



## ECOLOGICAL, GENETIC AND EPIGENETIC BASIS FOR BIOINVASIONS

### BASES ECOLÓGICAS, GENÉTICAS Y EPIGENÉTICAS DE LAS BIOINVASIONES

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#### ABSTRACT

From the moment small groups of individuals are introduced and become incorporated into a receptor environment, in addition to their obvious advantageous characteristics as potential invaders, complex interactions between the environment and genetic and epigenetic mechanisms arise to either thwart or foster the invasion. To understand invasions, different kinds of mechanisms that would allow the introduced organisms to become invasive in their new environments must be analyzed: enemy release, mutualist release, allelopathy, Darwin's naturalization hypothesis, breakdown of biotic regulation, empty niches, propagule pressure, genetic variation increase (by means of hybridization, genome and gene duplication, endosymbiosis, transposition, somatic mutations, mitotic recombinations, small regulatory RNAs), purge, adaptive mutations, phenotypic plasticity, and epigenetic changes. These processes are critical to explaining the success of some alien species in new environments.

**KEY WORDS:** Invasive species, phenotypic plasticity, epigenetic changes.

#### RESUMEN

Desde el momento en que pequeños grupos de individuos se introducen e incorporan a un ambiente receptor, además de sus características ventajosas obvias como potenciales invasores, se presentan complejas interacciones entre el medio ambiente y los mecanismos genéticos y epigenéticos para frustrar o fomentar la invasión. Para entender las invasiones, se deben analizar diferentes tipos de mecanismos que permitan a los organismos introducidos convertirse en invasores en sus nuevos ambientes: liberación de sus enemigos, mutualismo, alelopatía, hipótesis de naturalización de Darwin, ruptura de la regulación biótica, nichos vacíos, presión de propágulos, aumento de la variación genética (por medio de hibridación, duplicación de genes y el genoma, endosimbiosis, transposición, mutaciones somáticas, recombinaciones mitóticas, pequeñas moléculas reguladoras de ARNs), purificación, mutaciones adaptativas, plasticidad fenotípica y cambios epigenéticos. Estos procesos son fundamentales para explicar el éxito de algunas especies exóticas en nuevos ambientes.

**PALABRAS CLAVE:** Especies invasoras, plasticidad fenotípica, cambios epigenéticos.

#### INTRODUCTION

From the moment small groups of individuals are introduced and become incorporated into a receptor environment, complex interactions between the environment and genetic and epigenetic mechanisms may arise to either thwart or foster the invasion. In some of these cases, there is evidence that gene expression is affected by environmental influences, a challenge to the central dogma of molecular biology's traditional tenet that DNA base sequencing is unidirectional to RNA, and transcribed and translated into specific amino acids. The information flows in a one-way direction and there is no reverse flow of information. The reductionist view - that organisms can be understood using properties of their genes and nothing else must also be critically assessed.

Invasion biology is one of fastest growing fields in ecology and evolution, however still there is a long

way from being able to generalize about why invasions occur and predict which introduced species may become invasive. Many different mechanisms promoting invasion have been proposed, but actually it is impossible to say with when or where a particular mechanism is likely to be important. The present situation, with a multitude of particular supported hypotheses, is due less to a failure to identify the most important mechanism and more to an inadequate conceptual framework with which to organize our knowledge (Dietz and Edwards 2006).

According Dietz and Edwards (2006) an invasion can usefully be subdivided into a primary phase, in which the abundance of an often preadapted species increases rapidly (typically in resource-rich, disturbed habitat), and a secondary phase, in which further spread is contingent upon plastic responses or genetic adaptation to new ecological circumstances. Consideration of different invasion phases contributes to clarify the relative

importance of phenotypic plasticity and evolutionary change for invasions.

There are some advantageous characteristics of potential invaders such as:

### **Vegetative reproduction**

*Hydrilla verticillata* is highly aggressive invasive aquatic plant than can seriously degrade the ecology, recreational usage and water quality of freshwater system. It has growth habitats and reproductive strategies that allow for extremely rapid growth and extension. This specie is native to Africa that grows in still or slow-moving fresh water. This plant grows rapidly and can reproduce through seeds, plant fragments, tubers and turions. These characteristics allow hydrilla to spread easily to new sites, which it can then quickly dominate. Additionally, *Hydrilla* is quite adaptable, tolerating low light levels, a wide range of water depths and temperatures, and a high level of suspended sediments. *H. verticillata* is considered one of the worst aquatic in the United States; this weed can be spread by water, boats, trailers, fishing gear, birds and by dumping aquarium plants in waterways (Chetta *et al.* 2012).

### **Animal fast growth and early sexual reproduction (Strategy r)**

Studies in several taxa indicate that fast growth can have negative as well as positive effects. There appears to be a link between accelerated growth and lifespan: rapid growth is associated with reduced longevity (Metcalf and Monagan 2003). From an ecological and evolutionary perspective, there are two main advantages: *a*) Rapid gain in body size can improve short-term survival chances. For instance, the risk of being caught by a predator is strongly linked to body size (Metcalf and Monagan 2003). *b*) Rapid growth can lead to increased reproductive success. For example, larger males in many species may be either preferred by females or more able to compete with other males for access to females (Bowcock *et al.* 2013). In females, the advantage is fecundity, which often increases with body size (Luo *et al.* 2012).

Animal parental care: Parental care comprises a number of characteristics and activities undertaken by the parents to optimize the survival of the offspring and maximize reproduction (Granado 2002). Sometimes this care is taken to extremes, as when the young tilapias of the genus *Oreochromis* swim back into the protection of their mother's mouth (Schwanck 1989). Another example

occurs in *Cichla* species, among others: bi-parental care of eggs that have made their populations capable of expanding rapidly in the invasive range (Carvalho *et al.* 2014).

### **Generalist habits**

Generalists are organisms able to thrive in a wide variety of environmental conditions, using many food sources and being, therefore, able to flourish in many habitats, as opposed to specialist organisms, which can only thrive in a narrow range of environmental conditions and make use of a narrower range of food or resources. When environmental conditions change, generalists are able to adapt, whereas specialists are more likely. Most neoecological studies indicate that specialists suffer declines under recent environmental changes. This was confirmed by many paleoecological studies investigating fossil taxa in the geological past both milder environmental fluctuations and mass extinction conditions had occurred. Phylogenetic biologists, studying the histories of lineages, showed that specialists are not confined in evolutionary dead ends and could even give rise to generalists (Colles *et al.* 2009).

Van Tienderen (1997) indicated that the evolution of generalists and specialists is related with the evolution of the phenotypic plasticity. The contrast between generalists and specialists refers primarily to the fitness under different environmental conditions: specialists are superior under some but not all conditions.

According Van Kleunen and Fisher (2005) phenotypic plasticity is expected to coincide with generalist whenever plasticity is advantageous not constrained. If plasticity is advantageous but constrained, specialists with a phenotype suited to only certain conditions may evolve. Alternatively, individuals may evolve that have a compromise phenotype in between the demands of the different habitats, hosts, etc. Such compromises can still be considered to be generalist strategies.

On the other hand, many factors can dramatically affect the dynamics of biological invasions, such as the alteration of expected spatial ranges, distributions, and patterns in the presence of a demographic Allee effect (Taylor and Hastings 2005, Tobin *et al.* 2009). In other words, the *per capita* birth rate declines at low densities (Allee 1931). As Allee effects cause longer lag times and slower spread, invasive species are less likely to become established. In fact invasion biologists must consider Allee effects as auspicious deterrents of further spread by

an invading species (Tobin *et al.* 2011). The Allee effect will be more the case for animals. A highly-seeding annual plant can establish a population from a single propagule with no changes in per capita reproductive rate.

Numerous hypotheses address the reasons for successful biological invasion and most attribute it to characteristics of the invader or characteristics of the invaded ecosystems, with comparatively few integrating the two. Research studies have mainly focused on individual mechanisms and there has been no formal way to integrate findings. Invasion success is likely to be context-dependent and due to a combination of factors and mechanisms, so all of the possible reasons for successful invasion should be considered. The aim of this paper is to illustrate the major themes, currently cited in the literature, by which species may become invasive and how they are dealt with in different hypotheses.

## MECHANISMS BY WHICH SPECIES BECOME INVASIVE

### TRADITIONAL MECHANISMS

#### Enemy release

The so called “escape from enemy hypothesis” holds that transplanting a species into a new habitat separates it from natural enemies in the native habitat such as soil pathogens and parasites (Keane and Crawley 2002).

Keane and Crawley (2002) proposed that species are negatively affected to some degree by specialist herbivores or pathogens in their native ranges, and that escape from these negative interactions allows non native species to achieve higher individual growth and reproductive rates and subsequently higher populations and meta-populations growth rates relative to what they achieve in their native ranges, and relative to native species in their introduced range.

The subsequent evolutionary loss of defense in the absence of enemies enables internal resources to be allocated for growth, fecundity, and other performance-enhancing traits. This hypothesis can explain the lag period between the time of introduction and the invasion of some exotic species as local selection pressures reduce energy allocation to defense, but tests in support of the hypothesis have been inconclusive (Handley *et al.* 2008).

Invasive species, however, may not always experience enemy release, and this potential mechanism may not

always result in greater performance (Chun *et al.* 2010). For example, escape from one guild of enemies does not necessarily imply escape from other guilds. Because the effects of each guild are likely to vary through space and time, the net effect of all enemies is also likely to be variable (Agrawal *et al.* 2005). Given the complexity of the processes underlying biological invasions, there may not be a simple relationship between enemy release and the vigor, abundance, or impact of non indigenous species (Colautti *et al.* 2004).

#### Mutualist release

The so called “Endophyte-enemy release hypothesis”. Mycorrhizal symbioses are widespread, and mycorrhizal fungi commonly associate with the vast majority of plant species in terrestrial ecosystems. Alien plants, especially dicot hosts, arriving in exotic ecosystems would have a depauperate endophytic mycobiota, freeing up resources for increased growth and reproduction. This, together with the absence of co-evolved natural enemies (enemy release hypothesis) would enhance significantly their fitness. Given that these endophyte-free aliens have sufficient auto-defense mechanisms to overcome the pressure from indigenous natural enemies, they then would have increased competitive advantage (Evans 2008). Several criteria can determine the potential for mycorrhizal symbioses to constrain or facilitate the invasion process: the plant’s degree of flexibility in associating with a range of fungal species, and whether suitable fungi are transported with the plant or are independently introduced to a habitat (Pringle *et al.* 2009).

Dickie *et al.* (2010) studied the invasions of *Pinus contorta* over the past 800 years in New Zealand. In the absence of exotic mycorrhizal fungi, *Pinus* plantations failed to establish themselves, supporting the loss of mutualists as a factor limiting invasion; however, once these fungi were introduced both the fungi and the plant were able to spread widely. Intriguingly, *Pinus* spreads easily into grasslands and disturbed sites where no ectomycorrhizal trees are present and where native ectomycorrhizal trees are limited by a lack of mycorrhiza. A similar process may have occurred in Spain, where *Eucalyptus* has become more invasive following the introduction of Australian ectomycorrhizal fungi (Díez 2005).

#### Allelopathy

The so called “novel weapons hypothesis”. Another hypothesis to explain the success of some exotic plant

species to invade was proposed by Callaway and Aschehoug (2000). According to Hierro *et al.* (2005), the novel weapons hypothesis argues that exotics exude allelochemicals that are relatively ineffective against well adapted neighbors in the communities of origin, but highly inhibitory to native plants in recipient communities.

The negative effects of *Centaurea* species on native plants are well documented. *Centaurea maculosa* may reduce the cover and diversity of native grassland species by more than 90% (Callaway *et al.* 2001); *C. maculosa* and the closely related *C. diffusa* appear to suppress natives via a number of different mechanisms including allelopathy (Callaway and Aschehoug 2000, Callaway *et al.* 2004); the effect of *C. maculosa* on the composition of the soil microbial community to that of the native species, this effects not manifest as simple direct effects, but become apparent only when native plants, invasive plants, and soil microbial communities were interacting at the same time.

Caulerpenyne and catechin are two of the compounds that function as weapons to invade new territories. Caulerpenyne (metabolite synthesized by *Caulerpa racemosa* var. *cylindracea*) is a potential allelochemical present in this invasive Mediterranean seaweed. Caulerpenyne revealed its phytotoxic effect over the native sea grass, *Cymodocea nodosa*. The results of Raniello *et al.* (2007) suggest a possible allelopathic activity of the caulerpenyne, and a possible role in the successful competition of the invasive *C. racemosa* var. *cylindracea* over native sea grasses.

### Darwin's naturalization hypothesis

Darwin proposed in *The Origin of Species* (Darwin 1859) that introduced plants are more likely to invade and become naturalized in areas with distantly related native species, due to the absence of competition with the congeneric native species. Furthermore, introduced species are more likely to be attacked by native herbivores and pathogens that could use them as hosts, when native species are phylogenetically close.

A different explanation (also considered in Darwin 1859) and termed "pre-adaptation hypothesis" indicates that introduced species with native congeneric ones are more likely to share features that pre-adapt them to their new environment. Ricciardi and Mottiar (2006) indicated that Darwin's naturalized hypothesis has rarely been tested statistically, and results thus far have been equivocal; some studies support this hypothesis

(Rejmanek 1996), while others do not (Duncan and Williams 2002).

In an attempt to find which hypothesis best explains invasion, Jiang *et al.* (2010) used four species of bacteria: *Bacillus pumilus*, *B. cereus*, *Frigoribacterium* sp., and *Serratia marcescens* as residents in every possible 1, 2, 3, and 4-species communities, and invaded them with a subspecies of *S. marcescens*. What they found was that invader density was significantly related to phylogenetic distance, so that the invader reached its greatest density when communities contained only distantly-related species. Jiang *et al.* (2010) indicated that their findings support phylogenetic relatedness as a useful predictor of species invasion success. However, like Ricciardi and Mottiar (2006) using data on fish introductions, they failed to support either viewpoint.

### Breakdown of biotic regulation

Species within their natural ecological community collectively evolve restrictions on their functioning that serve to stabilize the community as a whole. As these restrictions are unknown to the exotic species, there is no correlated interaction between native and invading organisms and the ensuing perturbation prevents the community from efficiently controlling environmental conditions, causing the community to deteriorate (Gorshkov *et al.* 2004, Makarieva *et al.* 2004). As soon as the degree of deterioration becomes significant, all indigenous inhabitants lose competitiveness, and alien species encounter at least the same conditions as the local ones. Mitchell *et al.* (2006) pointed out that species introduction generally alter plant interactions with enemies, mutualists and competitors, and that there is increasing evidence that these altered interactions jointly influence the success of introduced populations.

### Empty niches

Although, by definition, a niche exists in the presence of an organism, this hypothesis refers to the possibility that certain exotics may be successful because they have access to resources in the newly-adopted community that no local species utilize (Hierro *et al.* 2005). Elton, 1985 first proposed that exotic species might more easily invade species-poor areas than species-rich areas. The hypothesis is based on the idea that species in species-rich areas must use limiting resources more thoroughly as a result of competition and specialization, leaving fewer open niches for invaders. On the other hand, in areas of low species richness, niches are filled less (whereas mean



there are not available resources, nor is competition any less intense). Since then, the Eltonian theory has been reinforced by considerable theoretical studies consistently supported by the predicted negative relationship between diversity and invasibility (Levine and D'Antonio 1999). However, the results of some empirical studies evaluating the effects of species richness on invasibility were mixed (Levine and D'Antonio 1999, Hierro *et al.* 2005, Ricotta *et al.* 2010).

In many cases, there are populations established for several decades that have failed to become invaders, undergoing instead a lag phase. If the conditions of the new environment change or the populations evolve, they might exit this lag phase as invaders (Zenni and Nuñez 2013).

Other populations, on the contrary, move speedily to take hold of the new habitat. The invasion of the Northwestern Atlantic and the Caribbean Sea by the Indo-Pacific lionfish (*Pterois volitans* and *P. miles*), for instance, has been one of the swiftest marine finfish invasions in history (Morris *et al.* 2008). Several scientists (Morris *et al.* 2008, Smith and Sullivan 2008) postulated the importance of the “empty niche hypothesis” in the establishment of these exotic species.

Lionfish are top-level predators and thus compete for resources with other native top-level predators such as the species of the snapper-grouper complex. This complex is heavily exploited by commercial and recreational fisheries, an ensuing niche vacancy resulting in the reef fish community. There are classic examples of niche takeover by one fish species following the removal of another. It is unclear if niche takeover by lionfish will impact stock recovery of threatened species such as the Nassau grouper *Epinephelus striatus* (Morris 2009).

### Propagule pressure

This term refers to the number of individuals introduced into a region and the number of release events, sometimes from different sources. In the face of this pressure, invasive species that are not as genetically poor as expected have been observed, partially explaining their successful invasion (Frankham 2005). Occasionally, hybridization provides introduced populations with more genetic variation than it does native ones of the same species (Kolbe *et al.* 2004). This explanation, however, is not useful for understanding successful invasions where only a single inoculation occurred, as in the cases of tilapia (*Oreochromis mossambicus*) and the marine

alga *Kappaphycus alvarezii* in Venezuelan waters; the amphibian *Rana catesbiana* in the Venezuelan Andes (Pérez *et al.* 2006a,b); the freshwater fish *Cichla ocellaris*, introduced into Lake Gatun in Panama (Zaret and Paine 1973).

### Genetic variation increase

Some mechanisms (other than mutations) allow the introduced species to increase their variation and adapt to new environments. Among them are: Hybridization: Provides genetic variation in a large number of genes in a single generation. Genome and gene duplication: Genetic variation is not directly increased (with the exception of allotetraploidy) but allowed to arise without the constraint of natural selection. Endosymbiosis: The fusion of the entire genomes of two organisms; it overlaps with horizontal gene transfer, the introduction of genes or parts of genes. Transposition: Small packages of DNA can splice into other sequences and provide fortuitous opportunities for evolutionary innovations. Somatic mutations and mitotic recombinations: Sources of genetic variation in species that mainly reproduce asexually by fragmentation. Small regulatory RNAs: Regulation can be exerted through chromatin structure modification either at the transcriptional level (epigenetic regulation) or post-transcriptional, affecting mRNA stability or translation.

### Purge

The low number of introduced organisms at the beginning of the invasion and the so-called founder effect will reduce genetic diversity and increase inbreeding, which can lead to inbreeding depression and, in some introductions, to the extinction of the invader. Since most cases of inbreeding depression are due to deleterious recessive alleles, their severity would be diminished if natural selection purged such alleles from populations during reproduction (Swindell and Bouzat 2006).

By using a worldwide invader native to Asia, the harlequin ladybird *Harmonia axyridis*, Facon *et al.* (2011) evaluated whether such purging could facilitate biological invasions. The species was repeatedly introduced (as a biological control agent) into North America and Europe, but for decades it failed to establish itself. However, by 1988, it had not only settled in North America, but had also rapidly become an invasive pest on a worldwide scale. As indicated by Facon *et al.* (2011) the invasions of *H. axyridis* followed a “bridgehead scenario”, in which the initial invasive population in

North America was the source of invasions worldwide. This result was associated with a founder effect, which was appropriate for purging to occur. Facon *et al.* (2011) demonstrated that introduced replicate populations experience almost none of the inbreeding depression suffered by native populations. Thus, rather than posing a barrier to invasion as it is often assumed, the founder effect, by purging deleterious alleles, can enable the evolution of invaders that maintain high fitness even when inbred.

### Adaptive mutations

The basis of genetics and the neo-Darwinian theory of evolution suggest that gene mutation occurs at random and independently of the environment in which the organism lives. The discovery of “adaptive” mutations in bacteria shook this dogma by suggesting the existence of a new kind of mutation that differs from spontaneous mutation and appears to be induced by stress (Rosenberg and Hastings 2004). A genetic method developed by Cairns and Foster (1991) to discern the effect of selection on the rate of appearance of adaptive mutations has been used by several authors (Rosenberg and Hastings 2003, 2004, Hastings *et al.* 2004, Kugelberg *et al.* 2006) to provide evidence that this kind of mutation does in fact occur.

In their method, Cairns and Foster (1991) created a strain of *E. coli* defective in the *lac* gene that determines the cells unable to grow on lactose. They plated out the bacteria on a minimal medium with lactose, and looked for mutants that revert to normal. As the cells used up the small amount of nutrients, they stopped growing. But after some time, mutants that could grow on lactose began to appear. However, the mutations were not strictly directed to the gene in which mutations could be advantageous, as unselected mutations also accumulated.

In eukaryotes, Denver *et al.* (2004) had suggested that cellular stress responses might provoke hypermutation in the round worm *Caenorhabditis elegans*. Most of these mutations would surely prove harmful or be neutral, but rare adaptive mutations have allowed some individuals in stressed populations to flourish (Rosenberg and Hastings 2004). An invasion is an unequivocal stress condition, and lends support to the idea that evolution might be hastened under stress.

## NEW CONCEPTS IN BIOINVASIONS

Now, we are going to attempt to integrate the

traditional mechanisms of invasion already analyzed, with new concepts in invasions: phenotypic plasticity and epigenetic changes.

Epigenetics (a suite of interacting molecular mechanisms that alter gene expression and function without changes in DNA sequence), has very much to do with phenotypic plasticity (the ability of a genotype to express different phenotypes in different environments) since a great amount of environmental-induced phenotypic changes will have some kind of epigenetic regulation component involved somewhere. The relationship between epigenetics and phenotypic plasticity is complex. Epigenetic modifications, whether heritable or not, are part of the mechanisms that allow phenotypic plasticity (Bossdorf pers. com.).

The study of Zhang *et al.* (2013) demonstrates that variation in DNA methylation (one of the epigenetic mechanism) can cause substantial heritability in ecologically important plant traits and their plasticity. Because there is selection acting on some of this variation, they predict rapid phenotypic evolution in this epigenetically based system.

The inheritance and the increasing evidence for natural epigenetic and phenotypic plasticity often highly variable in natural populations, suggest that it going to be necessary to expand the concept of variation and evolution in natural populations, considering several ecologically relevant inheritance systems. This may result in important expansion of the Modern Evolutionary Synthesis (Zhang *et al.* 2013, Bossdorf *et al.* 2008).

### Phenotypic plasticity:

Plasticity can play an important role in biological invasions by allowing individuals to colonize and establish themselves in diverse habitats.

Phenotypic plasticity is often cited to explain bioinvasions, despite the lack of knowledge of the underlying mechanisms that allow the production of different phenotypes from a single genotype (Ellers and Stuefer 2010). To analyze the importance of phenotypic plasticity in facilitating bioinvasions it is necessary to make a distinction between simple or within-generation phenotypic plasticity (WGP) and trans-generational plasticity (TGP), both important contributors to the establishment and spread of some invasive species.

WGP is the individual's response to variation in

current environmental conditions, whereas TGP is a response to the maternal environment expressed in the progeny. According to Dyer *et al.* (2010), when a new set of source conditions is encountered, individuals rely on WGP for survival, but after the first generation, TGP will provide the stronger driving force because it is more efficient than WGP.

In a recent study, tadpoles in threatening situations, such as an impending attack by a predator, released stress hormones that prepared the body to defend itself or quickly escape the danger. The study of tadpoles of the wood frog (*Lithobates sylvaticus*) and dragonfly larvae (Anoseptera) as predators found that tadpoles exposed repeatedly to predators released pheromones and stress hormones into the water to alarm other tadpoles (Maher *et al.* 2013). After several days tadpoles treated with the stress hormone or exposed to predators, developed larger tails than those of the control animals, and showed higher survival rates than the controls.

One example of TGP was observed when, exposed to search tracks from larval or adult convergent ladybird beetles (*Hippodamia convergens*) cotton aphids (*Aphis gossypii*) produced greater numbers of winged offspring. Apterous and related individuals on clean plants were found to have primarily normal and dwarf offspring respectively. Mondor *et al.* (2004), suggest that elevated predation risk may cause phenotypic changes in aphids over multiple generations, resulting in a more precipitous decline in herbivore population that could be explained solely by increase predation rates.

### Epigenetic change

In many species there is a natural variation in epigenetic modifications, very similar to that found in DNA sequences, and at least some of this variation is inheritable and independent of genetic variation, thus making it potentially subject to evolution by natural selection (Jablonka and Raz 2009, Bossdorf *et al.* 2010). Adaptation, as indicated by Jablonka and Raz (2009), can occur very rapidly through selection of these epigenetic variants, when populations are small and lack genetic variability, as in the case of bioinvasions. When environmental conditions change, these epigenetic variants are often induced into several individuals in the population, many acquiring similar modifications at the same time.

Crews *et al.* (2007) also demonstrated that inheritable epigenetic variation can even affect animal behavior. Given that behavior is regarded to be the most responsive

aspect of the phenotype of an animal, such epigenetic effects on behavior may have profound evolutionary consequences.

Stress conditions seem to be particularly important as inducers of heritable epigenetic variation, and lead to changes in epigenetic and genetic organization that are targeted to specific genomic sequences (Prentis *et al.* 2008).

A very important aspect related with biological invasions is to determine whether DNA methylation is variable and if this variation could compensate for decreased genetic variation associated with introductions. Schrey *et al.* (2012) looked for the answer working with the house sparrow (*Passer domesticus*), introduced in Nairobi (Kenya) less than 50 years ago; in Tampa (USA) about 150 years ago; and with native populations from Europe. They found that samples from Nairobi had less genetic diversity than samples from the native European and receiving North American ranges, whereas the introduced North American populations had a genetic diversity similar to that of native populations (Ho 2009).

On the other hand, they found that methylation was more frequent in Nairobi, and outlier loci suggest that populations may be differentiated. Methylation diversity was similar between populations, in spite of known lower genetic diversity in Nairobi. Therefore it is possible that this epigenetic mechanism compensates for the decrease in genetic diversity associated with introductions as a source of phenotypic variation.

Huang (2008, 2009) proposed the existence of an inverse relationship between genetic diversity and epigenetic complexity. Multicellular organisms differentiated into tissues and cells are epigenetically complex and do not tolerate much genetic variation, whereas unicellular organisms, being epigenetically simple, do. Genetic diversity is thus restricted by epigenetic complexity and *vice versa*. It is impossible to build complex epigenetic programs if the DNA is constantly changing. Gilchrist and Lee (2007) assert that an evolutionary response to selection may be produced depending on the genetic architecture (nature and number of genes, their regulation, dominance, epistatic and pleiotropic interactions influencing a particular adaptation) of the underlying traits. Highly canalized genetic architectures imply that the developmental program allows only a small number of discrete phenotypic states but a more rapid response to selection, since the alternative genetic and developmental pathways

are already in place and only minor transcriptional changes are needed to shift the phenotype. In contrast, highly plastic genetic architectures produce numerous trait variations that may allow for a more precise fit between trait and environment and thus, by reducing selective deaths and expanding the range of expressed genetic variation, accelerate the invasion process.

## CONCLUSIONS

The present situation in bioinvasions have a multitude of particular factors (advantageous characteristics of potential invaders, environmental characteristics, interactions, alle effect, life story and others) and supported hypotheses (enemy release, endophyte-enemy release, novel weapons, Darwin's naturalization, empty niche and others), all of this considered traditional mechanisms that are joined to the new concepts in bioinvasions like phenotypic plasticity and epigenesis to integrate an overarching framework.

A single explanatory factor for invasions is not expected to emerge from the numerous studies, although, in some cases a single factor seems to be of greatest importance. Species can use several mechanisms of invasion that are driven by different factors and it difficult to determine the relative influence of different mechanisms on invasion, and might have slowed down the rate of progress in invasion study.

Phenotypic plasticity and epigenesis are recently mechanisms, to explain bioinvasions. In relation with phenotypic plasticity, WGP is the individual's response to variation in current environmental conditions, whereas TGP is a response to the maternal environment expressed in the progeny. When a new set of source conditions is encountered, individuals rely on WGP for survival, but after the first generation, TGP will provide the stronger driving force because it is more efficient than WGP.

Epigenesis can play an important role in biological invasions. In many species there are epigenetic changes very similar to that found in DNA sequences. At least some of this variation is inheritable and independent of genetic variation, thus making it potentially subject to evolution by natural selection. Adaptation can occur very rapidly through selection of these epigenetic variants, when populations are small and lack genetic variability, as in the case of bioinvasions. When environmental conditions change, these epigenetic variants are often induced into several individuals in the population, many acquiring similar modifications at the same time.

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