

A general eco-evolutionary framework for understanding bioinvasions

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Studies of bioinvasions have revealed various strategies of invasion, depending on the ecosystem invaded and the alien species concerned. Here, we consider how migration (as a demographic factor), as well as ecological and evolutionary changes, affect invasion success. We propose three main theoretical scenarios that depend on how these factors generate the match between an invader and its new environment. Our framework highlights the features that are common to, or differ among, observed invasion cases, and clarifies some general trends that have been previously highlighted in bioinvasions. We also suggest some new directions of research, such as the assessment of the time sequence of demographic, genetic and environmental changes, using detailed temporal surveys.

Introduction

Bioinvasions (i.e. the successful establishment and spread of species outside their native range) are increasingly frequent, and can have detrimental consequences, including the erosion of biodiversity and the disruption of invaded ecosystem function [1]. They can also cause public health risks [2], and damages to agriculture and fisheries [3]. In a few instances, such as the invasion of the Great Lakes by the zebra mussel *Dreissena polymorpha* [4,5] or the invasion of North America by the plant *Silene latifolia* [6], the mechanisms of invasion are well understood. However, a general explanation for bioinvasions that extends beyond the particulars of biological systems is still lacking. A potential reason is that, until now, the search for general causes of bioinvasions has concentrated on two aspects: understanding what predisposes a species to become an invader and a community to be invaded. In spite of numerous comparisons between successful and failed species introductions [7] or between invasive and non-invasive species [8], there is neither a definitive list of characters that define a good invasion strategy [9] nor a general predictor of community invasibility (although disturbance is a possible exception [10]). These approaches thus do not converge to a unifying pattern,

suggesting that our ability to predict invasions is still limited.

In our opinion, these approaches have met with limited success because they focus separately on the properties of invaders and of invaded ecosystems. Invasions, however, represent a match between a species and an ecosystem [11] rather than an intrinsic property of either one. Indeed, a species can only invade if it has the adaptations that are necessary for success in the environment invaded. However, how can some species succeed in an environment that differs from their native one, sometimes displacing native species that should *a priori* be better adapted to the local conditions [12,13]? Here, we consider the corollary of this paradox: why were species that ultimately succeeded in invading a new environment not previously dominant in it? In other words, what limited their invasion potential?

Some species are naturally pre-adapted to exploit a particular environment but, owing to insufficient migration abilities, are unable to reach it. However, in other cases, this pre-made match is imperfect, and change in either the invaded habitat or the invading species is necessary before successful invasion occurs. In such cases, invasion involves ecological and/or evolutionary changes. Most studies of bioinvasions have thus far considered ecological changes, and have only recently begun to include evolutionary ideas [14–16]. However, a conceptual framework that combines these two types of change is still lacking. Here, we formalize this integration by examining three theoretical scenarios of invasion based on the respective roles of migration (as a demographic factor) and ecological and evolutionary changes in invasion success. We then evaluate whether such a framework can help us to find general rules for bioinvasions that could help to predict, prevent or control them.

Three theoretical invasion scenarios

Several invasion scenarios are possible depending on how migration and other ecological and/or evolutionary forces interact and vary during invasion. We describe here theoretical invasion scenarios that, for the sake of simplicity, represent the extremes of a range of situations.

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Available online 8 November 2005

Glossary

- Allee effect:** a situation where the density of a population is so low as to cause adverse effects on individual fitness owing to difficulties to find partners to mate with.
- Allogamy:** fertilization by the union of male and female gametes from different individuals of the same species (as opposed to autogamy, whereby male and female gametes are from the same individual).
- Bottleneck or founder effect:** the increase of genetic drift caused by a sampling accident in which only a few founders derived from a large population begin a new population.
- Genetic drift:** random changes in gene frequencies in a population.
- Introgressive hybridization:** the incorporation of genes from one species into the gene pool of another because some fertile hybrids are produced from crosses between the two species.
- K strategist:** a species with a set of life-history traits (e.g. large size, late reproduction, low fecundity, long-lived, etc.) that enables a high carrying capacity (K).
- r strategist:** a species with a set of life-history traits (e.g. small size, early reproduction, high fecundity, short-lived, etc.) that enables a high instantaneous rate of increase (r).

Scenario 1: migration change

In the case of a pre-existing match between an alien species and the novel environment that it encounters, invasion is only limited by demography when individuals are either absent or too scarce to initiate a viable population. A change in the migration regime, possibly as a result of human activity, is sufficient to initiate such an invasion (Figure 1). The invader was previously absent from the novel environment owing to its inability to get there. Such situations, reflecting so-called 'empty niches' or 'pre-adaptation of the invasive species', are more likely to involve species with low natural mobility and isolated or unsaturated communities. Invasions following intentional or accidental introductions onto islands [17] are good candidates for scenario 1. For instance, the brown tree snake *Boiga irregularis* has proliferated since its introduction to Guam during the late 1940s, consuming birds and lizards that had no previous experience of tree-climbing predators [18]. Scenario 1 can also occur in niches that are already occupied, as attested by the niche overlap between introduced grazers and the resident species that they have displaced (e.g. the overlap between European rabbit *Oryctolagus cuniculus* and Australian

herbivores such as the burrowing bettong *Bettongia lesueur* and the greater bilby *Macrotis lagotis* [19,20]).

Scenario 1, regardless of whether the niche is empty, raises the problem of why an alien species performs better in a particular niche than do local community members that have long experience of the local conditions. This reflects some form of adaptive deficiency of the local community, which can result from historical contingency (i.e. favourable mutations are rare and can appear only in some places). The lack of coevolutionary history can also be advantageous to the invader. This is the core of the enemy release hypothesis, whereby invaders benefit from the lack of specialized natural enemies in the recipient community [21]. Enemy release has often been found in transcontinental invasions, although there is currently little empirical evidence that it causes invasions. Hence, the environment in the new range can not only match the ecological requirements of the invasive species, but also be more favourable initially than is the native range.

Scenario 2: environmental change

Migration is sometimes not the main limit to the expansion of the range of a species. Once migration has occurred, the invasion only begins when a new match arises between the environment and the introduced species, possibly after repeated contacts with the new range.

The new match can arise via a biotic or abiotic environmental change in a given area. If these new environmental conditions fit the niche requirement of an alien species, this species might spread even without acquiring new adaptations (Figure 1). Range expansions of many species after Pleistocene glaciations from southern refugia towards the north (e.g. the brown bear *Ursus arctos* that has colonized most of Europe from an Iberian and Caucasian refuge [22]) are examples of a scenario 2 invasion type. Similar modifications of species ranges follow current global warming (e.g. the recent appearance of warm-water species in the Mediterranean Sea, such as the fish *Scartella cristata* [23]). Additionally, human-induced disturbances enhance invasions,

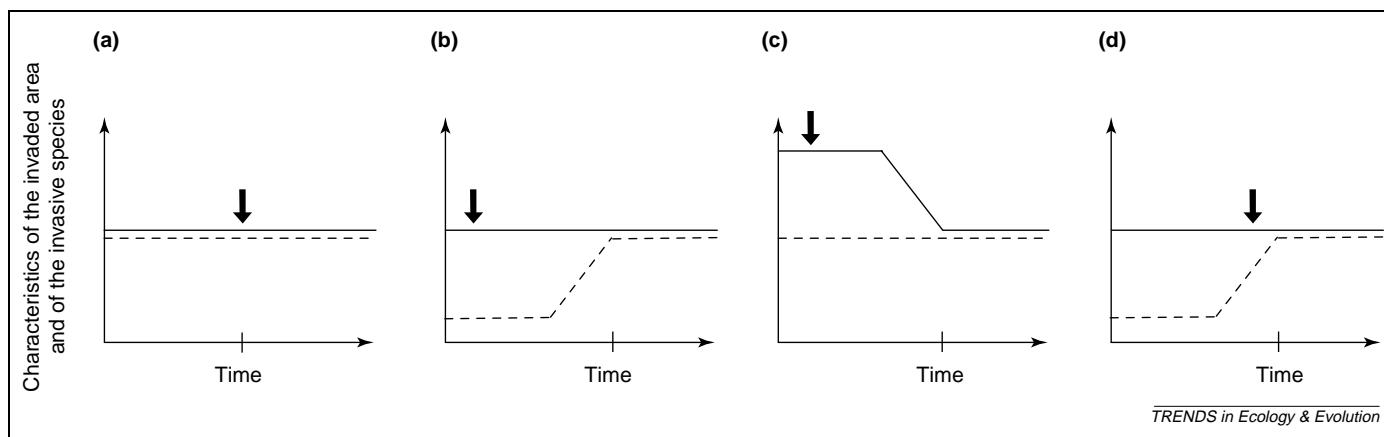


Figure 1. Theoretical invasion scenarios. Characteristics of the invaded area and of the invasive species are represented by a dotted line and a solid line, respectively. An arrow and a vertical stroke indicate the time of the first potential contact between the invaded area and the invasive species (through migration), and the starting point of the invasion process, respectively. Scenario 1 (a): only a change in migration regime is needed to initiate invasion. Scenario 2 (b): the invasion begins after a change in the invaded area that enables a new match between the invasive species and the invaded area. Scenario 3 (c): the invasion begins owing to genetic change(s) in the invader. Scenario 1+2 (d): mixed invasion scenario, where a change in migration regime and invaded area is needed to initiate invasion.

primarily of species that are commensal with humans [24]. For example, large-scale farming has promoted the invasion of weeds, diseases and pests of crops and domestic animals. Finally, some invasive species cause rapid changes in ecosystems and thereby pave the way for subsequent invasions ('invasional meltdown' [25]). For example, predation on tadpoles by dragonfly nymphs had previously prevented the invasion of Oregon, USA by the eastern North-American bullfrog *Rana catesbeiana*. However, introduced fish have reduced the density of predatory dragonfly larvae, enabling the bullfrogs to establish [26].

Scenario 3: evolutionary change

Under scenario 3, invasions start as a result of genetic changes in the invader that are a consequence of a combination of evolutionary forces (Figure 1). We assume here that the introduction has occurred (sometimes repeatedly), but without the establishment of self-sustaining populations. Several non-exclusive factors might have prevented the adaptations that are necessary for invasion [27].

Reduced genetic variance. Introductions can involve small populations containing little genetic variation. Genetic drift (see Glossary) in such populations can further diminish the genetic variation available for selection. Neutral genetic variation, although not necessarily representative of variation relevant for selection, might be extremely low following introduction [28], no different from that of the source populations [29], or greater than in source populations as a result of multiple introductions [30]. Genetically depauperate populations can gain evolutionary potential from new migrants that are either already suited to the new conditions or that provide the raw materials to generate new successful genetic combinations. For example, a Cuban lizard *Anolis sagrei* required multiple introductions from different source populations before it spread throughout Jamaica and Florida, but the process was different in each invasion [30]. In Jamaica, a first introduction remained latent for more than a century, and a later introduction spread across the whole island, suggesting that only the second introduction contained the genetic material that was appropriate for invasion. By contrast, all invasive populations in Florida are mixtures of haplotypes from several different source populations on Cuba. Increased genetic diversity might have promoted invasion success, although it is impossible to know whether invasion resulted from the arrival of the right genotypes at the right time or from new genetic combinations. Similarly, among successful plant invaders, multiple introductions appear to be the rule rather than the exception [31].

Inappropriate range of adaptive variation in the original species. Appropriate phenotypes for a target ecosystem might not exist in the natural range of variation of the candidate invader. Major genetic changes, particularly polyploidization and hybridization [32], can generate invasive strains that are sometimes considered to be new species, such as the allopolyploid invasive grass *Spartina anglica* [33] or the exotic saltcedar *Tamarix* spp. [34]. Hybridization can provide the raw material for rapid

adaptation by producing extreme or 'transgressive' phenotypes [35]. Hybridization can also enable introgression of adaptive alleles, as in the case of *Rhododendrum ponticum* [36]. Naturalized populations in the UK show evidence of introgression from North American *R. catawbiense* into Iberian *R. ponticum* for morphological and genetic markers. Introgression is greatest in populations in eastern Scotland, which is the coldest area of the invaded range. This suggests that hybridization introduced cold tolerance into *R. ponticum*, which then enabled this southern species to establish in northern climes [35].

Maladaptation owing to excessive migration. Theoretical studies demonstrate that range expansion along an environmental gradient can be limited by excessive gene flow from central to peripheral populations [37]. Therefore, a disruption in migration is sometimes necessary for local adaptation in peripheral populations, and could, paradoxically, trigger scenario 3 invasions, provided peripheral populations produce sufficient local recruits to persist [27]. The Argentine ant species *Linepithema humile* is a possible example because their invasive success relies on high-density supercolonies that exist through lack of genetic variation at loci used for colony recognition [38–40]. Isolation from the native range prevents the introduction of additional colony recognition alleles. Hence, although anthropogenic fragmentation of habitats has negative effects on population dynamics, it might trigger some invasions by enabling local adaptation.

Under scenario 3, to infer the respective magnitude of the different evolutionary forces and to then explain the observed genetic changes, it is crucial to know at which temporal and spatial scales they act [41].

Application of our approach

In practice, applying our proposed framework requires answering the following: (i) Has there been a major change in the invaded environment? Answering this requires long-term ecological data; (ii) Has there been evolutionary divergence in adaptive trait(s) between native and introduced populations? Answering this requires quantitative genetic investigations; (iii) Has there been a change in migration regime (e.g. artificial introductions)? This necessitates information about long-distance migration; and (iv) When did invasion occur relative to these events? This requires detailed historical information. Box 1 gives some examples of invasions analysed using our framework.

Obtaining the necessary information is difficult and all four questions have yet to be answered for most known invasions. In particular, the timing of invasion relative to other events is often impossible to establish, although this is crucial, as shown in the example of the freshwater snail *Melanoides tuberculata* (Box 1). Here, invasion occurred before evolutionary changes, rendering this a scenario 1 rather than scenario 3 situation. Furthermore, concluding causation from temporal successions of events requires previous ecological knowledge, as for the introduction of mycorrhizal fungi that enabled *Pinus* species to invade the southern hemisphere (Box 1). Finally, many invasions appear, at least at first, to combine characteristics of different scenarios. However, it is not clear whether this

Box 1. Application of the proposed framework on examples of invasion

There are three examples of successful invasions for which the proposed framework would enable further understanding of the mechanisms and processes involved.

Melanoides tuberculata: Scenario 1 in spite of subsequent evolution

Melanoides tuberculata, a tropical Asian and African freshwater snail, reached America on imported aquarium plants approximately 65 years ago. The snails reproduce mainly parthenogenetically and produce morphologically distinct clones. The best documented invasion, in Martinique, has seen the serial replacement of eight clones since 1979, which have sequentially outcompeted each other in a repeatable sequence [49] from least to most K strategist with decreasing clutch size but increasing juvenile size [45]. No environmental change occurred in the invaded area and changes in the traits of invaders arose *in situ*, with natural selection acting on variation arising from repeated introductions from different parts of the native distribution and sporadic sexual reproduction producing new recombinant clones [45,50]. Although this appears consistent with scenario 3, by 1980, most of the watersheds in Martinique had been invaded by only two poorly competitive clones. Therefore, although natural selection subsequently improved competitive ability in this species, evolutionary change at the species level was not instrumental for invasion.

Pinus pines in New Zealand: Scenario 2

Although *Pinus* pine plantations were established throughout the southern hemisphere by humans, they failed to escape and spread until suitable mycorrhizal fungi were also introduced. Pines are obligate ectomycorrhizal species and southern hemisphere soils are likely to have originally lacked suitable mycorrhizal fungi. Only when soil from the native range was imported did these fungi spread, ultimately enabling pines to invade New Zealand and South Africa [51]. Native and introduced pines do not appear to differ strongly in adaptive traits, although this remains understudied. Hence, although the initial introduction of pines was human mediated, their invasion ultimately required an environmental change in the form of the introduction of suitable mycorrhizal fungi.

reflects either our lack of information about which changes were instrumental to promote invasion, or the multifactorial nature of most invasions. In principle, the simultaneous occurrence of several necessary changes (in the environment, migration and adaptive traits) is less likely than just one, unless these changes are somehow correlated. Human activities causing major changes in the environment and migration might result in such correlations, thereby stimulating invasions with scenarios 1, 2 and a mix of both (Figure 1). Habitats that are subject to anthropogenic disturbance are thus more likely to be invaded [10]. However, it remains to be determined why this is the case. Did most of these species need migration and habitat change to invade (i.e. scenarios 1+2), or does the effect of human activities rely mainly on only one of these factors?

Toward a better understanding of the mechanisms underlying bioinvasions

Our purpose here is not to classify invasions into categories, but to generate a logical framework to further our understanding of the mechanisms and processes involved in invasions. Other than the role of anthropogenic perturbation, other general trends have been

Genetic change initiating invasion in *Senecio*: Scenario 3

In England, the invasive plant *Senecio vulgaris hibernicus* is an introgressed hybrid of the native *S. vulgaris* and the introduced *S. squalidus* from Sicily. *Senecio v. hibernicus* bears the allele at the RAY locus from *S. squalidus* that induces the production of radiate flower heads (Figure 1). These attract more pollinators and outcross more than do the discoid flower heads of *S. vulgaris*. The invasive hybrid often produces more seeds with longer dormancy than do its parents, which is advantageous under ecological conditions of high seedling mortality [52]. Here, a genetic change through introgressive hybridization appears to be the key process that resulted in invasion.

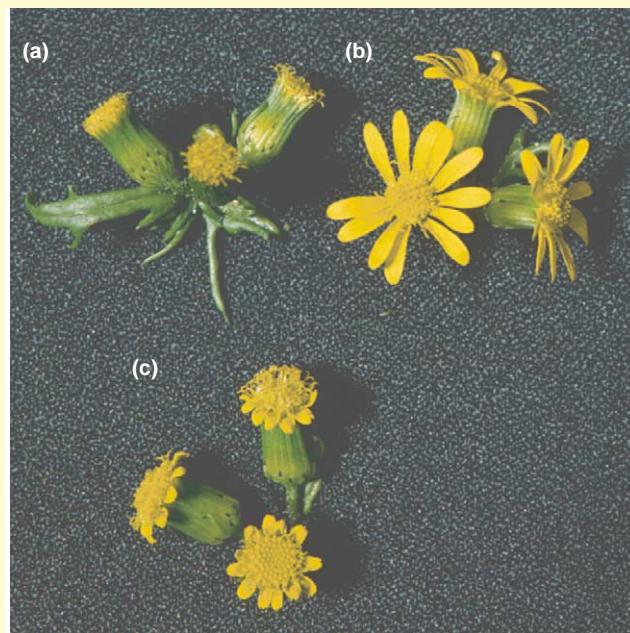


Figure 1. Flower heads of *Senecio vulgaris* (a), *S. squalidus* (b) and *S. v. hibernicus* (c). Reproduced with permission from R.J. Abbott.

previously highlighted in bioinvasions and can be interpreted within our framework.

Propagule pressure

Propagule pressure influences invasion success for species that are limited by migration (scenario 1) but can also promote scenario 3 invasions by providing more genetic variance on which selection can act [42]. Again, it is not obvious how to disentangle these factors.

Autogamy

Asexual reproduction or autogamy is often seen as a key advantage for invasion success [43] because of reproductive assurance of initially small populations. However, these reproductive systems restrict the generation of new variants. Asexuality or autogamy will thus be more likely under scenario 1, where arriving species already have the necessary adaptations to succeed in their new habitat. However, if adaptive change is required for invasion success (scenario 3), allogamy, or even a reversion from autogamy to allogamy is likely to promote invasion [44]. Sporadic sexual reproduction in predominantly asexual species, with generation of new variants, can also enhance invasiveness, as in *M. tuberculata* [45].

Time lags

A time lag is often observed between introduction and successful invasion, including further range expansion. This is expected for scenarios 2 and 3, because the species–environmental match required for invasion depends on a change in either the environment or the species. Introduced species that are adequately pre-adapted to their new habitat (scenario 1) should succeed immediately following introduction. However, purely demographic phenomena (such as Allee effects) or sampling bias (a density below detection thresholds) might also result in a transient lag time.

Life-history traits

Invaders are often *r* strategists [1], although high competitive ability (i.e. *K* strategy) also appears to be important [46]. Emphasizing the match between the organism and the environment, as in our framework, helps resolve this contradiction. Whether a strategy enables invasion to occur depends on the recipient ecosystem and resident community. In models of the competition–colonization tradeoff, when two sufficiently similar species meet, the better competitor excludes the other, regardless of the perturbation regime [47]. An invader encountering an already occupied niche will only succeed if it is a better competitor than the resident species. Established species therefore set up a competition threshold that invaders must exceed. However, species investing too much in competitive ability (i.e. *K* strategists) are poor colonists. Species that are more *r* selected will invade faster and/or more often provided they remain above the competition threshold set up by residents. This interpretation predicts successive waves of invasions of increasingly *K* strategists into occupied niches, as observed in *M. tuberculata* (Box 1), and invasion of *r* strategists into empty niches. For example, a particularly *r*-strategist variety of the grass *Spartina alterniflora* has invaded the previously grassless mud flats on the American Pacific Coast [48].

Conclusion

The present analysis examines the processes involved in bioinvasions that generate a match between the invader and its new home. Although the search for a single invasive strategy is illusory, attempts at meaningful generalizations could benefit from our proposed framework. It provides logical links between previous generalizations and enables insight into some of them (e.g. why are human activities important?). It also generates unexpected theoretical scenarios (e.g. invasion enabled by a rupture in migration leading to decreased inflow of maladapted genotypes) that deserve examination. Our framework might appear at first difficult to apply because, in most cases, the invasion scenario is not easy to infer or invasion can be perceived as a mixed situation. However, our inability to disentangle the role of simple causal categories such as migration, habitat change and trait evolution might rather reflect a lack of focus on some useful research directions, such as the establishment of precise temporal sequences of various events, and the simultaneous evaluation of environmental, demographic and genetic changes. We hope that our framework will

inspire multidisciplinary research looking for common causes behind the diversity of invasion scenarios to better predict and prevent future invasions.

Acknowledgements

We thank T. Giraud, T. Lenormand, I. Olivieri, V. Ravigné, the CBGP scientific community and reviewers for insightful comments on the article. We thank also R.J. Abbott for Figure 1 in Box 1. B.F. was supported by a PhD fellowship from the French Ministry for Research and Technology and a ‘Lavoisier’ post-doctoral grant from the French Ministry of Foreign Relationships.

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9–14 July 2006

11th International Deep-Sea Biology Symposium, Southampton, UK
http://www.noc.soton.ac.uk/GDD/DEEPSEAS/symp_pages/symphome.html

11–12 July 2006

BES/IEEM Ecological Impact Assessments: Science and Best Practice, Bath Spa University College, Bath, UK
http://www.britishecologicalsociety.org/articles/groups/conservation/bes_ieem_conf/

18–22 July 2006

International Fish Biology, St Johns, Canada
<http://www-heb.pac.dfo-mpo.gc.ca/congress/>

23–29 July 2006

11th International Behavioral Ecology Congress, Tours, France
<http://www.isbe2006.com/>

6–10 August 2006

Animal Behaviour Society, Salt Lake City, USA
<http://www.animalbehavior.org/ABS/Program/Snowbird05/>

6–11 August 2006

91st ESA Annual Meeting, Memphis, USA
<http://www.esa.org/memphis/>

13–19 August 2006

24th International Ornithological Congress, Hamburg, Germany
<http://www.i-o-c.org>

22–26 August 2006

1st European Congress of Conservation Biology, Eger, Hungary
<http://www.eccb2006.org/>

4–6 September 2006

ECBB: 3rd Joint European Conference on Behavioural Biology, Belfast, Northern Ireland
<http://asab.nottingham.ac.uk/meetings/asab.php>

5–7 September 2006

British Ecological Society Annual Meeting, University of Oxford, UK
<http://www.britishecologicalsociety.org/>

10–14 September 2006

American Society for Fish Biology, Lake Placid, USA
<http://www.fisheries.org/html/index.shtml>

3–7 October 2006

American Ornithologist Union, Veracruz, Mexico
<http://www.naoc2006.org/>

18–21 October 2006

Society of Vertebrate Palaeontology
<http://www.vertpaleo.org>