Bridgehead effects and role of adaptive evolution in invasive populations

Cleo Bertelsmeier[1] and Laurent Keller[1]

[1] Department of Ecology and Evolution, University of Lausanne, Switzerland.

Correspondence to: cleo.bertelsmeier@unil.ch, laurent.keller@unil.ch

Abstract

Biological invasions are a major threat to biodiversity, agriculture and human health. Invasive populations can be the source of additional new introductions, leading to a self-accelerating process whereby "invasion begets invasion". This phenomenon, coined "bridgehead effect", has been proposed to stem from the evolution of higher invasiveness in a primary introduced population. There is, however, no conclusive evidence that the success of bridgehead populations stems from the evolution of increased invasiveness. Instead, we argue that a high frequency of secondary introductions can be explained by increased abundance in the bridgehead region or the topology of human transport networks. We outline the type of evidence and experiments that are needed to demonstrate adaptive evolution and higher invasion success of introduced populations.

Key words:

Biological invasions, evolution of invasiveness, adaptation, globalization

i. Evolution as a potential driver of bridgehead effects

All species have limits to their geographical distributions [1]. Historically these limits were determined by a range of environmental factors such as climate or resource availability, biotic interactions and physical barriers to dispersal [1]. However in the current period, particularly since the Industrial Revolution, increased international trade and human movement have resulted in the accidental movement of many species worldwide. This on-going movement of species has brought about the breakdown of biogeographic boundaries that have historically limited the distributions of organisms [2] and some of these species become “invasive” (i.e., an introduced population maintains itself without human assistance, spreads further and has impacts on biodiversity, health, agriculture or ecosystem functioning) [3]. As biological invasions are a leading cause of global biodiversity loss and the erosion of ecosystem functions worldwide [4], it is important to develop a better understanding of the invasion process [5].

In several species, it has been observed that introduced populations are themselves the source of additional new introductions (e.g. [6–9]), leading to a self-accelerating process whereby “invasion begets invasion”. This phenomenon has been called the “bridgehead effect”, using the analogy of a military unit establishing a foothold at the far side of a bridge, prior to further incursions into hostile territories [10]. Recently, the bridgehead effect has been highlighted by a horizon scan identifying the most important issues likely to affect how invasion processes and dynamics are studied in the near future [11], because it could drive steep rises in global invasion rates [12]. A potential explanation for an introduced population being the source of several secondary introductions is that this bridgehead populations evolve “higher invasiveness”; that is, they acquire new traits increasing the probability of successful establishment and further spread relative to native populations [10]. While this idea of adaptive evolution as a driver of bridgehead effects is appealing, we argue here that there is currently no empirical support for this hypothesis. Most studies that suggested a role of adaptive evolution are based on the observation that introduced populations are the source of one or several secondary introductions of invasive species. In the first part of this review we show that none of these studies tested for the appearance of new adaptive traits in the bridgehead population. Moreover, we argue that a high frequency of secondary introductions can be explained by the topology of human transport networks, with species more likely to be introduced to, and spread from, highly connected hubs. Next, we discuss the few studies that actually demonstrated genetic changes in a bridgehead population, emphasising that these observed genetic changes have not been shown to increase invasiveness. Finally, we outline the evidence that would be needed to demonstrate adaptive evolution and higher invasiveness of introduced populations.

ii. Evidence for adaptive evolution in invasive populations

We conducted a literature search on Web of Science in July 2017 using the key words “biological invasions” OR “invasive” Or “introduc*” OR “alien” AND “bridgehead effects” OR “secondary introductions” OR “secondary spread” OR “multiple introductions”. For our review, we retained all papers that described invasion histories with secondary spread from an initial invasive population and which have hypothesized that this could be explained by evolution of higher invasiveness in the bridgehead population compared to native populations (listed in Table 1). These papers have used either a spatial spread pattern or genetic changes in the invaded range to suggest adaptive evolution as a driver of bridgehead effects.

Spread patterns as evidence of adaptive evolution in bridgehead populations

The vast majority of the studies suggesting a role of adaptive evolution used genetic markers to retrace the invasion history of a single invading species. Because a single bridgehead population was found to be the source of several secondary introductions (Table 1), while no (or few) new invasions occurred through direct introductions from the native range, the authors hypothesise that an adaptation for increased invasiveness may have occurred (Table 1). While some of these studies are careful to underline that the appearance of new adaptations in the bridgehead population is only one of the possible explanations, others such as Zepeda et al. [13] are less cautious, making statements such as “Biological invasions are rapid evolutionary events in which populations are usually subject to a founder event during introduction followed by rapid adaptation to the new environment”. For example, in the study that originally coined the term “bridgehead effect”, the authors concluded that adaptive evolution most likely occurred in the introduced population of the Asian harlequin ladybird in the USA because this population was the source of several secondary invasions in Europe, Africa and South America while all attempts to establish new populations for biocontrol purposes by releasing individuals from the native population failed [10]. However, there is currently no empirical support for adaptive evolution in the introduced US population. Moreover, and importantly, successful establishment is a rare event with the effect that in most cases a species needs to be introduced many times in sufficient numbers before a self-sustaining population establishes [14]. Therefore, the failure of individuals originating from their native range to establish a new population does not demonstrate an evolutionary shift in the invasive populations.

These studies have not demonstrated adaptation. But many suggest that adaptive evolution could drive the observed secondary spread, arguing that this would be “evolutionary parsimonious” because a single evolutionary shift in a single population, the bridgehead population would be required to explain increased invasion success (e.g. [10,15–19]). However, this argument is problematic because adaptation is often not necessary for establishment of a species outside of its native range. Recent studies indicate that in the majority of cases species invade habitats with environmental conditions similar to those in their native range [20–22]. Even in cases where the introduced populations occupy different environmental conditions, this is often within the species fundamental niche, with the effect that establishment requires no adaptation [23]. Moreover, there are two alternative explanations for bridgehead populations being the source of the majority of new introductions, in the absence of the evolution of any new adaptive traits. The first is associated with the fact that introduced populations frequently reach much higher densities than those in native range, because of increased resource availability, filling of an empty niche or release from natural enemies such as herbivores, predators, pathogens and parasites absent from the introduced range (reviewed in [24]). All of these can lead to increased biomass and abundance in the introduced range compared to the native range [25] with subsequent greater likelihood of movement to new non-native regions. The second explanation is associated with the network properties of human commerce. Dispersal of invasive species is tightly linked to trade networks. For example, the invasion history of *Solenopis geminata* seems to closely follow the Spanish trade routes in the 16th century [26]. Current human transport networks are heterogeneous with most nodes (cities, ports, countries) having few connections and a few nodes (e.g., transport hubs) having many connections and these nodes are transport hubs [27]. Moreover, these networks have small-world properties, meaning that any node in the network can be reached from any other node in a few steps [27]. Given these network properties, secondary spread can be expected to be the rule rather than the exception [27,28].

In summary, the statement that adaptive evolution in bridgehead populations is the most “evolutionary parsimonious” explanation for the bridgehead phenomenon is mistaken; the most parsimonious scenario is simply no adaptation at all. Therefore, in the absence of any convincing evidence for adaptive evolution, increased abundance in a primary invaded area or the peculiar topology of the transport network should be the null hypothesis for explaining bridgehead effects.

Genetic changes taken as evidence of adaptive evolution in bridgehead populations

Two studies suggested that genetic changes could underlie greater invasiveness of bridgehead populations [13,29]. However, none of these have demonstrated a causal link between the trait change and invasion success and cannot exclude that other processes have played a role in observed trait changes.

In the first study the authors provide a detailed study of how the tobacco aphid (*Myzus persicae nicotianae*) was first introduced in North America and then to South America [13]. They show that introductions were associated with bottlenecks. The authors also suggest that shifts in the mode of reproduction may mitigate the effect of reduced genetic diversity mentioning the Argentine ant as an example. In this species a reduction in genetic diversity has been suggested to be at the basis of the success through a shift in social structure of colonies [30]. However, a later study revealed that there is no difference in social structure between native and introduced populations of the Argentine ant, the only difference being the size of the supercolonies which is larger in the introduced range, probably as the result of ecological factors [31]. In the case of their study on aphids, Zepeda-Paulo et al. [13] mention that a shift to asexual reproduction might have been important to circumvent the loss of genetic variation associated with bottlenecks during introductions. However, there is yet not data showing that the establishment probability of asexual aphid populations is greater than sexual populations.

The second study suggested that increased genetic diversity, instead of reduced genetic diversity, may have conferred greater adaptive potential in a population of glossy buckthorn introduced from a bridgehead region [29]. Due to admixture resulting from several primary introductions, the bridgehead population had high allelic richness at loci with putative ecological functions. Moreover, there was evidence of selection on loci putatively involved in reproductive functions, which was interpreted by the authors as an adaptive shift towards more “reproductive” phenotypes. However, this study did not identify any phenotypic differences between individuals from the native and introduced range nor did it demonstrate that the introduced population had a greater colonization success compared to native populations. Although previous work has shown that admixture in invasive populations may increase fitness relative to native populations [32], it is currently not possible to conclude from the evidence in this study if adaptation played any role in the secondary spread of glossy buckthorn.

iii. Evidence needed

In order to demonstrate that adaptive evolution is an important driver of secondary introductions, one would need to first establish that a trait conferring greater invasion success evolved in the bridgehead population. Thus far, there is only limited evidence for adaptive evolution in introduced populations (reviewed in [33]), with the notable exception of a well-designed common garden experiment comparing the fitness of invasive plant populations along a climatic gradient over several growing seasons [34]. But there is currently no specific evidence of adaptive evolution in bridgehead populations, favouring secondary spread. Here, we outline what type of evidence would be required to test this hypothesis.

Demonstrating that a trait conferring greater invasion success evolved in a bridgehead population requires several steps (Fig. 1). The first is to determine the exact origin of the introduced population. Because organisms display geographical variation in many phenotypic traits, demonstrating a difference between a native and an introduced population does not allow one to make any conclusion about evolution in the introduced range as it may simply reflect variation in the native range. For example, most native populations of little fire ants thrive under tropical climatic conditions, while some introduced populations have established in colder locations [35]. This could be taken as evidence for a potential shift in climatic tolerances in the introduced population. However, a genetic study revealed that the source population of the introduction is located at the edge of the native distribution and was therefore already pre-adapted to establishing under a Mediterranean climate [35].

The second step is to demonstrate that phenotypic differences between a source and introduced population have a genetic basis. Many traits are plastic and differences between any two populations may simply reflect the effect of ecological and biotic factors. The third step consists in demonstrating that a genetic change that occurred in the primarily introduced population provides a selective advantage. This requires carrying-out well designed reciprocal transplant experiments to compare the native source and the bridgehead populations [33]. Ideally, such studies should measure fitness over multiple growing seasons or generations [33]. As this is not always feasible, an increasing number of studies use genomic screens to search for signatures of natural selection at loci possibly involved in adaptation [36,37]. For example, a recent study revealed that selection on loci associated with flowering time could play a role in adaptive evolution in the invasion of Pyrenean rocket [38]. It is however important to note that genomic screens are only correlative and that experiments comparing the fitness of organisms with identified genetic differences remain necessary to demonstrate adaptation.

The final step is to show that a genetic difference between a source and an introduced population is responsible for the success of the bridgehead population as a source of secondary invasions (i.e. that it is a pre-adaptation for further invasions). For example, an adaptation to the climatic conditions of a bridgehead population will act as a pre-adaptation only if the habitat where secondary introductions occur has climatic conditions more similar to those of bridgehead population than to those of the native population. In general, demonstrating that the bridgehead population is pre-adapted for secondary spread is difficult since it would require conducting controlled introductions, which raise ethical issues (fears that the invasive species may escape into the wild) and because, it is logistically challenging, as the experiment would have to be repeated at different locations to preclude the role of idiosyncratic ecological factors.

An alternative approach to testing experimentally if adaptive evolution is a driver of secondary spread is to investigate whether historical introductions from the introduced range more frequently lead to successful establishment than introductions from the native range. Given that this would require accounting for variation in propagule pressure from the native and invaded range [39], it may be difficult to obtain sufficient data for a single species because numbers of introductions are generally limited. Larger sample size could possibly be obtained using data from multiple species. Alternatively, it might also be possible to use data from biocontrol attempts, where species have been introduced by humans on purpose. The idea would be to test if introductions from the introduced range of a species are more successful than introductions directly from the native range, while accounting for propagule pressure. The advantage of this type of data is that there are observations of both successes and failures and perhaps even estimates of the actual propagule pressure, which would be important for this analysis.

Perspectives and Conclusion

The bridgehead effect has recently become a focus of invasion science because it has the potential to drive global increases in future invasion rates. A popular explanation for the bridgehead effect is that it stems from the evolution of higher invasion success of the bridgehead population. In many studies, authors are careful to suggest that alternative hypotheses are possible. However, collectively these studies placing the bridgehead effect in the context of an “evolutionary parsimonious scenario” give the impression that the evolution of traits conferring greater invasiveness in the bridgehead population is an important factor of the invasion process, in particular by favouring secondary spread. However, in the absence of empirical evidence for adaptation, the null hypothesis should be that secondary spread from bridgehead populations simply stems from increased abundance in bridgehead populations or general properties of transport networks. Yet, for the purpose of the management of biological invasions the point made previous authors [10] that there should be heightened vigilance against invasive bridgehead populations is still valid. This is because bridgehead population are generally more likely to generate new introductions than native populations, independently of the underlying process generating this secondary spread.

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		Evidence needed to demonstrate that adaptive evolution drives bridgehead effects					
Paper group	**Taxon**	Identification of the origin of the introduced population(s)	Genetic basis for phenotypic differences	Genetic phenotypic difference demonstrated to confer greater invasiveness	Pre-adaptation for secondary spread	**Alternative explanation(s) proposed for the observed pattern**	Ref.
Pattern of spread	Red imported fire ant (*Solenopsis invicta*)	Yes	No	No	No	Yes. High levels of secondary transport could reflect higher propagule pressure from the USA relative to native areas because the USA are highly connected to the transport network.	[40]
	Harlequin ladybird (*Harmonia axyiris*)	No	No	No	No	No	[10]
	Potato powdery scab pathogen (*Spongospora subterranea f.sp. subterranea*)	No	No	No	No	Yes. High levels of secondary transport from Europe rather than from the native range could be explained by historical colonization and exploration of Europeans, transporting contaminated potato specimens with them.	[41]
	Colorado potato beetle (*Leptinotarsa decemlineata*)	No	No	No	No	Yes. High levels of secondary transport from Europe could be due to higher levels of commercial trade than in the native range, resulting in more common long-distance transport.	[8]
	White campion (*Silene latifolia*)	Yes	No	No	No	No. But stated that a common garden would be necessary to test the hypothesis.	[42]
	Pathogenic citrus bacterium (*Xanthomonas citri pv. citri*)	Yes	No	No	No	Yes. Secondary transport from Mali could be explained by higher levels of exportation of citrus material from nurseries to neighbouring regions.	[19]
	Western corn rootworm (*Diabrotica virgifera virgifera*)	No	No	No	No	No. But stated that the hypothesis of adaptation needs further investigation.	[9]
	Western flower thrips (*Frankliniella occidentalis*)	No	No	No	No	Yes. Secondary spread from Kunming could be explained by the fact that Kunming is a center for floriculture transportation and a major center for international imports of plants in China.	[43]
Genetic changes	Glossy buckthorn (*Frangula alnus*)	Yes	Indirect evidence	Indirect evidence	No	Yes. Secondary spread could be attributed to role in the early trade of ornamental plants of New York. The invasion of more inland areas may have occurred from nurseries.	[29]
	Tobacco aphid (*Myzus persicae nicotianae*)	No	Yes	Indirect evidence	No	No	[13]

Table 1. Previous studies on bridgehead effects arguing that adaptive evolution may drive secondary spread, the type of evidence used to support the evolution of greater invasion success and alternative explanations proposed for the observed pattern.

Figure legend

Figure 1. Evidence needed to demonstrate that adaptive evolution is an important driver of secondary introductions.