

The comparative analysis of historical alien introductions

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Abstract The comparative analysis of past introductions has become a major approach in investigating the rules governing invasions, yet their utility to understand the invasion process is not exempt of problems. The relevance of some of these problems has not yet been fully appreciated, but it has now become clear that not taking them into account may lead to invalid conclusions. Taking examples of the plants' and birds' literature, this paper reviews these difficulties by discussing the comparative analysis of region invasibility. The difficulties include biased information toward successful introductions, confounded effects of many explanatory variables, statistical non-independence of introduction events and taxonomic levels, and inappropriate definition of the units of study. Provided that there is good information on introduction events at the appropriate spatial scale, reliable results may be obtained by using

modelling techniques that control for the effects of introduction effort and species properties while dealing with spatial and phylogenetic non-independence of introduction events. In conclusion, although important progress can be made in understanding the factors behind invasibility of regions by the comparative analysis of the past introductions, this will only be possible by acknowledging the existence of biases and confounding effects in historical introductions and by using appropriate methods to deal with them.

Keywords Invasion success · Invasibility · Comparative approach · Statistical techniques · Phylogenetic-based methods · Spatial autocorrelation · Pseudoreplication

Introduction

Concern over the impact of invaders on biodiversity and ecosystem functioning has prompted a plethora of research on the mechanisms that govern biological invasions. Much of the effort has been devoted to designing and performing experiments in the field and in controlled conditions. Experiments are the best approach to establish causal relationships, and hence are central to understanding the mechanisms of invasion (Schoener and Spiller 1999; Levine 2000; Levine et al. 2003). However, experiments are by itself insufficient to fully understand invasions. Due

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to the immense variability of ecological systems, one limitation of experiments is that the results might lack generality, being only related to the particular area, period of time or species selected as study case. Moreover, not all questions on invasions can be tackled by experimentation, for example those concerned to the resistance of entire regions to invaders. Finally, experiments are not always possible for taxa such as long-lived plants or vertebrates in which natural, large scale experimental introductions are not feasible for legal, ethical or logistic reasons.

One alternative to the experimental approach is the comparative analysis of past introductions (Kolar and Lodge 2001; Fisher and Owens 2004; Cadotte et al. 2006). In the last decades, the use of the comparative approach has greatly broadened our understanding of the invasion process, uncovering some of the general rules that govern the establishment and spread of species introduced into foreign regions (Brown 1989; Lodge 1993; Kolar and Lodge 2001; Duncan et al. 2003; Fisher and Owens 2004; Cadotte et al. 2006). A major advantage of the comparative approach is that it can help drawing general principles that apply over broad regions and across a great diversity of taxa, and may thus provide generalities that are realistic enough to be used in risk assessment of future invaders as well as provide the starting place for determining management of existing invasions (Kolar and Lodge 2002; Settele et al. 2005). The comparative approach can be used to evaluate a variety of hypotheses regarding the invasion process, such as identifying the properties that make some species successful invaders or assessing whether habitats differ in their resistance to invaders (Kolar and Lodge 2001; Sakai et al. 2001; Duncan et al. 2003). Human-driven introductions have thus been considered as one of the most important, albeit unfortunate, “ecological experiments” ever conducted (Rice and Sax 2005).

Yet, past introductions are not well-designed experiments, but quasi-experiments (see Table 1), and hence their utility for understanding the invasion process is not free of problems. In short, the problems of analysing past introductions arise from the non-random assignment of the species to the introduced regions, the impossibility of isolating a priori single treatment effects, and the lack of true replication, all of which makes the approach vulnerable to a number of biases and confounding effects that prevents

inferring causality. The relevance of some of these issues is, in our view, not fully appreciated, even though evidence indicates that not taking them into account may lead to invalid conclusions (Cassey et al. 2004). Continuing to add to this body of work without acknowledging the limitations of the comparative approach will do relatively little to advance our understanding of the invasion process.

Here, we constructively review the difficulties to detangle the factors underlying the process of invasion using the record of past introductions. We illustrate these difficulties by discussing the comparative analysis of region invasibility, defined as the ease with which new species become established in a region where they are introduced (Lonsdale 1999), although most of the difficulties also apply to other aspects of the invasion process. Our intention is not to exhaustively review the progress made to understanding invasibility with the use of the comparative approach, an issue that has been reviewed elsewhere (Smallwood 1994; Levine and D’Antonio 1999; Shea and Chesson 2002; Cadotte et al. 2006; Colautti et al. 2006). Rather, we use the concept of invasibility to illustrate the different caveats of the comparative approach when applied to historical introductions. Our goal is to illustrate with examples the nature of the problems, and then present some of the approaches to deal with them.

Confounding invasibility with invader pools

A main complication in assessing whether regions differ in invasibility is the necessity to disentangle the effects of the region from those associated with the frequency of introductions. The fact that some regions contain more invaders than others may simply reflect differences between regions in the number of species introduced deliberately or accidentally by humans (Lonsdale 1999). For example, a consistent pattern that emerges from the study of past introductions is that the number and proportion of naturalized aliens on islands is generally higher than in continents. In New Zealand, for instance, the number of naturalized birds is more than two times higher than that of Australia (Duncan et al. 2003). Such type of evidence has been used to support the viewpoint that island communities are more invasible than those of mainland areas, yet they simply reflect

Table 1 Comparison between experimental and comparative approaches in the study of differences in invasibility among regions

Aspect to consider	Experiment	Comparative analysis
Grain of the spatial scale	Fine	Coarse
Spatial autocorrelation	Controlled	Uncontrolled, usually present. Should be included in the analysis
Temporal scale	Contemporaneous Usually short, medium if permanent plots or long-term experiment available	Past Usually long, sometimes unknown if residence time was not recorded
Causality	Demonstrated by treatment manipulation	Inferred from statistical analysis with multiple predictors
Replication	True and random Low due to logistic and man-power constraints	Not random, biased towards certain regions and species Large sample size if many records available
Phylogenetic inertia	Considered as a fixed species effect because usually few species are tested	Considered as a random effect because usually the alien species dataset is large
Propagule pressure	Absent or controlled	Present and uncontrolled Should be estimated in the analysis even if only surrogates are available
Invasiveness	Controlled	Uncontrolled. Species traits should be included in the analysis
Logistical considerations	Field experimentation with birds is almost impossible	Advanced statistical software required
Ethical considerations	High if experimental introductions are required	Absent

the fact that humans had introduced more species to islands than to continents (Duncan et al. 2003).

The success in the comparative analysis of region invasibility depends thus on the availability of accurate information on the pool of introduced species (Duncan et al. 2003). While the species that have succeeded at establishing themselves are relatively easy to determine, it is much more difficult to know those that have failed, as they may have left no traces of their presence in the region. Indeed, for many taxa the record of species unsuccessfully introduced is quite incomplete. In plants, for example, we can recall on only a few studies which have attempted to estimate the success of naturalization based on species introductions rates (e.g. Duncan and Williams 2002).

The incapacity to control for the invader pools limits the possibility of using the comparative approach for some taxa (Lonsdale 1999). In addition, for those taxa for which information is available, the existence of differences in the quality of the historical record may lead to wrong conclusions when comparing invasibility among regions, the ecosystem resistance to invaders being under-estimated in

regions with a poorer record of failed introductions. Fortunately, appropriate data sets can be found for many plant and animal taxa. For example, Duncan and Williams (2002) used exotic angiosperm and gymnosperm species that have been introduced for cultivation into New Zealand to show that naturalization success is higher for introduced species belonging to genera already found in New Zealand, contradicting Darwin's naturalization hypothesis (but see Lambdon and Hulme 2006; Ricciardi and Mottiar 2006).

Confounding invasibility with propagule pressure

Accurate records of introduction successes and failures are not enough to study invasibility. We also need information on the effort with which the different species have been introduced. All evidence to date indicate that species that are introduced in larger numbers or more times are more likely to become established than those that are introduced in smaller numbers or fewer times (Lockwood et al. 2005), as the latter are highly vulnerable to extinctions by

demographic or genetic stochasticity (Legendre et al. 1999; Sax and Brown 2000). If species have tended to be introduced in larger number in some regions than in others (Cassey et al. 2004), this may lead us to erroneously conclude that they differ in invasibility.

Information on introduction effort is available in some cases of deliberate introductions, making it possible to control for the above biases with the appropriate statistical techniques (Table 2). In birds, for example, many of the introductions in the 18th and 19th centuries occurred during the great migrations of European settlers (Long 1981), a major motivation being that the introduced species reminded them of their European homeland. The process of transporting and introducing species was facilitated by the setting up of acclimatization societies, which kept accurate records of the year of introduction, its outcome and even the number of individuals released, providing high quality data that have been the basis of many comparative studies (e.g. Veltman et al. 1996; Green 1997).

The problem of confounding invasibility with introduction effort is particularly difficult to overcome in the case of plant invasions, given the obvious difficulties in measuring the number of seeds released and considering that many plant species have been introduced accidentally. Furthermore, the number of introduction attempts, which may be correlated with the number of introduced individuals (Veltman et al. 1996), is also of little use in this case, as the role of humans in secondary releases is virtually impossible to assess. However, there have been some imaginative attempts to deal with these limitations. For example, given that the effort of introduction is a function of human activities (Chaloupka and Domm 1986), some authors have suggested using the number of human visitors to an area as surrogate for propagule pressure in plants (Pysěk et al. 2002; Sobrino et al. 2002; McKinney 2004). This type of approaches can be useful provided that one can show a priori that the chosen variable is an appropriate surrogate for propagule pressure. For the above example, the assumption that the amount of human visitors to an area reflect propagule pressure is supported by the existence of a positive relationship between number of visitors and the percentage of alien plants in the area (e.g. Chaloupka and Domm 1986).

Confounding invasibility with invasiveness

Another complication in assessing whether regions differ in invasibility is the need to disentangle the effects of the region from those associated with invasiveness (i.e. invasion potential of the species introduced). To become established in a novel region, a species needs to find an appropriate niche there. The chances of finding a niche opportunity will depend on the presence of preys, competitors and enemies or pathogens in the community, but also will depend on the properties of the introduced species (Sol 2007). In fact, there is evidence that species differ in their invasion potential in virtue of their properties. In birds, successful invaders tend to be habitat generalists (Cassey et al. 2004) and to show a high degree of flexibility in their behaviour (Sol et al. 2005). In plants, more abundant naturalized species tend to have wider niche breadths regarding habitat and climate (Kühn et al. 2004). If species with features of successful invaders have been introduced more often in some regions than in others, this may lead us to believe that regions differ in invasibility when this is just a confounding effect of its co-variation with species properties.

There is evidence that the identity of the species introduced is non-random. In birds, most of the species chosen for introduction come from temperate regions, and hence it is expected that traits characteristic of the taxa in these regions are over-represented (Duncan et al. 2003). Moreover, introductions of behaviourally flexible species have been more frequent in some regions than in others (Sol et al. 2005). Thus, the risk is high that differences between regions in the likelihood of establishment are confounded by the invasion potential of the species introduced. This might be one of the reasons why species attributes related to invasion success differ depending upon the habitat type (Lloret et al. 2005) and spatial extent of the region to be analysed (Hamilton et al. 2005).

Assessing the effects of the region from those associated with propagule pressure and the properties of the introduced species is thus central to assess whether or not regions differ in invasibility. This requires statistical control of these factors using techniques such as multi-variable models (Veltman et al. 1996) or path analysis (Duncan et al. 1999; Sol et al. 2005).

Table 2 Overview on some software for methods to correct for phylogenetic or spatial non-independence or both

Software	Method	Source
<i>Spatial analyses only</i>		
SAM (spatial analysis in macroecology)	Conditional autoregressive models, simultaneous autoregressive models, spatial filtering, spatial generalized least squares	Rangel et al. (2006) http://www.ecoevol.ufg.br/sam/
SpaceStat	Simultaneous autoregressive models	Anselin (1995) http://www.terraseer.com/products/spacestat.html
<i>Phylogenetic analyses only</i>		
CAIC (Comparative analysis by independent contrasts)	Phylogenetic independent contrasts (PIC)	Pruvis and Rambaut (1995) http://www.bio.ic.ac.uk/evolve/software/caic/
COMPARE (Phylogenetic comparative methods)	Independent contrasts, phylogenetic generalized least squares, phylogenetic mixed model	Martins (2004) http://compare.bio.indiana.edu/
CACTUS (Comparative analysis of continuous traits using statistics)	Independent contrasts	Schwilk and Ackerly (2001) http://www.pricklysoft.org/software/cactus.html
<i>Both phylogenetic as well as spatial analyses</i>		
R (different packages)		R Development Core Team (2006) http://www.r-project.org/
ape (Analyses of phylogenetics and evolution)	Phylogenetic independent contrasts (PIC), Generalized estimating equations (GEE) in a phylogenetic context	Paradis and Claude (2002)
PHYLOGR (Functions for phylogenetically based statistical analyses)	Generalized least square models (GLS) in a phylogenetic context	Díaz-Uriarte and Garland (in preparation) http://cran.r-project.org/src/contrib/Descriptions/PHYLOGR.html
GEE (Generalized estimation equation solver), geePack; available for R and SPLUS	Generalized estimating equations	Yan and Fine (2004)
MASS (Modern applied statistics with S), lme4 (Linear mixed-effects models using S4 classes), nlme (Linear and nonlinear mixed effects models); available for R and SPLUS	General(ized) mixed effect models/ Generalized least squares models	Pinheiro and Bates (2000)
stats	Eigenvalue-based filtering	R Development Core Team (2006)
spdep (Spatial dependence: weighting schemes, statistics and models)	Conditional autoregressive models, simultaneous autoregressive models, spatial filtering	Bivand et al. (2006)
SPLUS		http://www.s-plus.com/
	Generalized mixed effect models/ Generalized least squares models	Pinheiro and Bates (2000)
	Generalized estimating equations	Yan and Fine (2004)
Spatial module in SPLUS	Conditional autoregressive models, simultaneous autoregressive models	
GLIMMIX in SAS	Generalized mixed effect models/ Generalized least squares models	http://www.sas.com/

There is a plethora of methods and software implementations available and we will only be able to present some few examples. Many of the programmes mentioned are able to do many more analyses. The list is by far not exhaustive. The spelling (including use of upper and lower case) is in accordance with the programmes themselves

Using the appropriate spatial level of analysis

Some comparative analyses have defined the regions of study based on geographical criteria rather than based on ecological similarity. While this may be appropriate for the specific purposes of these studies, examining regions with high heterogeneity in climatic and ecological characteristics is clearly inappropriate to study invasibility. All introductions into large countrywide regions (e.g. North America, Australia, etc.) should not be regarded as equivalent, as it seems clear that ecological differences within these large regions may in some cases be larger than among regions. These limitations may have concealed interesting patterns that could be important for better understanding the process of invasion (Kark and Sol 2005). One clear example is the finding in large-scale analyses that more diverse systems contain higher numbers of exotic species (Shea and Chesson 2002), an observation that is contrary to theory (Elton 1958). This discrepancy is attributed to extrinsic factors that vary at these spatial scales, which favour high numbers of native species and also increase niche opportunities for invaders (see Kühn and Klotz 2007 for details).

Thus, tests of the factors that make some regions more invulnerable than others should also define regions in a more ecological way (Kark and Sol 2005). The problem is that with historical introductions it often is difficult to know the exact environment where species have been introduced. Moreover, in mobile organisms, as in birds, the place of introduction can differ from the place of establishment. One possibility to overcome these difficulties is to restrict the analyses to islands (Cassey et al. 2005; see below), as ecological differences within island should generally be smaller than across islands. An alternative is to compare invasions across convergent ecosystems that share similar climates (Kark and Sol 2005). Such an approach enables one to investigate patterns and processes that affect the success and failure of species introductions while adjusting for fundamental climate region and ecosystem-type differences. Comparing convergent Mediterranean ecosystems, Kark and Sol (2005) reported evidence that regions are differentially invaded by birds, with the Mediterranean Basin showing higher invasibility than Mediterranean Australia and the South African Cape.

Spatial non-independence of introduction events

Theory predicts a number of reasons why some regions and ecosystems should be easier to invade than others, including variation in climatic conditions, species diversity and degree of environmental disturbance (Williamson 1996; Shea and Chesson 2002). However, if it is easier to establish at some locations than others, then the outcome of introductions to the same location will be correlated (Duncan et al. 2003). This means that introductions in the same region are unlikely to represent independent pieces of evidence for the influence of a factor on establishment success, because we should expect similar outcomes (either success or failure) for all species introduced to the same location, violating a core assumption of standard statistical tests. The pseudo-replication that arises if the probability of success in introductions is more similar between near-by regions than it is between more distant regions is the so-called spatial autocorrelation (SAC). The above-mentioned example of repeated introductions in the same region is the most extreme form of spatial non-independence or pseudo-replication.

Spatial autocorrelation can be particularly problematic in studies trying to characterize the factors that make some regions more resistant to invaders than others. On one hand, when data points are not independent, statistical tests are more likely to show that factors have a significant influence on establishment success when actually they have not (type I error). Maybe even more important, albeit less often appreciated, is the fact that ignoring SAC may yield incorrect parameter estimates for slopes and intercept (see Lennon 2000; Lichstein et al. 2002) as far as changing the direction of a relationship (Kühn 2007). On the other hand, if some of the characteristics that make some regions more resistant to invaders than others follow a similar pattern of autocorrelation than establishment success, then the association between these characteristics and establishment can be entirely caused by their geographical distribution (i.e. spatial) pattern. Therefore, ignoring SAC may often increase the variance around parameter estimates but not necessarily yield incorrect results as such (Hawkins et al. 2007).

There are several methods now available that correct for spatial non-independence (Table 2, see also review by Dormann et al. 2007). If we only want

to correct for a “region” effect in invasion analysis, we can do so with a (generalized) mixed effect model, such as in Blackburn and Duncan (2001), where the region is coded as a random effect. However, this would only correct for the effect of that “region” but would disregard smaller scale SAC. If we have information on spatial coordinates, then we should check for SAC of the residuals (e.g. computing Moran’s I). If SAC is present, the choice of methods is relatively easy when the data (or better the residuals) are normally distributed. For such data, there are broadly two classes of methods: conditional autoregressive methods (CAR) and simultaneous autoregressive methods (SAR) (Cliff and Ord 1981; Anselin 1988; Cressie 1993; Haining 2003; see Kissling and Carl 2008, for details in an ecological framework). With non-normally distributed data, such as binomial or Poisson, we will need a generalization of the methods described above. Generalized Estimating Equations (GEE) are generalizations of Generalized Linear Models (GLM) to include autocorrelation structures (Diggle et al. 1995; Yan and Fine 2004; Carl and Kühn 2007). Another option is the use of Generalized linear mixed effect models (Blackburn and Duncan 2001) or the use of and Generalized Least Squares, which are also apt to correct for SAC in analyses with non-normally distributed residuals when a correlation structure is defined. Diniz-Filho and Bini (2005) used an approach using spatial eigenvectors as covariates in a regression model as a useful tool. Very recently, Carl and Kühn (2008) developed a wavelet-revised method which proved to be very fast, stable and efficient in accounting for SAC when having gridded data. The use of the very popular autologistic methods, however, yields severe bias and incorrect parameter estimates and hence cannot be recommended (Carl and Kühn 2007; Dormann et al. 2007). The methods briefly introduced here are described in more detail by Dormann et al. (2007).

Phylogenetic non-independence of introduction events

Besides the likely non-independence between introduction events or spatial arrangements, species are themselves clustered to higher level units. This phylogenetic non-independence essentially mirrors

the effects of spatial non-independence and may therefore have similar problems. In particular, closely related species share many morphological, behavioural, physiological and ecological traits due to common ancestor rather than independent evolution (Felsenstein 1985; Harvey and Pagel 1991; Freckleton et al. 2002). If these shared traits affect the likelihood of establishment, then introduction outcomes will be clustered by phylogenetic or taxonomic relatedness. In other words, spatial proximity is exchanged by phylogenetic relatedness. Not taking into account the phylogenetic relationship between species overestimates the degrees of freedom in the analysis and increases the chance to obtain false positives. Additionally, phylogenetic relatedness that overlaps with environmental influences (e.g. due to niche conservatism) may interfere with such variables and lead to wrong parameter estimates. The importance of considering phylogenetic relationships when comparing species has long been recognized (Felsenstein 1985; Harvey and Pagel 1991; Freckleton et al. 2002). A simple example can illustrate the problem when studying the invasibility of regions. Let’s imagine that we want to test whether an ecological factor such as the degree of disturbance in the habitat facilitates establishment and survival of invaders, and we manage to obtain good data for 40 species’ introductions to do so (Fig. 1). In phylogenetically uninformed tests, these 40 species would be used as pieces of evidence to support or reject the hypothesis. As shown in Fig. 1a, in our working

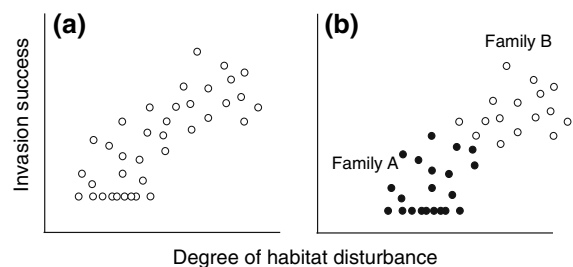


Fig. 1 Example of phylogenetic effects in interspecific comparisons ($n = 40$). In this example the graph (a) would suggest a link between an ecological variable such as degree of habitat disturbance and invasion success (e.g. species establishment or survival) when the association is the result of taxonomic relationship (b). Not taking into account the phylogenetic relationship between species may thus overestimate the degrees of freedom in the analysis and increases the chance to obtain false positives (See text for further details)

example the test would support the hypothesis that disturbance facilitates invasion. Let's now imagine that these species belong to only two different families, and that species from each family differ in their ability to survive in disturbed habitats (Fig. 1b). Would we still consider that there are 40 pieces of evidence? Figure 1b does not suggest any pattern within families, but just differences between them. Species from a same family are likely to share many characters thought to affect establishment that could be confounding the association. We only really have two independent data points with 20 pseudo-replicates, each, which is certainly not enough from which to draw any firm conclusions.

The degree of phylogenetic autocorrelation in a variable can be evaluated by a number of methods, including the Moran's I autocorrelation index (Paradis and Claude 2002) or phylogenetic generalized least squares (Freckleton et al. 2002). If phylogenetic effects are proved to be important, these should be controlled for either with methods aimed at removing phylogenetic influence from trait spaces (such as phylogenetic independent contrasts; (Felsenstein 1985) or with those that partition their influence between environment and phylogeny (such as eigenfactor based methods; Diniz-Filho et al. 1998; Desdevices et al. 2003). The eigenvector approach was used by Lososová et al. (2006) in an analysis of trait patterns in annual vegetation of man-made habitats in central Europe. There, among other results, alien status changed from insignificant to significant after accounting for phylogenetic information. When no adequate phylogenetic hypothesis is available, the problem of phylogenetic inertia may be partially solved by using taxonomic information. For example, the systematic hierarchy may be incorporated in (Generalized) Mixed effect Models as random effect (Cassey et al. 2004; Duncan and Blackburn 2004; Sol et al. 2005) or as autocorrelation matrix in Generalised Estimating Equations (GEE) (Duncan and Blackburn 2004).

Introduced success of birds as an example

The main conclusion drawn from the previous section is that to properly study region invasibility we not only need good information on introduction events at the appropriate spatial level, but we also need to employ

statistical techniques that can control for confounding variables (introduction effort and species properties) and incorporate information on non-independence of introduction events due to phylogenetic affiliation and SAC, so as to produce unbiased estimates of the effects of the different factors. As previously shown, there are several modelling approaches now available to do so. Admittedly, some of the advanced approaches are cumbersome in analysis and interpretation, and several are far from being perfect. However, it is better to use some improved though not perfect statistical method than a method where the basic assumptions are clearly violated.

Only a few studies have adopted the above principals to examine differences in invasibility between regions. One of these few examples is the analysis by Cassey et al. (2004) of global patterns of establishment success in birds. Following Blackburn and Duncan (2001), the likely non-independence of introductions of the same taxa or in the same region was modelled by using Generalized Linear Mixed Models (GLMM). The approach used was to assume a common positive correlation between introduction outcomes within the same taxa or region, but a zero correlation between outcomes involving different taxa or regions. This was achieved by including region of introduction and the taxonomic hierarchy as random effects in the model. Because the response variable was success or failure of introductions, Cassey et al. (2004) adopted a model with binomial structure of errors. The results confirmed the primary importance of propagule pressure for avian establishment success across regions. Moreover, propagule size was found to be correlated with a large number of variables previously thought to influence success. From all those variables, only habitat generalism was related to establishment success once the effect of propagule was controlled for with a multi-variable approach. The number of released individuals was not only the strongest correlate of introduction success, but was also non-randomly distributed across regions. Thus, differences between regions in invasibility could not be assessed without considering the confounding effects of propagule size and non-random distribution of species with varying invasion potential. When propagule size and habitat generalism were controlled for in the model, Cassey et al. (2004) found significant differences in the likelihood of establishment of birds across regions. For example,

while 56% of avian releases succeeded in Hawaii, only 35% succeeded in New Zealand.

When a comparative analysis has shown that regions do differ in invasibility, the next step is of course to try to understand why regions differ in invasibility. Provided that one defines the study units in ecological terms and uses appropriate statistical techniques, the comparative method may provide important insight into the factors that make some regions more invisable than others. Cassey et al. (2005), for example, used information for exotic bird introductions to oceanic islands and archipelagos around the globe to test whether invasibility is related to competition, predation, human disturbance or habitat diversity. Islands seem to be an appropriate unit of analyses, as ecological differences within each island should generally be smaller than across islands. Once controlled for confounding effects and spatial and taxonomic autocorrelation, there was a strong negative interaction across regions between establishment success and predation; exotic birds are more likely to fail on islands with species-rich mammalian predator assemblages.

Conclusions

In this review, we argue that the comparative analysis of past introductions can provide important insight into the factors that make some regions more invisable than others. However, we also highlight that the comparative analysis is only useful as long as the problems of this approach are fully appreciated, and these are mitigated by the use of appropriate methods. Because the risk of mistakes and biases is high for historical data, and because the chances to detect biologically meaningful signal can be significantly reduced when the information is inaccurate, checking whether the available information is reliable remains central in the comparative analyses of past introductions. Provided that this information is accurate, reliable results may be obtained by using appropriate modelling techniques that control for the effects of introduction effort and species properties while dealing with spatial and phylogenetic non-independence of introduction events. Of course, it can happen that some important questions can be addressed only by using relatively imperfect data (e.g. small data sets), but this should not prevent the use of comparative

methods as long as these imperfections do not alter the conclusions. Thus, rather than advocate for a conservative approach, which can reduce the probability of obtaining false positives (type I error) but at the expenses of increasing that of false negatives (type II error), we suggest a precautionary approach in which the limitations of the method are fully acknowledged and the assumptions adopted are reasonably well-supported. Used correctly, the comparative method can be a powerful tool to identify general principles underpinning the invasion process that apply over broad regions and across a great diversity of taxa. Yet used inadequately, the method will do relatively little to advance our understanding of the invasion process and may even yield incorrect results.

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