

The problem of prediction in invasion biology

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Abstract Invasion biology is a relatively young discipline which is important, interesting and currently in turmoil. Biological invaders can threaten native ecosystems and global biodiversity; they can incur massive economic costs and even introduce diseases. Invasion biologists generally agree that being able to predict when and where an invasion will occur is essential for progress in their field. However, successful predictions of this type remain elusive. This has caused a rift, as some researchers are pessimistic and believe that invasion biology has no future, whereas others are more optimistic and believe that the key to successful prediction is the creation of a general, unified theoretical framework which encompasses all invasion events. Although I agree that there is a future for invasion biology, extensive synthesis is not the way to better predictions. I argue that the causes of invasion phenomena are exceedingly complex and heterogeneous, hence it is impossible to make generalizations over particular events without sacrificing causal detail. However, this causal detail is just what is needed for the specific predictions which the scientists wish to produce. Instead, I show that a limited type of synthesis (integration of data and methods) is a more useful tool for generating successful predictions. An important implication of my view is that it points to a more pluralistic approach to invasion biology, where generalization and prediction are treated as important yet distinct research goals.

Keywords Invasion biology · Ecology · Prediction · Integration · Philosophy of science · Philosophy of ecology

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Introduction

Around the beginning of the nineteenth century, the giant African land snail *Achatina fulica* began its first of many invasions (Civeyrel and Simberloff 1996). By the 1950s, partly aided by the Japanese army during WWII, it had reached China, North and South America. In addition to consuming incredibly large amounts of plant matter, this snail is also a host for a number of organisms which cause disease in agricultural animals and humans (Thiengo et al. 2007). Consequently, when it reached the Pacific Islands in the 60s, there was great concern. It was decided that the best way to deal with this threat was to introduce predatory snails, including the species *Euglandina rosea*. Sure enough, the population of *A. fulica* declined and for a short while, the project was deemed successful. Unfortunately, this success was short-lived. Scientists subsequently found that the rapid decline in *A. fulica* had little to do with the introduction of *E. rosea*. As it turns out, *A. Fulica* populations often crash after their initial population boom. In addition, instead of preying on the giant African snail, *E. rosea* preferred the native snail species and decimated many native populations. In the end, *E. rosea* became a successful invader in its own right, while some scientists think that it has caused much more devastation on native ecosystems than the species it was intended to control (ibid).

This story exemplifies the problem of prediction in invasion biology, as it shows both how difficult it is to predict the outcome of an invasion, but also how making mistakes in predictions can result in serious problems. The first mistake was the overestimation of the scope of the *A. fulica* invasion and the second was the prediction that *E. rosea* would not itself become an invader. Unfortunately, the snails' sad tale is not a one-off case; indeed, the history of invasion biology is often a litany of misjudgements, error, and disaster. It is generally agreed that the science of invasion biology is not able to predict the outcome or scope of invasion events (Hayes and Barry 2007; Lodge 1993), despite the fact that we have extensive knowledge of the mechanisms of invasion (Dunstan and Johnson 2007; Jarchow and Cook 2009; Weiner 2004), the process of invasion (Blackburn et al. 2011) and the harmful effects of invasions (Jeschke et al. 2012).

In fact, the mismatch between the knowledge of how and why invasions occur and the inability to predict them is a persistent source of criticism of the entire discipline of invasion biology. Some of this criticism is external to the field, and comes from governmental agencies and other policy-makers, who often feel that they need more precise and accurate guides for their decisions concerning allocation of funds for research and management of invasions (National Research Council 2002; Shrader-Frechette 2001; Simberloff 2009). Even though successful invasions are costly,¹ they are actually quite rare, as very few of the species introduced to a new area actually succeed in invading (Zenni and Nuñez 2013), hence it would be extremely useful to be able to determine beforehand which of the potential invasions will actually succeed.

¹ According to the National Research Council, "[t]he aggregate figure for crop and timber losses and for the use of herbicides and pesticides to fight invasive species exceeds \$100 billion per year", in the USA (National Research Council 2002, p.15). This figure is restricted to crops and does not include the funds spent on managing invasions of natural ecosystems.

Some might think that asking for *highly specified* prediction is simply too much of an ask for the sort of science invasion biology is. Given the complexity of the subject matter, after-the-fact explanations and vague prognostication might be the best we can hope for. Perhaps surprisingly, a number of invasion biologists adopt this position and are quite pessimistic about the ability of their science to successfully make highly specified predictions. Some even take this to mean that there is no real future for invasion biology as a scientific (Simberloff and Vitule 2013; Williamson 1999).² However, I will put this pessimistic argument to one side, in part because of the applied nature of invasion biology—being able to predict when and where invasions will occur matters—and because I think there is something invasion biologists can do to make better predictions.

The alternative approach, from within in the field, is to argue that the situation can be remedied, provided that invasion biologists achieve greater ‘synthesis’ in their field. There are many proposals for how this can be achieved, ranging from large-scale syntheses of theoretical frameworks (Gurevitch et al. 2011) to smaller-scale syntheses of data and methods (Vitousek 1990).

In this paper, I will argue that extensive synthesis is not the key to achieving better predictions. I will start by identifying *causal heterogeneity* as an important source of difficulty for making predictions that are both specific and accurate. I will then examine the invasion biologists’ calls for *synthesis* in a philosophical light, employing O’Malley and Soyer’s distinction between different types of *integration* in biology (O’Malley and Soyer 2012). Illustrating with examples from current bioinvasion research, I will show that some kinds of synthesis are much too extensive and result in overgeneralizations which are of limited usefulness, especially when it comes to prediction. If invasive systems are causally heterogeneous—which undoubtedly they are—then aiming for a unified synthesis is no way to make better predictions. Finally, I will argue that a much more constrained approach to synthesis, exemplified by a study of pine invaders, is much more promising for the improvement of predicting bioinvasions.

Why is prediction a problem in invasion biology?

There are two issues which need to be addressed if we are to fully understand and appreciate the problem of prediction in invasion biology. The first is the notion of ‘prediction’, as it is used in the field. In invasion biology, ‘predicting an invasion’ means determining when/where a particular organism will succeed in invading a particular environment. This is a quite narrow conception of prediction, one which precludes less specific predictions such as qualitative trends etc. In fact, this focus on specific predictions is part of the reason why predictions are a problem in invasion biology.³

² In recent years there have been a number of papers published by practicing invasion biologists, with titles such as “Another call for the end of invasion biology” (Valéry et al. 2013).

³ I use the term ‘specificity’ in this paper, because it captures the fact that invasion biologists must *specify* which organism will invade, which particular environment (ecosystem or community) it will invade, how far it will spread, how fast it will spread, and of course whether it will succeed. I should note

Invasion biologists certainly make qualitative predictions, based on general statements such as: islands are more susceptible to invasions, temperate climates are more susceptible than the tropics, within a taxon smaller animals are more invasive than larger animals etc. (Lodge 1993). However, these qualitative predictions are considered inadequate by scientists and policy-makers alike (Hayes and Barry 2007; Simberloff 2009). The reason for this is the practical nature of the problem of invasion. As we saw in the introduction, we care about bioinvasions: they can be detrimental to the production of goods that are necessary for human survival, such as food and timber, they threaten the integrity of natural ecosystems, and managing invasions or overturning their effects is extremely costly. In the eyes of many scientists and policy-makers, the only predictions worth pursuing are those which can determine precisely whether or not a particular organism will succeed in invading a particular environment (Shrader-Frechette 2001; Simberloff 2009).

I can now give a detailed analysis of why prediction is a problem particularly for field of invasion biology. In what follows, I will argue that the phenomena of bioinvasions are causally heterogeneous and that this leads to a tradeoff between generality and predictive power.

Traditionally, the existence of a tradeoffs in ecology are thought to be caused by the complexity of the systems under investigation (Levins 1966; Matthewson and Weisberg 2009). For instance, Levins's argument that ecological models cannot simultaneously maximise realism, generality and precision, is because ecological systems are complex: they display many different interactions between their parts (Levins 1966). Therefore, if an ecologist wishes to construct a model which is a very close representation of an ecological system, she will have to sacrifice generality, as this model will not be applicable to other systems.

While I agree with Levins that complexity is part of the problem, there is more to this story. In a recent paper, John Matthewson argues that the tradeoffs Levins identifies do not explain why studying complex systems in some disciplines such as ecology is more difficult than it is in others, such as chemistry or physics (Matthewson 2011). According to Matthewson, the reason for this is that ecological systems are not merely complex, but also *heterogeneous*. While complexity refers to the number and type of interactions between parts of a system, heterogeneity refers to the diversity of the parts themselves. Matthewson acknowledges that Levins considers heterogeneity as an aspect of complexity, yet he argues that the two concepts should be pulled apart.

For example, he states "Airbus A380 airliners are complex entities, but it is possible to model their properties precisely, realistically and in a way that generalises across all of them. This is because they are very similar to one another. They are homogeneous, and so in spite of their complexity, these entities can be represented in a general way." (ibid p. 331). In contrast, models in biology face a

Footnote 3 continued

that invasion biologists often use the term 'precision' to refer to the types of predictions they should aim for. While there is overlap between these two terms, 'precision' is a technical term which is used differently in various contexts, some of which are not applicable to invasion biology (see Matthewson and Weisberg 2009). Instead, the term 'specificity' is meant to be a more neutral term, which captures only these aspects of 'precision' (see also pp. 5–6).

much stronger tradeoff between generality and precision, because the entities within the system are so diverse that they cannot be represented in a general way.

I agree with Matthewson that this is an important distinction. Complexity and heterogeneity are not identical, and it is the existence of heterogeneity *in addition to complexity* which explains why the tradeoff between precision and generality is much more pronounced in ecology. For the remainder of the section, I will argue that it is heterogeneity which explains why prediction in invasion biology is so elusive.

I should note that the notion of ‘precision’ which Levins and Matthewson refer to, is quite similar to the specificity that invasion biologists require for their predictions. For Levins, a model is more precise when its results or predictions are quantitative and less precise if they are qualitative. In the case of invasion biology, if the results of a model or experiment are specific, they take the form of quantitative claims about when/where a particular invasion will succeed. For example, a model which determines that a particular plant species will invade a particular ecosystem within three months, unless the population is reduced to x individuals, is a model which gives very specific predictions. In contrast, a model that predicts that island ecosystems tend to be more susceptible to invasion than continental ecosystems provides a qualitative/less specific prediction.

Applying the notion of heterogeneity to invasion biology requires some additional conceptual clarification. On Matthewson’s account, heterogeneity refers to the ontological nature of parts of systems, whether they belong to different taxa, are biotic or abiotic and so on. That is, different airliners are made up of the same types of entities, whereas different ecosystems are made up of very different types of entities. For my purposes, the more relevant type of heterogeneity is in the way the parts of an ecological system manifest as *causes* of an invasion. Of course, ontological heterogeneity contributes to causal heterogeneity, as different types of entities have different ways of causing invasion. Still, as we shall see, the same entity can have different effects in different invasions, hence it is the difference in causal power of a particular entity which is more relevant than the ontological nature of the entity itself.

Causal heterogeneity means that making generalizations of causes and their effects across systems is difficult, even impossible. This is because when we generalize, we focus on what is common between various instances of a particular phenomenon and abstract or leave out the aspects of each instance of the phenomenon which distinguishes it from other instances of that phenomenon (Cartwright 1994). However, in order to make successful predictions about the outcome of an invasion, we must take into account the details specific to each instance. Whether or not a particular invasion will succeed depends not only on the common aspects and mechanisms shared by a number of systems, but on the peculiar ways in which all the small details of a system interact. Therefore, in the process of generalizing we leave out precisely the type of information which is necessary for making predictions.

A good way to illustrate the effects of extreme causal heterogeneity for invasion biology is with an example from research on plant–soil feedback. There has been a relatively recent realization that abiotic factors and the soil microbes through which

plants absorb them are important, because they affect the ability of plants to grow and compete with their neighbours (Klironomos 2002). Generally, when plants accumulate microbes such as mycorrhizal fungi and nitrogen fixers near their roots, this results in a beneficial effect on the plant which is called ‘positive feedback’, while when they accumulate pathogenic microbes, they create increasingly hostile conditions for themselves in a process called ‘negative feedback’ (Weidenhamer and Callaway 2010). Moreover, this feedback tends to come about because of evolutionary interactions between plants and soil-biota, hence there is more negative feedback in a plant’s native community than there is if a plant invades a new area with different soil biota. This led some researchers to hypothesize that when plants invade a new area, they are freed from pathogens and enjoy just the benefits of positive feedback (van der Putten et al. 2013). It would make sense, therefore, to predict outcomes of particular invasions, based on an analysis of a particular invader and a particular soil community.

Unfortunately, it turns out that these types of predictions cannot be made (at least not at this stage). First, there are differences in how quickly plants accumulate pathogens, depending on the type of plant and the type of pathogen (Klironomos 2002). These lags greatly affect the outcome of an invasion, depending on a whole host of other factors including the relative abundance of the invaders and native plants, predation climate etc., and it is extremely difficult to predict how these interactions will play out in each new invasion. Second, and perhaps more importantly, there are a large number of cases where the situation seems perfect for an invasion to occur, because of a particular combination of invader and soil-microbes, yet the invasions ultimately fail (van der Putten et al. 2013).

This example serves to highlight the two important points which make prediction a problem for invasion biology. First, complexity alone is not the sole cause of the problem of prediction. Plant–soil feedback interactions are complex, yet they can be modeled quite extensively. Scientists can even use plant–soil feedback to make predictions about the relative abundance of different plants within a community, when all the plants are native. However, when it comes to invaders, the addition of causal heterogeneity means that each invasion is highly idiosyncratic and the very slight differences between each instance of invasion are actually important in determining the outcome. Therefore, extrapolating knowledge from one invasion does not guarantee that predictions of other invasions will be accurate, even when the instances of invasion are quite similar to each other.

Second, this example also implies that expanding our understanding of which factors cause invasions does not automatically ensure that our predictions will be successful. Even if invasion biologists continue to identify new causes of invasions, such as plant–soil feedback, this will not automatically ensure the success of future predictions in new systems. The reason I bring up this point is because, as I stated in the introduction, many invasion biologists have argued that achieving a more general understanding of invasions is the key to making better predictions. This example shows that there are at least some cases where explanatory generality actually detracts from predictive power.

There is one more conceptual point of which needs some clarification, before I examine the extent to which invasion biology is causally heterogeneous. It could be

argued that the problem of prediction in this field is merely a symptom of a more general issue, the alleged *lawlessness* of all ecological systems (Lawton 1999; Scheiner and Willig 2008). The claim here is that it is simply impossible to make any kind of meaningful generalizations in ecology, hence there is no reason to expect invasion biology to be any different. If this is the case, then it is the lack of generalizability, not causal heterogeneity, which is the cause of the problem.

The debate concerning the status of laws in ecology is important in its own right, yet I think it is actually orthogonal for the problem of prediction in invasion biology.⁴ Even if we settled the issue of laws for ecology, and even if some of these laws can be applied to invasion biology, the problem of prediction in invasion biology would remain. The kinds of generalizations in ecology which are considered as candidates for laws or ‘useful regularities’, are already applicable to invasion biology, yet they have not led to better predictions. For example, there are generalizations in invasion biology based on theoretical frameworks, mechanisms, types of causal factors etc., all of which are sufficiently general to apply to most cases of invasion, and which can even provide good explanations of invasions, but which do not lead to predictions. For example, all invasions can be seen as instances of *interspecific competition*, where populations of invaders outcompete populations of native organisms.⁵

Therefore, there *already exists* a common underlying mechanism, shared by all invasions and most other ecological interactions. In addition, there are many established methods study competition, including predictive models. In other words, the problem is not the lack of generality, as generality is possible. Nor is the problem that there are exceptions to the rules. The problem is that achieving generality relies on leaving out causal detail, and while this can help with explanation or general understanding, it does not help with prediction.

Thus far, I have given conceptual reasons for why causal heterogeneity leads to difficulty in making successful predictions. But in order to show why this is a problem for invasion biology, I must determine whether invasion biology is, in fact, causally heterogeneous, and whether seeking generality does have the adverse effect that I claim. I will examine both in the next section.

⁴ A popular view that has emerged in philosophy of science is that laws do not have to be universal in order to count as true laws, (Colyvan and Ginzburg 2003). In other words, laws in biology (just like laws in physics or chemistry) can have exceptions. Therefore the generalizations and regularities that we find in ecology can count as laws (Colyvan and Ginzburg 2003; Cooper 1998). If we adopt this position, we may be able to find laws or at least regularities in invasion biology, which could prove to be useful for explaining invasions. Yet even if this is the case, this will not help in the case of predictions.

⁵ In fact, interspecific competition is considered to be one of the few unifying themes in ecology. Many of those who argue that ecology is lawless believe that the problem applies mainly to community ecology, while population ecology (especially competition and predation) fare much better (Lawton 1999; Roughgarden 2009). However, the approach to studying invasions as a type of competition was very popular in the 1960s and 1970s and became one of the two major conceptual frameworks of invasion biology. Yet despite important advances models and experiments of interspecific competition, predictions of invasions remained elusive (Davis 2011; Zenni and Nuñez 2013). A similar point can be made with respect to ‘macroecology’, which refers to the study of ecological interactions at large scales, in terms of both time and space. The idea here is that at these scales general patterns re-emerge. Again, while this approach became popular in invasion biology, in the study of biodiversity and resistance to invasion it did not yield any important predictions.

Causal heterogeneity and generalization in invasion biology

In the previous section I gave one example of causal heterogeneity in invasion biology, the various instantiations of plant–soil feedback. Yet this is not a unique example. A short survey of the literature shows just how many different factors have caused invasions. On the one hand, there are particular traits of invaders which have been shown to cause invasion. For example, traits as diverse as small seed size (Richardson and Rejmánek 2004), phenotypic plasticity (Daehler 2003; Geng et al. 2006), allelopathy (Jarchow and Cook 2009), adaptation to fire (Buckley et al. 2007), small size, large size, flowering late, flowering early, dormancy and non-dormancy (Richardson and Pyšek 2006) have all been described as causes of invasions, *within plant taxa*. There are similar lists for marine ecosystems, insects, vertebrates etc.

On the other hand, there are a number of traits of communities which have also been shown to cause invasions, such as human facilitation (Levine and D’Antonio 1999), disturbance (Buckley et al. 2007; Hayes and Barry 2007), biological inertia (Holle et al. 2003), plant–soil feedback (Callaway et al. 2004; Klironomos 2002), high diversity, low diversity (Kennedy et al. 2002; Levine and D’Antonio 1999) and resource fluctuation (Davis et al. 2000).

There are also a number of conceptual papers which explicitly identify the ‘idiosyncrasies’ or context dependence of invasion phenomena (Moles et al. 2007) while a few even acknowledge the tradeoff between generality and predictive power:

If th[e] conclusion [that there are no species-level traits common to all invaders] is true it imposes a tension between the generality and the accuracy of risk assessment schemes that rely on species-level characteristics to prevent introductions. Furthermore this conclusion cautions studies that promote risk assessments, based largely on species-level characteristics, as accurate and readily generalised to new locations (Hayes and Barry 2007).

However, most of the papers which cite causal heterogeneity as a problem for invasion research do not make the connection with prediction, but think that greater generality will solve the problem. The standard term which is used to refer to greater generality is ‘synthesis’ and it comes in many shapes and sizes. The following is a typical quote from a current paper in invasion biology, which advocates for an extensive conceptual synthesis in the field: “[I]nvasion biology is clearly ripe for conceptual synthesis and integration, by subsuming these individual hypotheses in a broadly applicable conceptual framework grounded in basic principles of ecology and evolutionary biology” (Gurevitch et al. 2011, p. 407).⁶ In addition, the authors of this paper also provide a list of terms and phrases which other invasion biologists have used to denote desired synthesis in their field: ‘comprehensive synthesis’, ‘conceptual synthesis’, ‘conceptual framework’, ‘synthetic framework’, ‘general

⁶ I should note that this is just one of many of calls for synthesis in recent invasion research. More examples can be found in: (Blackburn et al. 2011; Catford et al. 2009; Gundale et al. 2013; Kolar and Lodge 2001; Milbau et al. 2008; Moles et al. 2012; Perkins et al. 2011; Richardson and Pyšek 2006; Richardson and Ricciardi 2013; Romanuk et al. 2009; Sousa et al. 2011; Van Kleunen et al. 2010).

conceptual framework', 'unifying framework', 'single theoretical framework', 'conceptual ecological model', 'general eco-evolutionary framework', 'integrated approach', 'hierarchical framework' and 'merging'.

The type of synthesis I will examine here is what I call 'extensive synthesis', as it aims to provide a single conceptual framework which can explain the phenomenon of invasion and guide further research. These syntheses are inherently general, as they aim to subsume most or all instances of invasion under the proposed framework. While I don't think that these syntheses are problematic per se, I do think that they cannot help with the problem of prediction. This is because extensive syntheses 'over-generalize', by leaving out the causal factors which are necessary for prediction.

I will start by giving two examples of extensive synthesis from current invasion research. These examples differ in the way they have attempted to synthesize, as the first sacrifices causal detail, while the second abandons causes altogether. I have picked these examples for two reasons. First, they are examples of the two most common ways in which explanatory integration is achieved in invasion biology and second, they are both explicitly intended, by the authors themselves, as extensive syntheses. In both cases, we will see that the frameworks provided do not increase predictive power.

Insufficient causal detail

The first of the two examples comes from the conceptual paper mentioned above, which provides the list of uses of synthesis (Gurevitch et al. 2011). The authors of the paper provided an overarching conceptual framework which is aimed at subsuming all instances of invasion. The approach is called the 'Synthetic meta-framework' (SIM) (see Fig. 1). According to the authors, any specific invasion, invasion hypothesis and prediction about invasion can be accounted for by some subset of the SIM.

For example, the authors consider a hypothetical case where the invasion is caused by enemy escape. In this example, an invading plant is subject to reduced predation on its seeds and seedlings (population interactions). This leads to an increase in survival at particular life history stages (invader demography), which can then result in rapid population increase. Finally, if conditions are favourable, then this can lead to range expansion and altered landscapes. Hence, this invasion is explained by invoking particular set of 5 causes/processes out of the 17 possible ones.

According to the authors, the important innovation of the SIM is that it provides a more in-depth understanding of invasions. For example, 'enemy release' is a recognized cause of invasion, yet the authors believe that it is a black box explanation, one which does not give the full picture. With the SIM, the box can be opened and broken down, so that a more accurate picture of the invasion emerges. A second advantage is that it allows for the formulation of new hypotheses, as it facilitates the combination of processes and causes and the discovery of new connections between them.

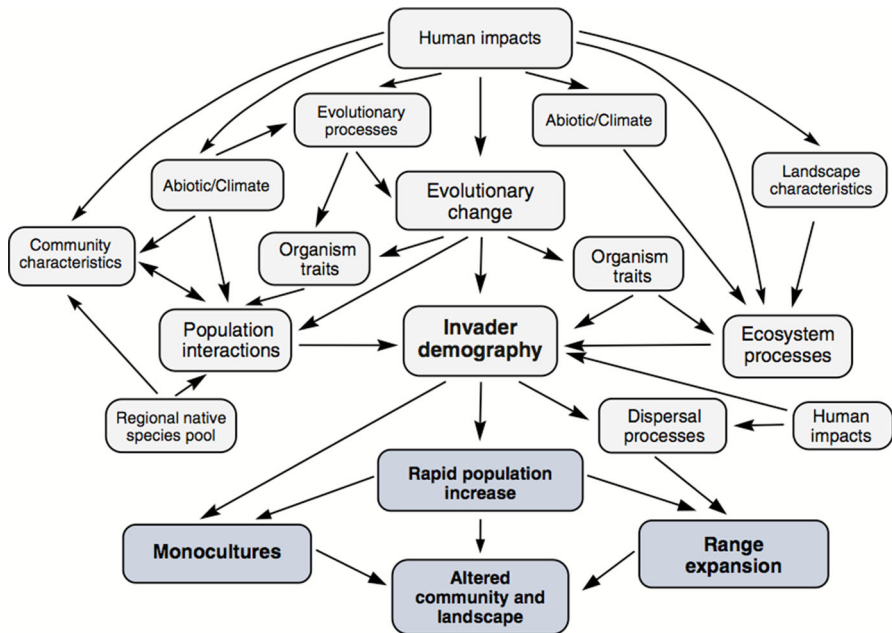


Fig. 1 The SIM (reprinted from Gurevitch et al. 2011)

I agree with the authors that their framework is an example of extensive synthesis and that it provides a framework which can incorporate all instances of invasion. However, I think that the SIM suffers from two important limitations. The first is that it is not clear that this framework is explanatory in a useful sense. That is, even though instances of invasion can be categorized within the framework, it is not clear how this can help to explain particular invasions any better than the pre-existing theories explained them.

Going back to the example of enemy release, the authors claim that the SIM opens the black box and give much more detail about the causal process which results in a successful invasion. Yet this doesn't seem to be accurate. Despite the claims of the authors, there are numerous existing studies which explain 'enemy release' in great detail. For example, there is a study that provides an extensive analysis of positive and negative feedback in plant communities which gives a finely specified explanation of what is necessary for different types of feedback to occur (Bever 2003). At the same time, there are numerous biogeographical studies which show that soil biota generally have more positive effects on invaders than on native species (Klironomos 2002).

What additional information does the SIM provide? The SIM does make the case that population interactions, demographical factors, population increase, range expansion and the altered community landscape must be taken into account. Yet these are factors which are already known to affect invasions, as they appear in studies like the ones of Bever (2003) and Klironomos (2002). In other words, the SIM seems like a disjunctive list of factors which potentially cause invasions.

In fact, the SIM actually provides us with less information than these other studies, because it leaves out the important causal details of how enemy release affects invasions. As we have seen, especially in the cases of plant–soil feedback, this causal detail is extremely important, as the same causes differentially affect individuals and communities and hence the outcomes of different instances of invasion.

It could be argued that the SIM provides us with a *general* explanatory framework for invasion biology, even though it does not do a very good job of explaining particular invasions. I would cautiously agree with this characterization, as the SIM does provide us with a set of all the possible causes of invasions, hence it explains invasions in a weak sense. However, I would also argue that as far as general explanations go, the SIM explanation is neither particularly informative, nor particularly useful. Merely categorizing possible causes of a heterogeneous phenomenon is only one aspect of explanation, one whose value for understanding invasions is quite limited.

The second important limitation of the SIM is that does not make the right sort of predictions. The authors assert that the SIM can help with predictions, because having a complete theoretical framework protects against predictions that are “incomplete, ambiguous, inaccurate or misleading” (Gurevitch et al. 2011). However, they do not explain how it is supposed to work. In fact, it seems to me that because of the way the SIM is constructed, by abstracting causal detail, it is more likely that the SIM’s predictions will be ambiguous, inaccurate or misleading.

Consider once more the example of enemy release. The SIM could provide the prediction that a particular invader x will be more likely to invade community A rather than community B , if A does not have the same soil pathogens that B and x ’s native community have. However, as it stands, this prediction is not sufficiently specific. It does not tell us whether or not x will succeed in invading A , as there a whole host of other causal factors which can change the outcome. In addition, given what we know about the intricacies of plant–soil feedback, a more specific prediction is very likely to be inaccurate.

The SIM is an interesting example of extensive synthesis, which unfortunately does not seem to achieve its aims. This is because it aims to provide ‘better’ explanations and predictions in a way which does not take into account the causal heterogeneity of invasion systems, and sacrifices too much causal detail in the interest of greater generalizability.

Abstracting causes altogether

An alternative solution to the tradeoff between causal detail and generalizability could be to eliminate causes altogether, and focus exclusively on achieving generality. If generality were the key to better predictions, we would expect a general, unifying framework to fare quite well in its predictive success. An example of such a framework can be found in a theoretical paper titled ‘A proposed unified framework for biological invasions’ (Blackburn et al. 2011). The authors of this paper re-conceptualize the phenomenon of invasion as a singular process rather than

the identification of causes and effects. In other words, the point is not to determine why a particular organism becomes an invader but to explain how it does so. They understand the phenomenon of invasion in very abstract and general terms, a process that can be divided into a series of stages (transport, introduction, establishment and spread) with barriers at each stage (geographical, captivity/cultivation, survival, reproduction, dispersal and environmental) that need to be overcome for a species or population to pass on to the next stage (see Fig. 2). If an invader is stopped by a barrier at any stage, then the invasion is considered a failure.

For example, the budgerigar *Melopsittacus undulatus*, an Australian native is considered an introduced species (in the UK), as there are individuals released into the wild (i.e. outside of captivity or cultivation), which are nonetheless incapable of surviving for a significant period. In this framework the budgerigar has passed the transport and introduction stages, overcoming the geography barrier (by traveling to the UK, with some help from humans) and the captivity barrier (by outsmarting said humans and escaping captivity) and is about to enter the establishment stage. Unless the population overcomes the survival and reproduction barriers (by surviving long enough to reproduce in sufficient numbers), it will not pass into the next stage and the invasion will fail.

This framework seems to be precisely the type of framework invoked by the calls for ‘extensive synthesis’. It is a complete ‘re-conceptualization’ of the phenomenon of invasion as an ongoing process rather than a singular event, and has the ability to subsume every instance of invasion as all invasions pass through the same stages. In this sense, it is a unifying framework in the philosophical sense mentioned above, as it cuts through ‘idiosyncrasies’ of particular invasions and provides a common explanatory framework for all invasions.

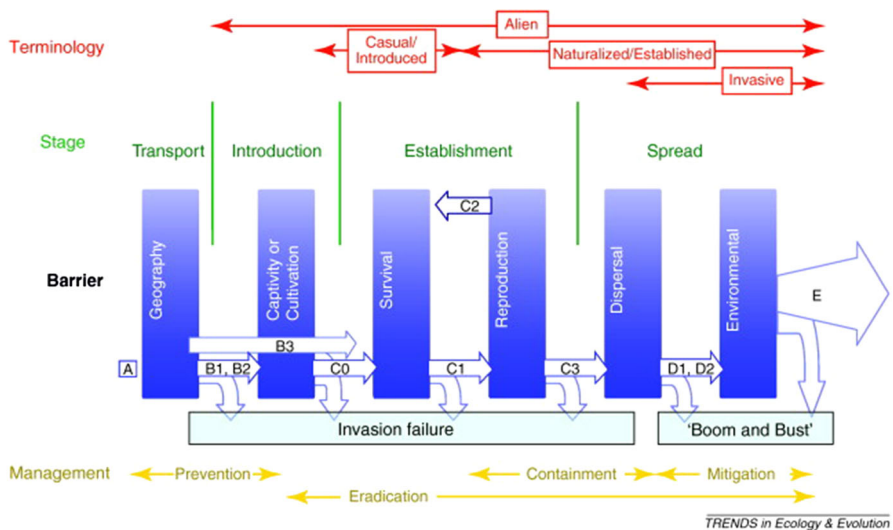


Fig. 2 The unified framework (reprinted from Blackburn et al. 2011)

One of the effects of this ‘re-conceptualization’ is that there is no need to invoke particular causes to explain an invasion. The framework contains no references to particular traits of organisms and particular characteristics of communities, which are traditionally identified by invasion biologists as causes of invasions. One might argue that re-conceptualizing invasions as a process does not get rid of causes, only some type of causes, as the whole process of invasion can be seen as causal. A full examination of this topic is beyond the scope of this paper, yet it seems to me that the stages of invasion are causal in a weak sense. Of course, if the framework is correct, then each stage is a prerequisite for the subsequent stage, and hence causally connected. However, a particular stage or barrier is not a cause of a successful invasion, it is particular traits of organisms and characteristics communities are the true causes of why an invader passes a barrier or not.

Does this unifying framework fare any better with respect to predictions than the previous one? It seems that it actually fares even worse, as there is not a single mention of the word ‘prediction’ in the paper. Instead, the authors substitute talk of prediction with management.⁷ Even though it might be possible to make some predictions, such as the next stage of the invasion if a barrier is overcome, this sort of prediction is not very informative; hence the authors do not seem interested in pointing them out. If the framework gave us the tools to predict whether or not the invasion will pass onto the next stage or not, that would be a very useful kind of prediction, one which the authors would presumably take care to point out.

Extensive synthesis leads to over-generalization

The two syntheses outlined in this section both fail to meet the standard of finely specified predictions. Yet this is not a feature of these two examples, but a more general problem of extensive syntheses in invasion biology (of which there are many, see footnote 5). This is because the main aim of extensive syntheses is to be explanatory in a *general sense*, and as we have seen this is at odds with prediction.

In order to explain this point, I will make use of a philosophical distinction between different types of *integration*. I am referring to O’Malley and Soyer’s analysis, which was developed to describe the different types of integration found in systems biology. O’Malley and Soyer distinguish between *data integration*, *methodological integration* and *explanatory integration* (O’Malley and Soyer 2012). The first type of integration refers to the creation of common data sets used by different groups of scientists. The second type, methodological integration “involves directing a range of methods at a particular biological phenomenon or research problem in order to achieve multiple perspectives on how a system works or what the dimensions of the problem are” (ibid 552). The third type, explanatory integration, is the synthesis of ‘previously unconnected theories’ and the application of explanatory models to new disciplines.

⁷ Of course, management of invasions is an important goal for invasion research, and it is quite well funded. However, management of invasions that have already occurred or have already started is very costly, whereas predictions could lead to the complete *avoidance* of invasions, greatly reducing economic and environmental costs.

According to O'Malley and Soyer, data integration and methodological integration are more practical or technique-driven, as they start off with a particular problem which needs to be solved and apply a certain method or technique to solve it. In contrast, explanatory integration is more theory-driven, as it aims to provide a conceptual or theoretical framework in order to explain a particular problem. I think that these distinctions are useful for understanding the different ways in which synthesis is used in invasion biology and for explaining the link between extensive synthesis and over-generalization.

The two examples of extensive synthesis are clear examples of theory-driven explanatory integration, as they aim to create of a new conceptual, explanatory framework, with various (mathematical, computational, statistical) models embedded within them (O'Malley and Soyer 2012). In fact, these syntheses seem to be examples of a very particular type of explanatory integration, which has echoes in accounts of theoretical unification, such as the covering law model (Hempel and Oppenheim 1948) or explanatory unification (Kitcher 1981) (O'Malley and Soyer 2012, p. 61). In these philosophical accounts, a good scientific explanation is one which explains a large number of diverse facts, by subsuming them under a simple explanatory framework. The simpler the framework (in terms of the number of explanatory principles and 'brute facts' it appeals to) and the greater the number of phenomena it can explain, the better it is. Integration of previously existing theories can lead to more unified theoretical frameworks which can explain a number of diverse phenomena.

Why is it that these explanations are meant to provide better predictions? The connection between explanatory integration and theoretical unification provides some insight. Hempel and Oppenheim's covering law model of scientific explanation, a phenomenon can be explained by showing that it is a particular instance of a general pattern, which comes about due to the existence of a natural law (Hempel and Oppenheim 1948). On this account, prediction is understood as having the same logical structure as explanation, but with the phenomenon occurring in the future rather than the past. Therefore, whatever is necessary for the production of successful explanations is also what leads to good predictions.

It seems that this is the type of reasoning which invasion biologists are following, when they invoke greater synthesis as a solution to the problem of prediction. However, I think that this focus on theory and explanatory unification is precisely what leads to syntheses that over-generalize and lose predictive power. Given the causal heterogeneity of invasions, such generality will frequently come at precision's price. Theory-driven syntheses are meant to provide overarching frameworks which explain most, if not all, invasions and the only way to achieve this is by focusing on what diverse instances of invasion have in common. Yet, this necessitates leaving out causal detail, which is exactly what is necessary for making specific predictions. Thus, theory-driven syntheses are simply not equipped for making predictions. This means that the calls for extensive theoretical synthesis in the invasion literature are actually misleading, as they cannot solve the problem they are intended to solve.

It is important to note that the problem of overgeneralization is not caused by the explanatory aspect of the integration, but by the theory-driven nature of extensive syntheses. There are a number of explanations and explanatory frameworks, which are limited in their scope and generalizability. This is because, even though can be are synthetic (as they often come about as a result of data or methodological integration), they are focused on a particular aspect of a particular problem, and so remain technique-driven rather than theory-driven. For example, as I will show in the next “[An example of data integration](#)” section, there are explanations of invasiveness which are only meant to apply to particular plant taxa (pines and conifers) and cannot be generalized further. In contrast, it is when the aim of the integration is to provide a *general explanatory theory*, applicable to all instances of a particular problem, that over-generalizing occurs.

A danger of accepting the position that theory-driven integration leads to over-generalization is a relapse into pessimism, both for theory-driven syntheses and for the field as a whole. However, this would be premature for two reasons. First, while theory-driven syntheses are not useful for prediction, this does not mean that they have no other uses. It is important to have a general conceptual framework of the phenomenon invasion for the purposes of explanation, especially in the pedagogical sense, for the purpose of guiding research and for management. Understanding the basic mechanisms and processes of invasion are a necessary pre-requisite for more specific problem-oriented research. Nonetheless, given that there are now a number of fully formed conceptual frameworks of invasion biology, it seems unnecessary to spend any more resources in creating additional conceptual frameworks.

The second reason not to give into pessimism, is that there are other types of syntheses (data and methodological integration) which do not over-generalize, as they manage to balance the tradeoff between generality and predictive power.

An alternative solution: constrained integration

The existence of a tradeoff between two aspects of a model does not preclude either aspect in its entirety, it merely shows that they cannot both be simultaneously *maximized* (Levins 1966). The same applies to the tradeoff between generalizability and predictive power, that is, it does not preclude *all* generalizability, merely that generality and predictive power cannot be maximized. This is important because it leaves open the possibility for predictions which are not limited to a single instance of invasion. However, this also leaves the issue of determining exactly what level of generality invasion biologists should aim for.

Unfortunately, I think that this can only be determined on a case-by-case basis, as it depends on the subject matter, i.e. the type of organism or community which is involved in invasion. As we shall see, some taxa or types of communities display less heterogeneity and allow for some generality and for sufficiently specific predictions.

An example of data integration

An example of a synthesis which successfully balances generality and prediction comes from a series of papers by David Richardson, Marcel Rejmánek, Peter Pyšek and colleagues on pines (Rejmánek and Richardson 1996; Richardson and Rejmánek 2004). The study focused on invasive and non-invasive species of pines and showed that invaders shared three important traits (see Fig. 3): small seed mass, small juvenile periods and short intervals between seed crops (Rejmánek and Richardson 1996). The authors were able to identify species of pines which pose particular threats to ecosystems. For example, they identified *P. radiata*, *P. contorta*, *P. halepensis*, *P. patula*, *P. pinaster* as the five most invasive species of pine and also identified 14 species of pine which do not pose a threat to invasion (Fig. 3).

Richardson and colleagues argued that the three traits taken together can explain why some pines disperse, become established and spread in new habitats, sometimes at the expense of native species. More specifically, they claimed that plants which exhibit these traits have a high “index of invasiveness” (number of

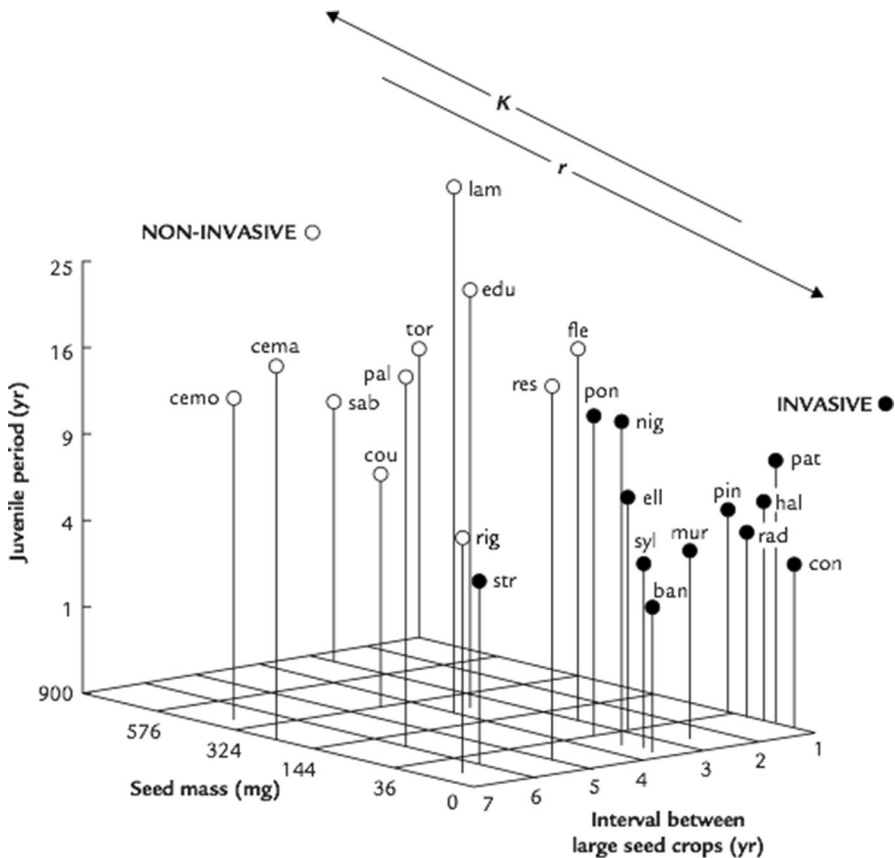


Fig. 3 Traits of invasive and non-invasive pines (Reprinted from Rejmánek and Richardson 1996)

invasive species/number of rare/threatened species). Small seed mass helps plants to disperse over long distances, without the aid of mutualists. It also helps them to compete against other plants because of the sheer number of seeds which germinate. Short juvenile periods and intervals between seed crops further increase a plant's competitiveness as it reaches the reproductive stage earlier than its competitors and can proliferate more extensively. This is especially important in disturbed habitats, which are the kind of habitats most susceptible to invasion.

This framework is first and foremost an example of data integration, as O'Malley and Soyer define it. The authors took data in the form of results from other studies, pertaining to the traits which have known to cause pine invasions. They then organized and analyzed this data, and found that a certain pattern emerged. In other words they were engaged in "quantifying data accurately, developing standardization procedures, cleaning data, and providing efficient and user-friendly interfaces to enable data not only to be reused, but reanalyzed and combined in novel ways" all of which are the hallmarks of data integration (O'Malley and Soyer 2012).

However, while the *process* of the integration was technique-driven, the *product* of the integrative study is quite explanatory. In fact, it does more than explain why a particular invasion occurred, as it provides an explanation for *pine invasions* in general. Nonetheless, there is a very important difference between the generality of this study and the ones in the previous section. The generalization here is inherently constrained to a particular taxon (pines) and makes no claims to explain or predict *all* invasions. Thus, even though it is more general than a particular invasion, it is not an example of an extensive synthesis, such as the SIM or the process synthesis. In fact, I think that it is precisely because this synthesis was driven by method rather than theory, and the theory emerged from the synthesis of data, that it was not over-extended.

Perhaps the most important achievement of this data synthesis, is that it yielded specific predictions, precisely the types of predictions which invasion biologists advocate. For example, Rejmánek and Richardson concluded that the dispersal of pine seeds from plantations into adjoining natural or seminatural habitats is a major threat, especially in the Southern Hemisphere. They also identified particular forests in Sweden as a potential danger zone, as they are susceptible to invasion by *Pinus contorta*, a North American pine. Finally, judging by responses to these studies from the literature, these predictions seem to be considered successful by the community at large (Milbau et al. 2008).

There are two main reasons which explain this study's success. The first is that pine are widely studied, as they appear in many ecosystems across the globe, and are frequent invaders. The second is that pines have a certain reproductive strategy which means that the traits which enable them to compete in their native ecosystems are the same traits which give them a competitive advantage in new ecosystems. Pines are gymnosperms (they do not rely on other organisms for their dispersal) and invest little into each seed, which means that they have quite simple 'regeneration requirements' (Richardson and Rejmánek 2004).

In other words, the particular reproductive strategy of pines provides the context in which the three traits become causes of invasion. If a plant had the same traits within a different reproductive strategy, one which did not reproduce as fast or in

large enough numbers, or which invested much more into each seed, then the same traits would not make it more likely to invade. This does not mean that the traits would not confer any other advantages to the plant, just not advantages sufficient for invading.

The general point is that given the heterogeneous nature of invasion systems, what counts as a causal factor in one group of organisms or species is often completely absent in other groups. This means that it is very unlikely that identifying the cause of a successful invasion in one group of species will help us determine anything about behaviour of species which do not have that trait. This is the main reason why plant invasions and animal invasions are so different. Yet even within smaller taxa, identifying a known causal factor in one species' invasion, does not mean that it will be a causal factor in another species invasion. Whether or not a trait becomes a causal factor depends, in part, on the context within the organism itself, its other traits, strategies and interactions with other organisms. Still, as we have seen, there are some cases where a particular context is such that it becomes possible to identify a small number of causal traits which can be used to predict invasions.

Does invasion biology require any more synthesis?

Despite the acclaim that these authors have received for their success in predicting pine invasions, their study has been criticized as being much too limited, precisely because it only applies to one genus. The critics believe that analyses which are limited in this way do not cut across the 'idiosyncrasies' of invasions.⁸ Yet I think that this criticism is misplaced, both in the case of this particular study, and in the field of invasion biology as a whole. Starting with the particular, as we have seen, the success of this study is due to the fact that it was restricted to pines. If my analysis of causal heterogeneity is correct, then we would predict that if the same traits were used to predict invasions in other taxa, these latter predictions would be less accurate.

As it turns out, the authors did extend their analysis to conifers and to woody angiosperms.⁹ As pines are conifers, we would expect some success there, though less pronounced than in within the pine genus, while we would expect even less success in the case of woody angiosperms (mainly because they rely on other organisms, not the wind for dispersal of their seeds). The results were as expected. There were some taxa (e.g. cypresses) which turned out to be more invasive overall, yet even within this family, there were quite a few exceptions, mainly in terms of species that displayed the traits and yet were not invasive. In the case of angiosperms the results were even less robust, with many more exceptions.

⁸ I should note that data integration and methodological integration are the most prevalent types of integration in invasion biology. Other examples of data integration include meta-analyses, (see for example Davidson et al. 2011). Other examples of methodological integration include mathematical and computational models from a range of different ecological sub-disciplines, laboratory experiments, field experiments etc (such as Dunstan and Johnson 2007).

⁹ The new studies were published about a decade later, perhaps in response to the criticism the authors received from the community.

The next question to ask is what we should make of results like these for the field of invasion biology. So far, I have argued against the idea that extensive synthesis, in the form of extensive explanatory integration, will be useful for the field, at least when the goal is to make more accurate and more finely specified predictions. However, this does not preclude integration which is more extensive than the data integration presented here, yet less ambitious than the extensive integration outlined above.

For example, it may be possible to apply the technique used in the pine study to other species, as an instance of methodological integration. Then, instead of using the same three traits to analyze other taxa, invasion biologists could look for whatever traits conferred a high 'index of invasiveness' to other species, starting anew with each new species. This may not be equally viable in all species, as it is the particular combination of context and causes which made it possible in pines. Other contexts or advantages conferred by traits might not be sufficiently robust to enable predictions. Still, there are at least good theoretical reasons to attempt this type of integration.

It also might be useful to attempt new types of explanatory integration, provided that we do not expect predictions to be as highly specific. For instance, given the way in which the climate of the earth is changing, it may be useful for scientists to conduct integrative data-driven analyses to determine whether some ecosystems are generally going to be more at risk from invaders. This type of analysis will not provide clear predictions of which ecosystems will be invaded and when, but it may help to scientists focus their research on particular invaders which are more dangerous or ecosystems which are more at risk.

Finally, we should not forget the importance of the instances of constrained integration, and make sure that the results they provided are utilized to their fullest extent. For instance, in one of their papers, Rejmánek and Richardson mentioned their surprise that a recent global assessment of criteria and indicators for sustainable forest management did not mention the invasiveness of many pine species (Richardson and Rejmánek 2004). It seems that based on their predictions measures should be taken to ensure that pine invasions do not occur.

Conclusion

The aim of this paper was to examine the claim made by invasion biologists, that extensive synthesis is essential for progress in their field. I argued that synthesis is not a singular concept in invasion biology, and could be understood as referring to three distinct types of integration. While I agree with invasion biologists that some types of integration (data and methodological) can lead to better predictions, extensive explanatory integration will actually hinder the production of predictions that are both accurate and specific. The reason for this is that the systems invasion biologists study are extremely causally heterogeneous, hence there is a tradeoff between generalizability and predictive power. Fortunately for the field of invasion biology, data and methodological integration are already established in the field and are yet to be utilized to their full extent.

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