Parendes & Jones, 2000) and weather extremes (Hobbs *et al.*, 2007) and hurricanes (Thompson *et al.*, 2007) that affect invaded ecosystems. An emerging challenge is also to understand the role of gradual changes of regional species pools and environmental factors – through climate change, nutrient deposition, land use changes and other global change – in determining invasion trajectories (e.g. Smith *et al.*, 2009). In model ecosystem sites it will often be possible to reconstruct past dynamics through the combination of multiple quantitative and qualitative data sources. More importantly, comprehensive monitoring of model ecosystems will in the future help to detect unexpected dynamics that will increasingly happen in ecosystems characterised by novel species composition and global change; a rationale that led to the formation of the emerging research field on ‘novel ecosystems’ (Hobbs *et al.*, 2013).

Forestry research in Puerto Rico provides a unique example of in-depth place-based research on such emerging novel ecosystems. Through many decades of research the emergence of a landscape mosaic of novel types of forests with new species compositions, plant–plant and plant–animal interactions, and ecosystem processes and characteristics has been documented that are co-determined by land use legacies, climate, soil factors, disturbances such as hurricanes, and local species pools (e.g. Lugo, 2004; Thompson *et al.*, 2007; Brokaw *et al.*, 2012). Thanks to such comprehensive research Puerto Rico has become an important model in debates about novel ecosystems, and conservation in the tropics and on islands.

Similar in-depth studies are missing from most other types of alien species-influenced and human-modified ecosystems. Ecologists working on invasions, restoration, global change and ecosystem succession need to join forces to establish long-term ecological research sites in novel ecosystems characterised by major past and current anthropogenic disturbances and where alien species are well represented (compare Robertson *et al.*, 2012). These should cover a broad range of different types of novel ecosystems including those involving shifts in disturbance regimes (e.g. grasslands affected by fire cycles), habitat transitions (e.g. grassland–forest transitions), habitats that are comparable across biogeographic regions (e.g. riparian or Mediterranean), and habitats that may become more vulnerable to anthropogenic changes in the future (e.g. as yet relatively undisturbed habitat such as mountain ecosystems) (for more information see Table S1). Indeed, most established long-term ecological research sites will increasingly be novel in the future, and invasion scientists are starting to exploit information from existing long-term studies (e.g. Parendes & Jones, 2000; Cleland *et al.*, 2004; Hobbs *et al.*, 2007). Often it will also be particularly fruitful to associate long-term studies with conservation management activities and design them as part of adaptive management (e.g. Foxcroft & Freitag-Ronaldson, 2007; Kueffer *et al.*, 2010b; Weller *et al.*, 2011; Florens & Baider, 2013; Hobbs *et al.*, 2013). We expect that such place-based research on invaded and human-modified ecosystems might develop into a major new

research avenue over the coming years and might greatly help to overcome the suggested dissociation between invasion science and succession and restoration ecology (Davis *et al.*, 2001; Hobbs & Richardson, 2011; Prach & Walker, 2011).

IV. Multi-site studies: evaluating context-dependencies

Research on particular model organisms or ecosystems must be complemented with comparative research across a broad range of study systems to evaluate how widely the knowledge gained from a particular model system may be applied. Thanks to an increasingly interconnected global research community, such multi-site studies are rapidly becoming more feasible (Sagarin & Pauchard, 2012; Fraser *et al.*, 2013).

1. Multi-site studies with a species-focus

Until recently, few studies had compared the invasive behaviour of the same species across multiple sites, although available data suggest that the demography and ultimately fitness ('invasiveness') and effects on the environment of populations may be highly variable at different sites (Kueffer *et al.*, 2010a; Drenovsky *et al.*, 2012; Pyšek *et al.*, 2012; Richardson & Pyšek, 2012) (Fig. 2). Such differences in invasion dynamics between sites might stem from

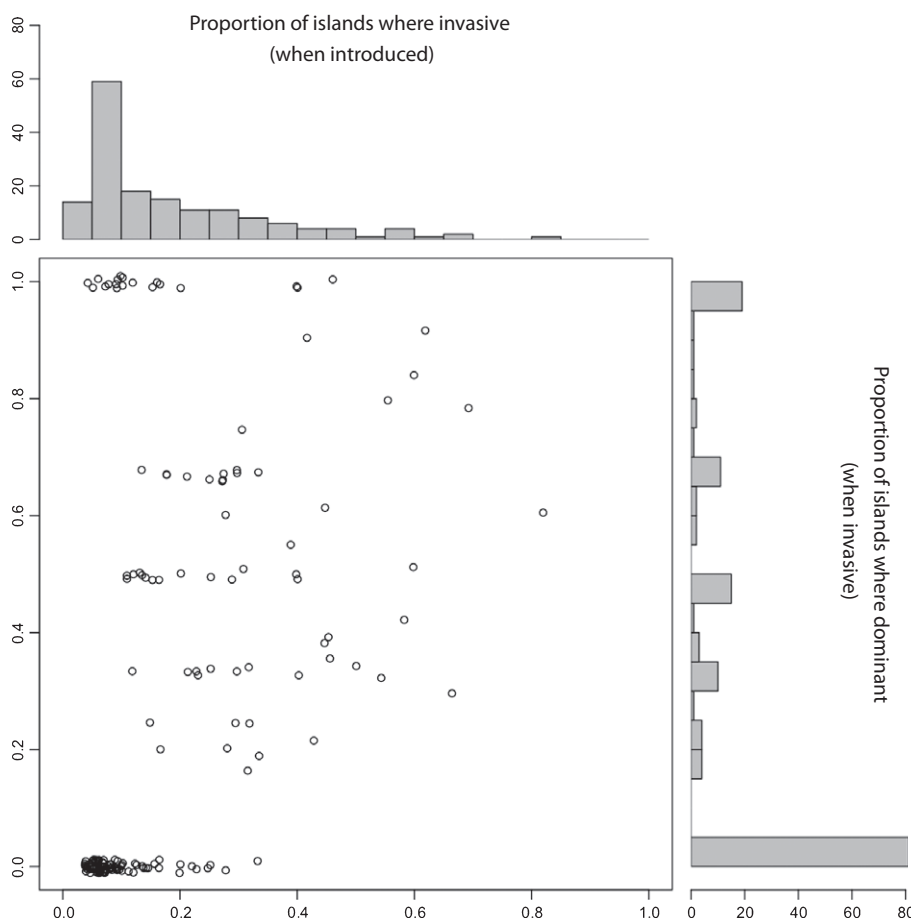


Fig. 2 Consistency of invasive behaviour across (sub)tropical islands worldwide. For 30 island archipelagos lists of introduced, invasive (> 5% maximal cover in natural areas) and dominant invasive alien plants (> 25% cover) were compiled (Kueffer *et al.*, 2010a). Data is shown for the 159 species that are present on at least 10 islands. The x-axis shows the proportion of islands where an introduced species became invasive, and the y-axis the proportion of islands where an invasive species became dominant. Histograms show the number of species per classes of a width of 0.05. Each dot in the scatter plot represents a species.

(1) the variability of the biology of a species between sites – through genetic differentiation and/or phenotypic plasticity; (2) species \times environment interactions – for example, fitness of an invasive species under certain abiotic conditions or presence of a particular enemy; or (3) contingencies of the invasion history such as differences in past human-mediated introduction or management efforts (Richards *et al.*, 2006; Drenovsky *et al.*, 2012; Strayer, 2012; Kueffer, 2013). Comparing a species across multiple sites acknowledges that *populations* (often representing different genotypes), and not species, become invasive (Parker *et al.*, 2013).

More studies that compare the biology of a species in native and invaded ranges are needed (van Kleunen *et al.*, 2010a), because such insights form the baseline necessary for drawing conclusions about the importance of the alien origin of species in invasions (Parker *et al.*, 2013). Given the variation in performance of a species' populations at sites within both native and invaded range, studies that compare data only from one site from each range are very likely to arrive at spurious conclusions, especially when populations are sampled from different habitats or different, and sometimes limited, parts of broad environmental gradients (Colautti *et al.*, 2009; Moloney *et al.*, 2009) (Fig. 3). Indeed, invasive species are generally abundant only in part of their potential (climatically suitable) range (Bradley, 2013). Consequently, studies should involve field observations or experiments from multiple sites distributed across complete environmental gradients in both

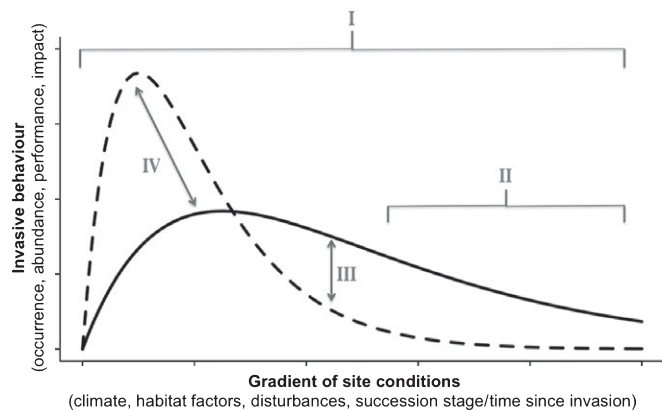


Fig. 3 Accounting for environmental gradients in comparative studies in invasion science. Different types of comparisons (e.g. of the same species in the native and introduced range, or between native and invasive species in the introduced range, for a comprehensive overview of possible comparisons see van Kleunen *et al.*, 2010a) are central to invasion science. However, these must account for variation of species behaviour across environmental gradients. The figure shows two hypothetical response curves of, for instance, the same species in the native and introduced range across a gradient of site conditions (in reality these may be multiple interacting gradients in multidimensional space; and they need not be gradual, e.g. different habitat types). There are different valid comparisons that can be made and specifying them is important in any study that aims to detect a novel behaviour of a species: the response curves can be compared across complete environmental gradients (I) or across a subsection that is relevant for a particular research question (i.e. a particular theoretical domain, e.g. only undisturbed habitat, II). Alternatively, invasions of sites characterised by the same conditions (e.g. early invasion stages in tundra habitat, III) or maxima in both ranges (IV) might be compared. Arbitrary comparisons that do not control for comparable site conditions can come to widely varying conclusions and therefore yield spurious results.

ranges; or clearly specify the type of comparison that is being made to detect the novel behaviour of a species (Fig. 3). Such comprehensive data are especially needed also from the native range, because only a thorough understanding of abundance patterns (Firn *et al.*, 2011), trait variation (Hornoy *et al.*, 2011) and ecological interactions (Hierro *et al.*, 2005) in the native range facilitates detection of novel behaviour in the invaded range (Fig. 3). One example of a comprehensive comparative effort is the 'Global Garlic Mustard Field Survey' (www.garlicmustard.org), which measured performance of *Alliaria petiolata* across almost 400 sites in both its introduced and native ranges (Colautti *et al.*, 2013). Genotypes included in common-garden experiments must also be collected from many different populations in both ranges (Alexander *et al.*, 2012; Kumschick *et al.*, 2013). The knowledge of the invasion history of particular populations should form the basis for a targeted selection; if such information is not available, then random sampling of genotypes is preferable (Richards *et al.*, 2006).

Some multi-site studies found consistent behaviour between native and invaded ranges (e.g. Erfmeier & Bruelheide, 2004; Herrera *et al.*, 2011; Moroney & Rundel, 2013), but often the variation within ranges is more pronounced than differences between ranges (e.g. Edwards *et al.*, 1998; Maron *et al.*, 2004; Pergl *et al.*, 2006). For instance, differences in the population ecology of *Heracleum mantegazzianum* between the native and invaded range are minor once differences between ranges in climate and land use are accounted for (Pergl *et al.*, 2006). Meaningful comparisons need to examine many sites per range because of such large within-range variation. For instance, although Moroney & Rundel (2013) found, on average, higher relative abundances of *Centaurea melitensis* in two introduced ranges (California and central Chile) than in the native range (Spain), some sites with the lowest dominance were in an introduced range. Also, one (out of five) high-density population was in the native range. Biased selection of study sites can (and probably has in many past studies) lead to spurious results (Fig. 3).

The impacts of invasive species are also strongly co-shaped by species \times environment interactions (Hulme *et al.*, 2012; Pyšek *et al.*, 2012) which can only be understood through comparative studies across sites. Nitrogen availability on young volcanic flows in Hawaii invaded by the nitrogen-fixing tree *Falcataria moluccana* was up to 121-times higher than in native stands. Phosphorus availability also increased, which, in turn, facilitated the invasion of other alien species such as *Psidium cattleianum* (Hughes & Denslow, 2005). By contrast, the invasion of *Falcataria* on very phosphorus-poor soils in the Seychelles did not increase soil nitrogen or phosphorus, or the growth of juveniles of other alien species (Kueffer *et al.*, 2008; Kueffer, 2010a). Similar opposing effects on soils depending on invaded site were, for instance, found for *Bromus tectorum* invasion in the USA, *Hieracium pilosella* invasion in New Zealand, and *Carpobrotus edulis* invasion on Mediterranean islands (Hulme *et al.*, 2012).

2. Multi-site studies with an ecosystem-focus

In order to move towards generalisation of knowledge about the vulnerability of ecosystems to invasions it is useful to perform

comparative research in the same ecosystem types across multiple sites. This requires measures of the level of invasion to be standardized across sites (Catford *et al.*, 2012). What is ideally defined as an ecosystem type for such comparisons depends on the research question. It can be useful to employ a narrow definition of an ecosystem type (e.g. arid grasslands invaded by *Bromus* species in North America) or a much broader one (e.g. arid grasslands anywhere in the world and invaded by any type of invasive species). Only such multi-site studies can help to disentangle the role of different factors such as propagule pressure, composition of regional alien and native species pools, disturbances, variation of abiotic factors, land use legacies, or landscape matrix in determining ecosystem invasibility and the ecology of invaded ecosystems (Richardson *et al.*, 1994).

As discussed above, some secondary successions of invaded tropical forest in Puerto Rico led to mixed native–alien forests in which native biodiversity is well represented (Lugo, 2004). Indication for the coexistence of native and alien species was also found for other invaded island ecosystems including some forests in the Seychelles and the Galapagos islands (Jaeger *et al.*, 2009; Kueffer *et al.*, 2010b). However, in other cases invasive plant dominance persisted over the long term and native island biodiversity recovered only after removal of the dominant alien tree; for example, in the case of invasions of *Psidium cattleianum* in Mauritius (Baider & Florens, 2011), *Miconia calvescens* in French Polynesia (Meyer & Fourdrigniez, 2011) and *Leucaena leucocephala* in Puerto Rico (Wolfe & Van Bloem, 2012). Understanding the reasons for these differences through multi-site comparative research would be of major relevance for island conservation.

New opportunities for such research across multiple ecosystems are opening as ecology enters an age of global collaboration through research networks and data-sharing (Hobbie *et al.*, 2003; Coleman, 2010; Sagarin & Pauchard, 2012). In the next section we will

discuss new perspectives for meta-analysis of emerging large datasets across ecosystems, while this section focuses on coordinated multi-site research (Sagarin & Pauchard, 2012; Fraser *et al.*, 2013; Kueffer *et al.*, 2013b). Such comparative research across multiple sites involves performing standardised observational or experimental research focused on specific research questions across sites and collaborative interpretation of data by cross-site teams.

For example, a comprehensive multi-site study on the invasibility of mountains has recently emerged which illustrates how social and ecological factors can co-shape the invasibility of a particular type of ecosystem and how such interactions can be elucidated through multi-site studies (Fig. 4). Mountains have long been considered relatively resistant to plant invasions (cf. Pauchard *et al.*, 2009). Indeed, the number of alien plants in mountains decreases strongly with increasing elevation independent of continent or climate zone (Alexander *et al.*, 2011). Comparative research of invasion patterns across multiple sites around the world has revealed that these patterns can be understood by integrating information about introduction pathways, changing anthropogenic and abiotic factors along elevational gradients, and species characteristics (Kueffer *et al.*, 2013b). Alien floras of mountains comprise almost exclusively species with broad climatic tolerances, whereas mountain specialists are conspicuously lacking (McDougall *et al.*, 2011). This pattern can be explained by the fact that most past human introductions of alien plants were to low or mid-elevation sites; consequently only species with wide climatic tolerances that can establish at both low and high elevations are currently found in mountains (Alexander *et al.*, 2011). The influence of past introduction pathways means that alien mountain floras around the world comprise mainly European herbaceous species associated with agriculture (McDougall *et al.*, 2011). The high spatial and temporal (ice ages) climatic variability of temperate Europe has pre-adapted many of these species for spreading along climate gradients (Alexander *et al.*, 2011). Rapid evolutionary change might also be

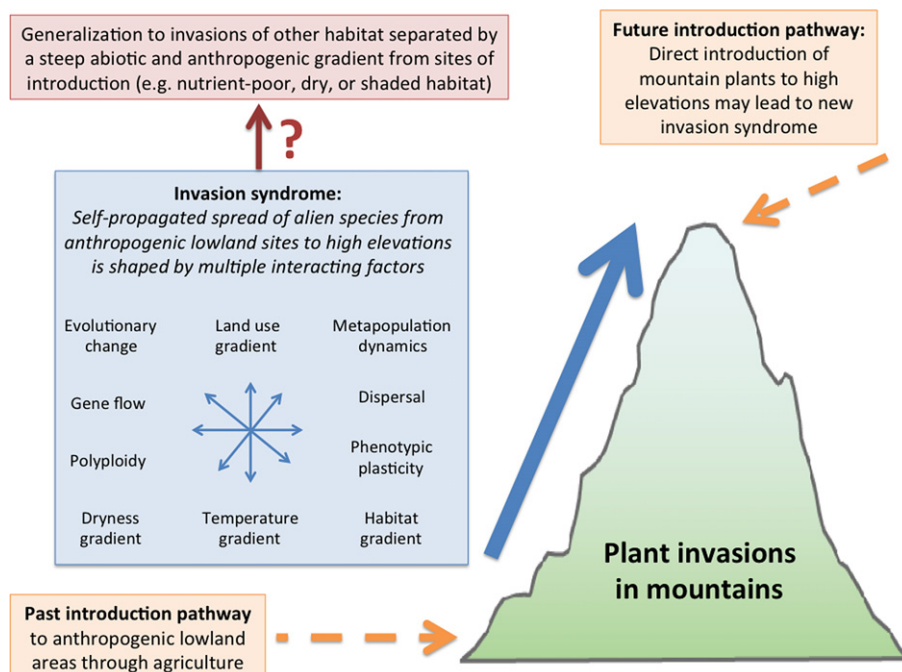


Fig. 4 Invasions in high-elevation sites in mountains often result from self-propagated spread of climatically plastic species along elevational gradients, from introduction sites in the human-modified lowlands to more natural habitats in the mountains with strongly contrasting abiotic conditions. Understanding these invasions requires an integrative grasp of species traits, and anthropogenic, ecological and evolutionary factors that facilitate such spread. These processes may also be relevant for understanding invasion in other habitats that are separated by a steep abiotic and anthropogenic gradient from sites of introduction; and may thus represent a generalizable invasion syndrome. However, mountain specialists are increasingly being introduced directly from native to alien mountain areas, and such changing introduction pathways may produce a new invasion syndrome – invasions of pre-adapted and deliberately introduced mountain plants.

important in enabling expansion to high elevations (Leger *et al.*, 2009; Monty & Mahy, 2009); this might explain why on Tenerife (Canary Islands) older introductions tend to reach higher elevations (Haider *et al.*, 2010). Understanding both the species and site characteristics that shape dynamics along elevational gradients is necessary to understand invasion patterns at high elevations (Kueffer *et al.*, 2013b).

However, mountain specialists are increasingly being introduced directly from native to alien mountain areas, and some of these species are highly invasive and have the potential to impact natural areas (McDougall *et al.*, 2011). Changing introduction pathways might lead to new invasions of pre-adapted and deliberately introduced mountain plants (Fig. 4). These species will have different traits, will experience different ecological and evolutionary dynamics, and will pose different threats to mountain biodiversity. Therefore, understanding land-use changes is crucial for anticipating future invasion risks in mountains (Kueffer, 2010b).

V. Focused meta-analysis: improving prediction through fine-tuning synthesis

Analyses of large datasets from different invasive species or invaded ecosystems compiled from the literature or gathered through coordinated efforts such as large multispecies experiments (Godoy *et al.*, 2010; Schlaepfer *et al.*, 2010) – meta-analyses in the broad sense – have become a backbone of invasion science. These are used to synthesise empirical information on (1) invasiveness and impact across species (Daehler, 2003; Liao *et al.*, 2008; Morales & Traveset, 2009; Van Kleunen *et al.*, 2010b; Vilà *et al.*, 2011; Godoy *et al.*, 2012; Pyšek *et al.*, 2012; Sorte *et al.*, 2013), (2) ecosystem invasibility (Lonsdale, 1999; Levine *et al.*, 2004; Chytrý *et al.*, 2009; Kueffer *et al.*, 2010a; Polce *et al.*, 2011), and to (3) investigate the role of mechanisms such as enemy release or phenotypic plasticity (Mitchell & Power, 2003; Vilà & Weiner, 2004; Chun *et al.*, 2010; Davidson *et al.*, 2011). In the next two paragraphs we posit that substantial progress in addressing these three types of questions through synthetic quantitative analyses requires a shift from opportunistic analyses of existing datasets (a shotgun approach) to a much more focused three-step methodology whereby: (1) the theoretical domain across which generalisations are made is objectively defined; (2) care is taken to use datasets that are appropriate for addressing particular research question and domains; and (3) multivariate analyses are appropriately applied to account for interactions and to avoid spurious conclusions due to confounding factors. Following such a strategy would, we suggest, allow us to advance from compiling lists of processes and mechanisms potentially implicated in invasions to an understanding of the relative importance of different mechanisms under different conditions, which is necessary to make invasion science more predictive.

1. Defining the theoretical domain

When generalising ecological knowledge it is crucial to explicitly specify the domain – that is, the phenomena such as organisms,

ecosystems, invasion phases, invasion mechanisms, as well as temporal and spatial scales – for which statements are meant to apply (Pickett *et al.*, 2007). Thus, synthetic analyses in invasion science must be constrained to appropriate subsets of invasions, rather than seeking universal explanations (Pyšek & Richardson, 2007; Jeschke *et al.*, 2012a; Kueffer, 2012). Indeed, meta-analyses generally reveal that no single explanation – such as enemy release, competitive superiority or physiological traits – applies to all invasions (e.g. Daehler, 2003; Blumenthal *et al.*, 2009; Cavaleri & Sack, 2010; Chun *et al.*, 2010; Jeschke *et al.*, 2012a; Moles *et al.*, 2012). For instance, those traits that are most frequent among invasive species across all life forms might not be relevant for predicting invasive species within a specific group of species (Fig. 5). Furthermore, insights gained from plant invasions are often not directly transferable to animals and *vice versa* (Jeschke *et al.*, 2012a,b).

The normal strategy is to focus on phylogenetically constrained groups at various taxonomic levels: different cultivars, hybrids or genotypes of the same species; or different species within a genus or family (Richards *et al.*, 2006; Pyšek & Richardson, 2007; Van Kleunen *et al.*, 2007; Richardson & Rejmánek, 2011). Taxonomically constrained comparisons can be combined with the source-area approach in which introduced or invasive species that originate from the same native source flora rather than those present in the same non-native target area are compared (Prinzing *et al.*, 2002; Pyšek *et al.*, 2004; van Kleunen *et al.*, 2010a). Ideally, reciprocal comparisons of invasions between source and target areas should be performed (Petitpierre *et al.*, 2012). However, important biases are often only weakly related to taxonomic patterns and other types of constraints must be defined to elucidate the limitations of particular comparisons. In particular, correlative studies are often biased by the unequal representation of different functional groups (Fig. 5), and especially by over-representation of species invading disturbed habitats (Pyšek *et al.*, 2004). It is thus not surprising that many studies of invasiveness identify the same traits as those described decades ago for weeds (Baker, 1974) – in most cases probably very broad sets of ‘general weediness’ characteristics that reflect the ability to tolerate and proliferate in the face of moderate levels of disturbance.

Ultimately the goal must be to understand which traits equip species to become invasive and problematic in different contexts (e.g. Daehler, 2003; Kueffer & Daehler, 2009; Drenovsky *et al.*, 2012). A first important consideration is that plants invading ecosystems with different abiotic and biotic conditions – such as temperate grasslands (Seastedt & Pyšek, 2011), Mediterranean-type ecosystems (Gaertner *et al.*, 2009), shaded forest understoreys (Martin *et al.*, 2009) or high-elevation sites in mountains (McDougall *et al.*, 2011) – are characterised by different traits that interact with the local environment in a different way. For instance, focussing on those life-history traits of invaders that are particularly important in early successional stages neglects the importance of traits that are important at late-successional stages and those associated with stress-tolerant species that are problematic invaders of resource-poor or undisturbed habitat (Martin *et al.*, 2009). There is also a growing interest in understanding the factors that determine invasion success in different invasion phases such as

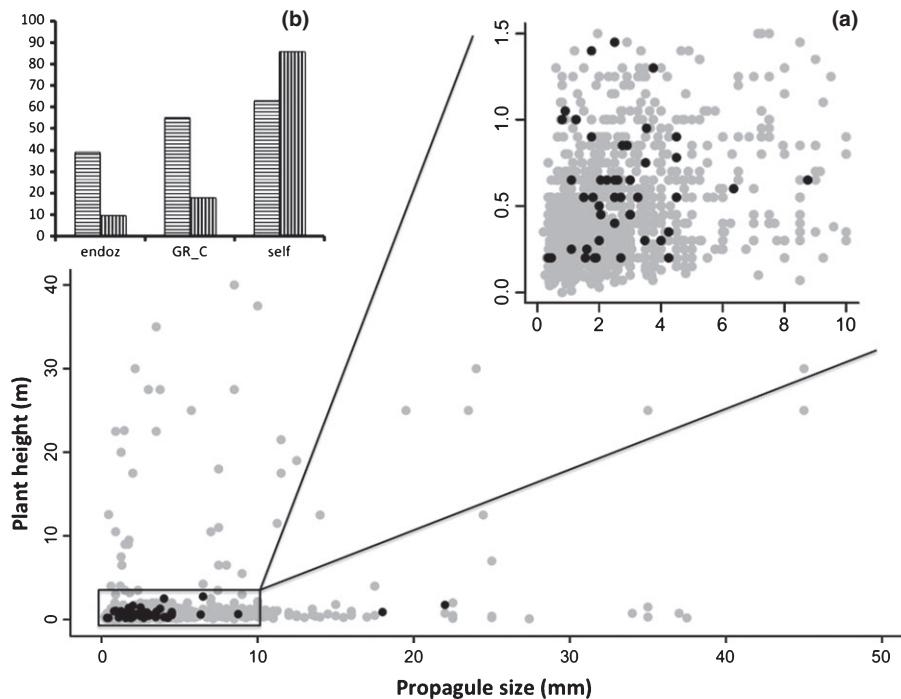


Fig. 5 The need for more focused meta-analysis in invasion science. For 1389 species native to central Europe that are reported as alien in other parts of the world, documented by at least 10 records in the Global Weed Database (Randall, 2002), plant height and propagule size was compiled (from Pyšek *et al.*, 2009a). Species for which weedy behaviour was recorded in at least 33% of all records are shown in black (53 species), other species in grey. Within this dataset, weedy species are clustered among herbs and short shrubs, and species with smaller propagules. However, 80% of species in the dataset are shorter than 1.5 m and have propagules smaller than 10 mm in diameter ('small species' as opposed to 'large species'); for these species neither of the two traits is a good predictor of weediness (inset a). Constraining analysis to this subset of species may also be important because frequency of traits is correlated with groups (see e.g. inset b, percentage representation among small (bars, vertical stripes) and large (bars, horizontal stripes) species for endozoochory ('endoz'), competitor growth strategy *sensu* Grime ('GR_C'), and ability for self-pollination ('self')).

introduction, establishment, naturalization, spread, or invasion and impacts (Dietz & Edwards, 2006; Williamson, 2006; Theoharides & Dukes, 2007; Gravuer *et al.*, 2008; Hanspach *et al.*, 2008; Milbau & Stout, 2008; Chrobok *et al.*, 2011; Richardson & Pyšek, 2012). Indeed, dispersal pathways strongly affect invasion processes (Wilson *et al.*, 2009), and the invasiveness of alien species dispersing along different pathways must therefore be analysed separately (Kueffer, 2012). For instance, unintentionally introduced species must be able to establish from small founder populations often characterized by low genetic diversity. Many such species depend on effective dispersal mechanisms and broad ecological amplitude to spread without deliberate human assistance across heterogeneous landscapes from anthropogenic sites of introduction to natural areas. However, many other invasive plants became invasive thanks to large-scale deliberate planting close to the areas that they eventually invade (Křivánek *et al.*, 2006; Kueffer, 2013). Invasive species in this category depend less on traits facilitating establishment and spread. Lastly, in order to make risk assessment more relevant for management it is particularly important to understand whether the same traits that are associated with invasiveness also determine impact (Drenovsky *et al.*, 2012; Pyšek *et al.*, 2012). There is growing evidence that transformer species (*sensu* Richardson *et al.*, 2000) have different traits than less problematic colonisers of natural areas (Kueffer *et al.*, 2010a; Speek *et al.*, 2011).

We see two strategies for constraining meta-analysis to address issues like those discussed above. First, existing data can help to identify context-dependencies and appropriate domains for generalisation. To date, meta-analyses often aim at identifying general trends and highlight those cases where differences between study groups (e.g. native vs invasive species) are the most consistent and pronounced. However, it may often be more useful to address cases where within-group variation is higher than between-group differences and investigate the reasons for such inconsistency. Indeed, meta-analyses that use such an approach have yielded important insights. For instance, Daehler (2003) found that native species often outperformed invasive species under low resource (nutrients, light, water) conditions. Cavaleri & Sack (2010) concluded that differences in water use by native and invasive species depended strongly on climate, with enhanced water use of invasives (in particular) in hotter, wetter climates. A related strategy is to utilise existing data and knowledge to formulate more specific hypotheses and to sharpen the focus of meta-analyses. Studies of the enemy release hypothesis, for instance, led to a rich understanding of the interrelated factors that co-shape the role of enemy release in plant invasions including habitat conditions such as shade (DeWalt *et al.*, 2004), high nutrient concentrations (Blumenthal, 2006; Blumenthal *et al.*, 2009), tolerance of enemy attack (Chun *et al.*, 2010), differences between functional groups of enemies (Agrawal *et al.*, 2005; Joshi & Vrieling, 2005), residence time (Hawkes,

2007), stages in population dynamics (Williams *et al.*, 2010) or rapid evolution (Müller-Schärer *et al.*, 2004). Such information needs to be more cleverly applied for designing and interpreting meta-analysis. For instance, the hypothesis that the effect of enemy release is more pronounced in fertile habitats was confirmed through a quantitative analysis across several hundred species (Blumenthal *et al.*, 2009).

2. The use of balanced datasets and multivariate analysis to avoid biases

Within domains of study, datasets should be comprehensive and balanced, so as to cover all relevant types of invasion. To date, available data on invasions is heavily skewed towards particular taxonomic groups and geographic regions, introducing a severe bias to analyses (Pyšek *et al.*, 2008; Hulme *et al.*, 2012; Jeschke *et al.*, 2012b; Strayer, 2012). Compiling more comprehensive and balanced datasets will be more achievable for focused meta-analysis, especially as new data sources are emerging including open-access data depositories (Sagarin & Pauchard, 2012), large-scale networks of field sites (e.g. Polce *et al.*, 2011), large data collection efforts such as multispecies studies (Godoy *et al.*, 2010; Schlaepfer *et al.*, 2010) and collaborative research across multiple sites (Colautti *et al.*, 2013; Fraser *et al.*, 2013; Kueffer *et al.*, 2013b).

Finally, it is usually not a single factor but a combination of traits that explains the invasiveness of species. Consequently, more attention must be given to analyses of multivariate datasets (Gravuer *et al.*, 2008; Küster *et al.*, 2008; Pyšek *et al.*, 2012). This approach can reveal how the importance of one species trait for invasiveness depends on other traits and factors (Küster *et al.*, 2008; Pyšek *et al.*, 2009a) as well as scale (Hamilton *et al.*, 2005), and will help to understand the role of confounding factors such as propagule pressure or introduction history (Lonsdale, 1999; Wilson *et al.*, 2007; Bucharová & van Kleunen, 2009; Pyšek *et al.*, 2009b). Thorough studies that take account of many possible factors and their interactions will make it possible to improve the predictability of impacts and accuracy of weed risk assessment schemes (Hulme *et al.*, 2012; Pyšek *et al.*, 2012).

VI. Invasion syndromes: advancing theoretical integration

We think that overcoming one weakness of past invasion science might help to greatly advance theoretical integration in the field. Invasion science has classically focussed in two separate directions: invasiveness of species and invasibility of ecosystems (Fig. 1). The impressive accumulation of information on these two aspects has paved the way for much progress in the field, but ultimately it may be of limited use to gain and generalise insights separately for species and ecosystems (Richardson & Pyšek, 2006; Kueffer & Daehler, 2009; Drenovsky *et al.*, 2012). Rather, recurrent patterns of species \times ecosystem interactions may be a more appropriate focus of study; we call these patterns 'invasion syndromes'. According to the Merriam-Webster dictionary a syndrome is 'a set of concurrent things that usually form an identifiable pattern'. Seed dispersal syndromes – correlations between seed/fruit traits

and animal disperser traits (van der Pijl, 1982) – might come first to the mind of an ecologist when she/he reads the term. Similarly, invasion scientists have previously used the term syndrome to denote the co-occurrence of different traits that together characterise invasive species (e.g. Hobbs & Humphries, 1995; Lloret *et al.*, 2005; Schmidt *et al.*, 2012). We propose expanding the concept of 'invasion syndrome' to encompass 'typical recurrent associations of species biology and invasion dynamics with particular invasion contexts such as an invasion stage, invaded habitat and/or socioeconomic context'.

The example of plant invasions in mountains discussed above (section IV.2 Multi-site studies with an ecosystem focus and Fig. 4) illustrates the usefulness of the invasion syndrome concept. Understanding mountain invasions requires an integrative grasp of species traits, and anthropogenic, ecological and evolutionary factors that enable self-propagated spread of species along steep climate gradients (Kueffer *et al.*, 2013b). Such a scenario might more generally help to understand invasion risks of habitats generally considered resistant due to harsh abiotic conditions, for example, shaded forest understoreys (Martin *et al.*, 2009), or nutrient-poor or dry ecosystems (Alpert *et al.*, 2000). In all of these cases alien species have to spread along steep environmental gradients from anthropogenic introduction sites that are rich in resources and/or characterised by a favourable climate, to recipient habitats that are geographically isolated and characterised by strongly contrasting abiotic conditions. Considering these invasions together as one invasion syndrome might help to gain general insights across the different cases, for example, about the role of phenotypic plasticity, rapid evolution or enemy release in enabling alien species to grow under strongly contrasting abiotic conditions, and about how impacts of species that colonize a habitat in an environmentally contrasting landscape matrix differ from those of pre-adapted species that were directly introduced to a particular habitat. This approach will also have important implications for management: harsh environments might not be inherently resistant to invasions, rather invasion risks might increase greatly once habitat specialists are directly introduced to these habitats (Bossdorf *et al.*, 2008; Martin *et al.*, 2009; Kueffer, 2010b). Consequently, we suggest that a focus on the process of spread along steep environmental gradients from anthropogenic sites of introduction to environmentally contrasting sites of invasion – which might be termed the 'spread along steep environmental gradients' syndrome – will help to generalise insights across invasions that might else be considered unrelated such as those in mountains and in shaded forest understoreys. Invasion syndromes also help to separate different scenarios that result in invasions of the same habitat. In particular, the direct introduction of pre-adapted species to a harsh environment is not part of the 'spread along steep environmental gradients' syndrome because it involves very different ecological processes and represents different invasion risks. In summary, invasion syndromes are a means for defining appropriate theoretical domains for generalisation in invasion science.

We hope that the concept of invasion syndromes can advance theoretical integration in other situations characterised by recurrent associations of species ecologies, habitat characteristics and socioeconomic factors, for example, invasion risks resulting from alien

tree plantations (Richardson, 1998, 2011b; Richardson & Rejmánek, 2011), restoration programmes of degraded land (e.g. on islands, Woodcock, 2003; Kueffer *et al.*, 2010a), the horticultural trade (Dehnen-Schmutz *et al.*, 2007; Hanspach *et al.*, 2008; Chrobock *et al.*, 2011) or the planting of novel biofuel crops on marginal land (Barney & DiTomaso, 2008; Davis *et al.*, 2010). In each of these cases a functionally and taxonomically biased group of species is involved, the invaded habitat is characterised by particular biotic and abiotic conditions, and the location, magnitude, timing and characteristics of human-assisted species introduction and dispersal are similar.

VII. Conclusions

Since the 1980s, invasion science has grown to become one of the most active research directions in ecology. Our objective in this article was to outline a research strategy that builds on the strengths of past invasion science – especially its broad interdisciplinary scope and use of invasions as natural experiments that allows for studying multivariate processes under field conditions and across multiple sites and scales – but which circumvents some of the weaknesses of past approaches. Significant advances, both in terms of improving the fundamental understandings of the processes driving invasions and in achieving better guidelines for management, call for a multi-pronged approach that recognises the complexity of invasions and combines in-depth studies on particular model systems with cross-site comparisons, focused meta-analyses that aim at generalising knowledge for well-specified theoretical domains, and a better integration of species-focused and ecosystem-focused research. We hope that our framework will trigger new interest, especially among graduate students, in projects that: (1) comprehensively study different aspects of a particular invasive species or invaded ecosystems; (2) expand the scope of comparative multi-site studies by building on the emerging research opportunities that the increasingly global and more closely inter-connected research community provide; or (3) treat in-depth a particular mechanism such as the role of novel weapons or hybridisation by comparing its importance and functioning between different theoretical domains (e.g. different organisms or ecosystems) through sophisticated data synthesis.

We expect that these different approaches in concert will help to move invasion science forward in several important ways. For example, by moving away from the unrealistic aim of making robust generalisations for all types of invasions the proposed approach has the potential to provide a better understanding of those invasion patterns that have (so far) been less frequently addressed. This will enhance the implementation of effective preventive action against future invasion risks that require an understanding of specific factors that drive rare or emerging, yet often highly problematic, invasions. These include those in less invaded habitats (e.g. undisturbed or geographically/ecologically marginal habitat), as well as invasions whose impacts may materialize only over the longer term. The approach we advocate also paves the way for the objective formulation of diverse management strategies, ranging ‘from complete eradication to tolerance and even consideration of the ‘new’ species as an

enrichment of local biodiversity and key elements to maintain ecosystem services’ (Walther *et al.*, 2009). Evaluating such alternative management scenarios and informing controversies among experts and stakeholders requires an integrative understanding of the multiple interacting factors, including socioeconomic ones, and their underlying mechanisms that determine the dynamics of particular invasions. Invasion science has identified a catalogue of mechanisms that potentially mediate invasions (Catford *et al.*, 2009). These are often used relatively arbitrarily in constructing *post hoc* explanations of past invasions, but their predictive power remains low. Better predictions rely on an improved understanding of the conditions that make particular mechanisms, such as enemy release, influential – and of how such factors interact with others to mediate invasions. In this review we have focused on plants, but an important implication of our article is that new breakthroughs in invasion science could arise through comparative studies of different types of organisms including alien plants, animals, pathogens, GMOs and spreading native species (Pyšek *et al.*, 2008; Jeschke *et al.*, 2012a,b, 2013).

By taking this avenue of research invasion science could become an important model for integrative research in ecology in general. Combining macroecology with mechanistic research, exploiting natural experiments and building generalised knowledge from multiple in-depth organism-centred or place-based studies are research strategies that are of increasing importance for ecology and conservation science.

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Additional supporting information may be found in the online version of this article.

Table S1 Interesting model systems for invasion science

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