Genetic and behavioral changes in introduced species

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Abstract

Biological invasions can have huge ecological and economic impacts, but the biological processes leading to the success of introduced species are not yet well understood. An important process is that during each step of the introduction, a subset of individuals may be selected. My question in this essay is whether the introduction process would cause behavioral and/or genetic change through a series of selective processes. The initial introduction stages act as a bottleneck, reducing genetic diversity relative to the original population. Invasive Argentine ants show reduced intraspecific aggression, but it is unclear if this change is an adaptation. Invasive cane toads evolve to disperse at a faster rate.

However, there is not enough research available of this subject to proof any patterns. Biological invasions are highly complex and unique, and make it hard to discover any patterns.

Introduction

Invasive exotics tend to have negative to disastrous effects on the invaded ecosystem, as native species can be decimated and may go extinct [1]. Ecosystems are “globalized” as they become more uniform. Biodiversity often drops and ecological and economic impacts may be disastrous. It is alarming that the rate of the establishment of alien species still increases [2].

This rise has been proven correlated to the increase of human travel and trade. Animals also benefit of our technological advances. We and our belongings can travel around the globe in hours, and so can possible stowaways. Human efforts to scan and eradicate for stowaways, do not suffice [3]. Individuals nowadays have the ability to travel over the former impenetrable ocean, and former evolutionary isolated species are joined. This often results in dramatic ecological consequences.

With the eye on the prevention of negative impacts, biological invasions are well studied. The path an invasive species passes is described in the introduction process [3]. The introduction process (see figure 1 [3]) is described in four stages; transport, introduction, establishment and spread. The transport and introduction stage succeed quickly and involves anthropogenic involvement. Establishment and spread includes less external time pressure and resemble population dynamics and ecology.

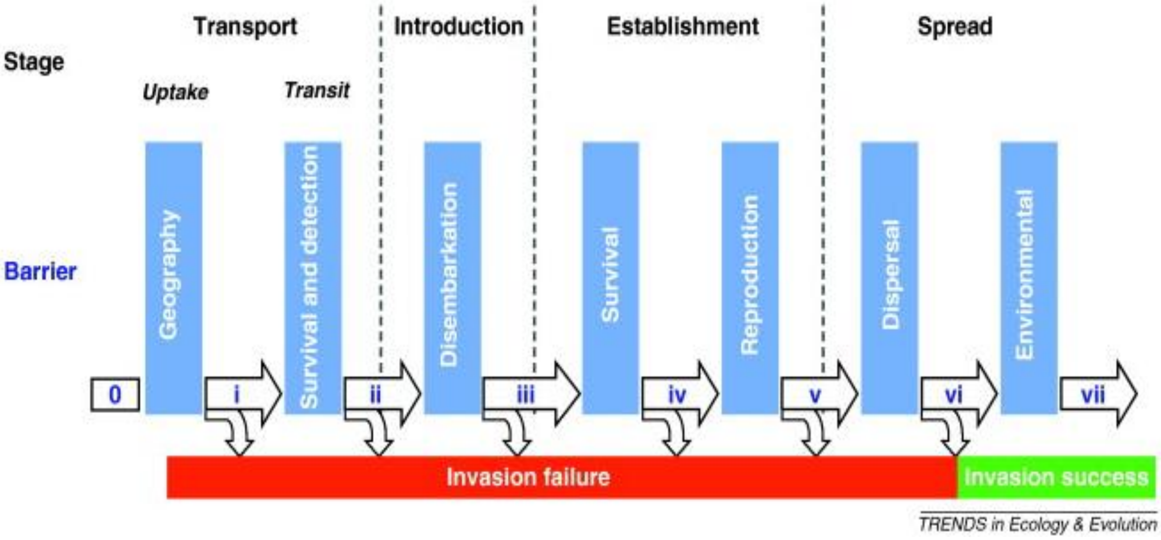

Figure 1: A schematic survey of the introduction process [3].

tep	Explanation
	Individuals in their native range that have not entered a transport vector
	Individuals that have entered a transport vector and are en route to a destination beyond the limits of their native range
i	Individuals within a transport vector that have survived transit and reached the non-native destination without detection
ii	Individuals that have disembarked from the transport vector and continue to evade detection
v	Individuals that are capable of surviving and go on to reproduce
	Individuals that are capable of surviving, reproducing and maintaining a self-sustaining population in the non-native region
i	A self-sustaining introduced population where individuals are able to survive and reproduce beyond the origin area of introduction
ii	An invasive species where individuals are capable of dispersing, surviving and reproducing at multiple localities across the introduced region

Table 1. Steps in the pathway to the success of unintentional species invasions [3]

Each step in the introduction process causes dropouts, therefore potentially selecting for traits. Many introduction attempts fail and even a successfully established species is not defined as invasive before it disperses again [4]. As behavioral traits have an important role in invasion success, populations can undergo behavioral change [3,14]. The major question I want to address in this essay is: Do introduced populations genetically or behaviorally differ of native populations? The appearance of genetic and behavioral traits beneficial for invasion success is expected to amplify in introduced populations.

Knowledge of biological invasions is important, for the phenomenon is not yet fully understood. Understanding how a species matures to an invasive one, should further raise awareness of the possible harmful impacts a still harmless species may cause. Besides, biological invasions are a perfect opportunity to study evolutionary processes on a relatively short time span.

There are many invasion pathways. The different methods of transportation to a non-native area, can be described in great detail, for humans can contribute to biological invasions in many ways. [5]. For example, human infrastructure which connects two formerly segregated areas, already can result in an unintentional introduction. By adopting the introduction process model, this article focuses on stowaways on human transport vectors.

Some biological invasions are the result of escalated intentional introductions. The introduced species are primarily selected for traits which serve human purposes. These species did not run entirely through the introduction process, as they surpass the transport and introduction stage. As establishment and spread should be similar for deliberate and accidental introductions, results of these stages of deliberate introductions are allowed for extrapolation.

Background

Genetic change

To harbor genetic change, a population needs to have variation in its genetic material. Subsequently, after an event the abundance of a gene can change. Therefore, genetic diversity in a population is a requirement for evolution of this population. This genetic diversity can be used to adapt to changing circumstances. For example, after a bottleneck event, a part of the population may not be able to reproduce. Subsequently, the genetic material in the remaining population increased in its abundance.

In an introduction event a subset of individuals of the original native population enters a new environment. This newly arisen introduced population has undergone a bottleneck with respect to the native population.

The important question here is whether the genetic composition of this introduced population changed in a particular direction. The bottleneck may be the result of selection on a trait. No selection has to be subjacent. Merely by the decline of the number of individuals, the effects of chance (genetic drift) on gene abundances increases.

In relation to the introduction concept, bottlenecks are induced till the species disembarks the transport vessel. When a stable population has settled, more gradual evolutionary forces can occur.

In the view of punctuated equilibrium [6], a population bottleneck such as in the introduction process, would be exactly the event needed for the adaptation of an exotic to a new environment. Punctuated equilibrium states that mutations in large populations cannot fixate. In this case, only small populations can exhibit evolution.

Behavioral change

Intraspecific behavioral variation in the success of introductions is important [3] . Therefore selection on behavioral traits which enhance invasion success, should be severe. Behavior is a manifestation of the phenotype, and therefore is not necessarily heritable. If behavioral changes by the introduction event are to be sustained, it should be passed on to the next generation one way or another.

Behavior has an underlying genetic base, or the instinct, as it is often called. Partly it is composed out of past experiences and thus is dependent on environment influences. Offspring can acquire a part of their parents behavior by learning, enabling some kind of behavioral inheritance, called cultural inheritance.

Thereby, certain behavioral types are interrelated [7]. A set of these related behavioral types is called a behavioral syndrome, like aggressiveness and boldness. It can severely restrict the behavioral flexibility. Behavioral syndromes and cultural inheritance are important, for unintentional introductions are mostly noticed when the introduced population is already established. In the time that has passed, the original individuals could easily have reproduced and relevant acquired behavior can already become lost for observation.

Capacity for change

Species with a large relative brain size are proven to be more successful at invasions for mammals [8], birds [9], amphibians and reptiles [10]. The common explanation is that large brains grant an individual higher behavioral flexibility. In turn, behavioral flexibility can enhance survival in the challenges faced in the introduction process. This further emphasizes the role of behavior in invasions. Besides, behavioral flexibility supports more behavioral change, which is important for the main question.

The genetic counterpart in behavioral flexibility, is found in evolvability. Evolvability is defined as the capacity of a population for adaptation. Evolvability is presumed high in generalists in comparison with specialists [21]. Generalists thrive in a variety of circumstances and food sources, as specialists are more narrowly connected to one habitat and one food source.

So, as behaviorally and genetically flexible species have an higher invasion success, the capacity for behavioral and genetic change should certainly be present in invasive species.

The introduction process

Along each step of the introduction process, I shall describe the matching circumstances or conditions which define that step. Afterwards, the traits which have been found beneficial in that stage, interspecific or intraspecific, as an indication for possibly the direction of selection in that step. If present, an example of intraspecific change derivable to this introduction stage is depicted. This specific way is chosen for the elaborate amount of studies devoted to interspecific traits beneficial to invasion success, presumably for the cause of prevention of invasions.

Table 2. Potential behaviors that can influence success of unintentional species introductions at each stage of the introduction process[a] [3]

Behavioral traits	Transport		Introduction	Establishment	Spread	Refs
	Uptake	Transit	Disembarkation			
Actively hide and/or seek shelter	+[c]	+[c]	+/-	-	+[c]	[16], [18] and [45]
Activity	+	-	+	+	+[c]	[19]
Antipredator behavior 1	?	?	?	+/-	+/-	[15],[17],[34],[40] and [51]
Antiparasite behavior	?	?	?	+/-	+/-	[44]
Attraction to and/or tolerance of human-occupied environments	+	?	+	+[c]	+/-	[12],[14],[22] and [23]
Boldness 1,4,5	+	-	+	+	+[c]	[19],[20],[40] and [50]
Dispersal tendency 3,4,5	+	-	+	+/-[c]	+[c]	[13],[15],[19],[33],[37], [38], [46-50]
Exploratory behavior 4	+[c]	-	+	+/-[c]	+[c]	[17], [18], [19], [43] and [52]
Foraging behavior and flexibility 1,2	+	?	+	+[c]	+	[13], [15], [17], [34], [35], [40], [41] and [43]
Habitat preferences and flexibility	+	+	+	+[c]	+[c]	[13], [15],[17],[21] and [22]
Intraspecific aggression 1,2,4	-	-	-	-[c]	+/-[c]	[14], [15], [17], [24-27], [29], [32], [40-42]
Interspecific aggression 3	?	?	+	+[c]	+[c]	[14], [15], [28], [30], [31], [36], [37], [39], [42], [48] and [49]
Mate choice and recognition	?	?	?	+/-[c]	+/-[c]	[13] and [53]
Nesting and/or oviposition behavior	+[c]	?	?	+[c]	+[c]	[11], [12], [22], [24], [27] and [28]
Parental care	+	+	?	+	+	
Social tendency 4,5	+	+/-	+	+[c]	+/-[c]	[19], [25] and [50]
Species recognition	?	?	+	+	+	
Thermoregulatory behavior and flexibility	+	+	+	+	+	[21],[54],[55]

Transport

Uptake

An individual that is to be transported has to gain access to a human transport vehicle. So, an individual living close to human communities has a higher chance to be introduced. Living alongside humans requires a particular set of characteristics.

Urban animals are commonly more aggressive, bold and exploratory [3]. This can be thought of as a pre-adaptation to invasiveness. Adaptation to human disturbance within the native population can result in an increased uptake [56]. Introduced populations therefore will be more of a sample of urban than rural animals.

There are two ways an individual enters a transport vector [3]. Animals enter the vehicle on its own accords and hide in the exterior or interior. Additionally individuals can find shelter inside commercial goods, personal belongings or clothing and are embarked by humans [57]. Ballast water of ships can contain aquatic life, which can be transported through non-native ranges.

Actively hiding or sheltering, social tendency and flexibility in foraging behavior, habitat preferences and nesting behavior promote entering to be transported cargo [3]. Activity, boldness, exploration and dispersal tendency increases the chance an individual enters a transport vehicle (see table 2 [3]).

The garden skink and the delicate skink are two sympatric lizards and possess almost identical traits [18]. Both species have been found in freight, cargo and personal affects. However, only the delicate skink managed to establish outside its native range. The delicate skink has a higher propensity to explore and hide than the garden skink. It is believed these behavioral traits increase uptake of delicate skink and decrease detection during transit. This is supported by interceptions of the biosecurity checks, with an higher uptake frequency of the delicate skink in comparison with the garden skink [18]. This is a perfect example for the significance of certain behavioral traits.

Transit

Depending on the means of transport, transit can provide challenging environmental conditions for an individual. Aircraft are exposed to strong biological screening, but the travelling time to the destination is minimal. A commercial ship has less severe biological screening and is innumerable times bigger, whereby more cargo can be transported. On the contrary, the travel speed is much lower.

Due to longer travel time, the animal transported by ship may have to find a new food source, while an individual on a plane should have no trouble surviving without food. Conditions can vary between transport methods [2,3], but in both transport vessels, flexibility in habitat preference and thermoregulatory behavior can benefit survival. The temperature in the luggage compartment of aircraft can be low.

Once aboard a transport vessel, some personality traits enhancing uptake counteracts the transit stage. In the transit stage, individuals should evade detection by humans, so any conspicuous behavior must be avoided. Obviously hiding behavior is advantageous, as boldness and activity, dispersal tendency and exploratory behavior should be avoided. Therefore, these activity-related traits have adversative effects in uptake and transit. Behavioral tendencies in these traits should be accompanied with behavioral flexibility to grant success in the transport stage.

Introduction

The introduction stage originally includes the escape of captivity or cultivation of intentionally transported individuals [3]. Here, it covers the disembarkation of the transport vector, and is practically the opposite of the uptake stage, where exploratory behavior is encouraged to disembark the transport vehicle. The animal should continue to evade detection and reach a habitable environment.

The transport and introduction stages often happen in very quick succession, and individuals go through multiple bottlenecks [22,58]. Therefore genetic variation will decrease. However, there is no proof these bottlenecks are the result of an underlying selection.

The introduced populations of a much studied invasive organism, the Argentine ant, do socially behave differently of native populations. Introduced communities merely show intraspecific competition, resulting in a gigantic colony in which resources and workers are freely distributed [22]. This phenomenon is also found in other introduced ants. Two possible explanations were proposed.

One explanation was that intraspecific aggression was lost due to the reduced genetic variation after introduction. The genetic similarity between colonies of the introduced ants is increased, by what the colonies recognized each other as kin, as normally occurs between members of one colony.

The other option is that it is an adaptation to compete against native ant populations. The lowering of intraspecific aggression is believed to increase the ability to compete interspecific (see table 2 [3]). Along with human tolerance and escape from natural enemies, it is one of the main reasons this ant is believed to be such a successful invader.

Whether it is caused by selection or not, this reduced aggression is a clear example of genetic and behavioral change in the introduced population, caused by the introduction bottleneck.

Establishment

Introductions often result in the arrival of single individuals or small groups at different times and of different source populations [3]. A much used term to quantify arrivals is propagule pressure [59]. A propagule is a group of stowaways arriving together. Propagule pressure is composed by the amount of introduced individuals (propagule size) and the number of separate release events (propagule number) in a non-native region. It is an effective indication of success at the transport and introduction stage.

As low densities of conspecifics may lead to reduced population fitness (Allee effects) [60], as the initial population must overcome this barrier. As high propagule pressure is considered to be a key element to evade Allee effects. However, some behavior can render its significance minimal [42], like the locating, recognizing and interacting of individuals between propagules. This enlarges the effective population and lowers Allee-effects [3]. This applies to social tendency and species recognition.

Besides, as propagules can origin from different source populations, successful interactions between members of these possibly reproductively isolated populations is necessary. Compatible interactions in mate choice and recognition, nesting and/or oviposition behavior and parental care can degrade isolation barriers and increase population size (see table 2 [3]).

Differential personality types in sociability can decrease Allee-effects and stimulate spread [61,62]. Asocial individuals tend to disperse more at high densities of conspecifics and thrive in low density populations. Oppositely, social individuals disperse at low densities and thrive at high densities. These traits are density dependent and allow for a relatively high population growth at both low and high densities. Concisely, polymorphism in sociability should enhance population growth and spread.

Apart from the possible negative effects of inbreeding depression, genes in small populations more easily fixate (genetic drift), further diminishing genetic variation. With lowered genetic diversity, the population will lose its ability to evolve. This is very detrimental, as the new population will most definitely face new challenges in its new environment and adaptation is important for survival.

However, genetic variation can be replenished by interbreeding with propagules of multiple native origins. In an invasive lizard, the brown anole, admixture of genetic variation of propagules of various geographic origins occurs. Hereby the introduced population gains an even higher genetic diversity than native populations [58,63].

When this theory is tested for the delicate skink [64], the result subverts the importance of admixture. Establishment success for both populations with admixture and without admixture was the same. Admixture in invasions does not seem to influence establishment success.

To self-sustain, the new population must occupy an ecological niche, either by successfully competing with native species, or by finding a non-occupied niche [58]. Occupied niches can more easily be overtaken by expressing a high level of interspecific aggression. As intraspecific aggression lowers the ability to interspecifically compete [22], it negatively impacts the occupation of a niche (see table 2 [3]).

Human presence often disturbs ecosystems [65], weakening the local wildlife. Niches can become vacant and the interspecific competition in occupied niches is lowered. Introduced species [22] with tolerance for (human) disturbance can more easily occupy a niche in these disturbed ecosystems.

Spread

After establishment, the population must disperse away from the introduced range to become truly invasive. This dispersal can be either natural or human-mediated. Dispersal tendency, exploratory behavior and activity are behavioral traits positively correlated with natural dispersal. Also different behavioral types can enhance the spread of the initial population [61,62].

For human mediated dispersal, the same traits mentioned in the uptake stage are useful. For passive uptake, that is actively hiding or sheltering, flexibility in habitat preferences, foraging behavior, nesting behavior and sociality [3]. For active uptake these traits are boldness, exploratory behavior and dispersal tendency, which also benefit natural dispersal.

Generally there is a certain time lag between the establishment stage and the spread stage. It is interpreted as either an ecological or an evolutionary phenomenon [58]. The time lag can be interpreted as the lag phase in an exponential population growth curve. It can also be the time needed for evolutionary adaptation to the new environment.

Cane toads, which momentarily are invading Australia, have an increased invasion rate by fivefold since they were introduced 70 years ago [46,47]. There are indications of rapid adaptive evolution by the emergence of different dispersal types. Cane toads from the invasion front have greater endurance [46] and longer leg length [47] than cane toads in long-colonized areas.

Are this selection processes widely applicable?

Aforementioned selecting forces in the introduction process may seem true for a specific species in a specific invasion site, but do these also find expression among different species or different invasion sites? Here a subdivision is made for within taxa comparison. For example, higher vertebrates should have more trouble evading detection during transit than insects, alone for their sheer size.

Among species

In a comparative article, correlations between species and event traits and invasion success have been tested for 49 studies [66], within and among species of seven taxa (birds, finfish, insects, mammals, plants, reptiles/amphibians and shellfish). The study mostly addresses deliberate studies and focuses on the transition between introduction and establishment, and establishment to spread. Among the investigated species traits, such as migratory tendency, diet, human commensalism, reproduction traits, size and geographic range size, none were consistent.

From the event traits, traits connected with the introduction event, propagule pressure and habitat/climate match was correlated with establishment success. As the article uses the results of mostly deliberate introductions, propagule pressure is determined by human interference and not associated with the effort of the species itself. However, it shows that propagule pressure is important for the establishment success.

A history of invasion success also ensures establishment success. This would imply that establishment success is coupled with a species and the existence of characteristics associated with success. A match between habitat/climate in the native and non-native range, would imply no need for evolutionary or behavioral change, as the species can thrive on pre-introduction traits.

Among invasions

Establishment success can be to a greater or lesser extent independent of invader traits. Success can closely be related with the novelty of the invader in the introduced range and the composition of the host community [67,68,69].

There is a range of possible disadvantages and advantages to being “novel”. Most of them can go both ways. For example, the lack of co-adaptation to native predator, pathogen, parasite and prey can drive the invader to local extinction. In addition, it can give an advantage over native competitors for the lack of recognition mechanism (naiveté) of the natural enemies. Advantages of being novel limit the selection pressure and therefore the adaptation by the invader, as it is independent of invader traits.

Also, some ecosystems are impenetrable for invasions. This is defined as biotic resistance. A fine example is the reduced success of exotic wasps in Patagonia [68]. Wasp abundance in this area is lowered compared to other invaded regions. Native to this area are the competitively superior ants, which effectively put a halt to its success. The issue is that invasion success can greatly be affected by the invaded ecosystem. This makes every invasion more unique and complex, and invasion success is less dependent of the invasive species.

There is also controversy about the importance of genetic diversity in the success of an invasion. In some studies, genetic diversity is called the driving force for a successful invasion, as seen in lizards. However, the success of invasive ants is attributed to a decrease in genetic diversity. Ants have a hive structure, in which altruism is important. The existence of this structure heavily relies on genetic similarity to benefit from this altruism. Ants have methods to recognize genetically similar individuals, and failure to recognize results in the display of intraspecific aggression. As genetic similarity is correlated with intraspecific aggression, this construction may not work for invasive species without kin recognition.

Discussion

Introduced population show behavioral [22,46] and genetic [22,46,63] change. In different invading species, invasion success is appointed to a rise [63] or a decline [22] in genetic diversity. Besides, the severity of selection between invasion sites and species differ. No uniform pattern seems to arise. There is no proof any selection and adaptation has to take place.

In many cases, traits which positively contribute to invasion success are already present in the source population, also called pre-adaptations. Besides, it is hard to determine whether a species even needs or can adapt during establishment, for the invasion success can be a consequence of factors independent of the invasive species. The introduction event itself or the consistence of the host community can greatly determine success.

Bottlenecks are induced upon the introduced population, but there is no evidence this actually is the result of a selection. So yes, introduced populations show behavioral and genetic change, but no striking pattern arise.

An aspect which received little attention, is how selection acts on the transport and introduction stage. Is the genetic and behavioral consistence of the initial population a random portion of the source population, or is it a particular set of individuals with the eligible traits? How many propagules fail before one successfully arrives?

The transport and introduction stage are still underexposed in literature. Propagule pressure is given great significance in invasion success, but the variables which define it are not. This would be a difficult task, as successful invasions are recorded in great detail, the failures mostly are poorly represented, as they are less distinct.

There are articles of behavioral and genetic change in an invasive species, but there are too few to form a valid conclusion. More research of the genetic composition of an introduced population should clarify more of the peculiarities in the genetic variety.

The discussed interspecific behavioral traits have been proven to enhance invasion success. Most of these behavioral traits are not proven to be the direction of behavioral change within introduced populations. It would be interesting to see some behavioral experiments testing for instance intraspecific aggression. The reduced aggression of Argentine ants does not yet have much credibility as a general rule for other invasives, for the strong correlation in relatedness and intraspecific aggression is specific to social insects. The next step is to demonstrate reduced aggression in other invasive species.

Biological invasions are highly complex and depend on a lot of variables. Therefore, each invasion is unique in its own way, making it more difficult to generalize. It is certain that there are not many similarities among taxa. The amount of genetic diversity, the potential for evolution, is furthermore not a useful indicator among invasions, nor for success or evolution.

Yet invasive species show genetic and behavioral change, advantageous to the invasion effort. This should be an aspect which should be accounted for, as most studies focus on species traits to predict invasion capability. Behavioral and genetic potential should also be part of the picture, as it seems relevant in invasions.

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