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**HOW SOME ALIEN SPECIES BECOME INVASIVE. SOME  
ECOLOGICAL, GENETIC AND EPIGENETIC BASIS FOR  
BIOINVASIONS**

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Julio E. Pérez, Carmen Alfonsi, Carlos Ramos, Juan A. Gómez, Carlos Muñoz  
and Sinatra K. Salazar

*SUMMARY*

Genetic, epigenetic and environmental factors determine that some exotic species invade and become established, whereas most apparently either fails to become established or persist as small, isolated populations. To understand invasions we analyze different kinds of mechanisms that would allow the introduced organisms to become invasive in their new environments: enemy release, allelopathy, Darwin's naturalization hypothesis, empty

niches, propagule pressure, breakdown of biotic regulation, phenotypic plasticity, variation increase (by means of hybridization, genome and gene duplication, endosymbiosis, transposition, somatic mutations and mitotic recombinations, small regulatory RNAs), purge; adaptive mutations; and epigenetic changes. These processes are key to explain the success of some alien species in new environments.

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**Introduction**

It is generally accepted that genetic variation is a prerequisite for evolution, offering a selection of traits and adaptation to new environments, and avoiding inbreeding depression (Frankham, 1995). Nevertheless, increasing evidence suggests that some species become success-

ful colonizers in the absence of genetic variation. The population of brown trout (*Salmo trutta*) of German origin, for example, introduced in 1905 into the Patagonian National Park, Argentina, prospered despite its reduced genetic variability. Valiente *et al.* (2010) attribute this success to the trout's plasticity in life-history traits such as hatching

time and migratory strategy, and suggest that these traits are far more important than genetic variability. Recent research suggests that epigenetic changes are more determinant than genetic variability in the success of invasions: Jablonka and Raz (2009) indicate that adaptation can occur very rapidly, without genetic change, through the selection

of epigenetic variants, especially when populations are small and lack genetic variability, as is the case in most bioinvasions (the expansion of exotic organisms into regions where it had not previously existed, often as a result of human activity). Huang (2008, 2009) proposed the existence of an inverse relationship between genetic diversity and

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**Julio E. Pérez.** M.A. in Zoology, University of Kansas, USA. Ph.D. in Biology, University of Southampton, UK. Professor, Instituto Oceanográfico de Venezuela (IOV), Universidad de Oriente (UDO), Venezuela. Apartado 245 Cumaná, Venezuela. e-mail: jeperez@yahoo.com

**Carmen Alfonsi.** M.Sc. in Marine Sciences, IOV-UDO, Venezuela. Doctor in Zoology, Universidad Central de Venezuela. Professor, IOV-UDO, Venezuela. e-mail: calfonsir@hotmail.com  
**Carlos Ramos.** Ph.D. in Molecular Biology, University of Puerto Rico. Professor, Universidad de

Panamá, Panamá. e-mail: laito52@gmail.com  
**Juan Antonio Gómez.** M.Sc. and Doctor in Marine Sciences IOV-UDO, Venezuela. Professor, Universidad de Panamá, Panamá. e-mail: juanay05@hotmail.com  
**Carlos Muñoz.** M.Sc. in Marine Sciences, IOV-UDO, Venezuela.

Professor, Universidad Arturo Prat, Chile. e-mail: carlosmufoa@gmail.com  
**Sinatra K. Salazar.** M.Sc. in Marine Sciences, IOV-UDO, Venezuela. Professor, UDO, Venezuela. e-mail: kate\_salazar@yahoo.com

## COMO LAS ESPECIES EXÓTICAS SE CONVIERTEN EN INVASORAS. ALGUNAS BASES ECOLÓGICAS, GENÉTICAS Y EPIGENÉTICAS PARA LAS INVASIONES

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### RESUMEN

Factores genéticos, epigenéticos y ambientales pueden determinar que algunas especies exóticas invadan y se establezcan, mientras que la mayoría aparentemente falla en llegar a establecerse o persisten como pequeñas poblaciones aisladas. Para entender las invasiones se analizan diferentes mecanismos que permitirían a los organismos introducidos llegar a ser invasores en sus nuevos ambientes: la ausencia de enemigos, la alelopatía, la hipótesis de naturalización de Darwin, los nichos vacíos,

la presión de propágulos, la ruptura de la regulación biótica, la plasticidad fenotípica, el aumento de la variación (a través de la hibridización, la duplicación de genoma y genes, la endosimbiosis, la transposición, las mutaciones somáticas, las recombinaciones mitóticas, la regulación por pequeños ARNs), la purga, las mutaciones adaptativas, y los cambios epigenéticos. Estos procesos son claves para explicar el éxito de alguna especie invasora en ambientes nuevos.

## COMO AS ESPÉCIES EXÓTICAS SE CONVERTEM EM INVASORAS. ALGUNAS BASES ECOLÓGICAS, GENÉTICAS E EPIGENÉTICAS PARA AS INVASÕES

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### RESUMO

Fatores genéticos, epigenéticos e ambientais podem determinar que algumas espécies exóticas invadam e se estabeleçam, enquanto que a maioria aparentemente falha em chegar a estabelecer-se ou persistem como pequenas populações isoladas. Para entender as invasões são analisados diferentes mecanismos que permitiriam aos organismos introduzidos chegar a serem invasores em seus novos ambientes: a ausência de inimigos, a alelopatia, a hipótese de naturalização de Darwin, os

nichos vazios, a pressão de propágulos, a ruptura da regulação biótica, a plasticidade fenotípica, o aumento da variação (através da hibridização, a duplicação de genoma e genes, a endossimbiose, a transposição, as mutações somáticas, as recombinações mitóticas, a regulação por pequenos ARNs), a purga, as mutações adaptativas, e as mudanças epigenéticas. Estes processos são chave para explicar o sucesso de alguma espécie invasora em ambientes novos.

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. Thus, to compensate for a loss in the range of genetic diversity, adapt to environments, and evolve new phenotypes, complex organisms program their gene sets in ways other than mutation. Observations that support this hypothesis have long been noted. For example, Wallace *et al.* (1971) found that frogs are genetically much more diverse than mammals, but are much less diverse in phenotypes. Phenotype or epigenetic diversity/complexity is not possible if

genetic diversity is not somehow curtailed.

On the other hand, 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 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.

This paper analyzes different mechanisms by which species become invasive and thus attempts to help understanding bioinvasions. The study considers genetic, epigenetic and environmental approaches.

### Mechanisms by Which Species Become Invasive

Besides some obvious advantageous characteristics of potential invaders, such as vegetative reproduction, omnivorous feeding, fast growth and early sexual reproduction, parental care, disturbed conditions of the new environment, and generalist habits; a number of mechanisms allow introduced organisms to succeed in their new environments. Such mechanisms are:

### Enemy release

The so called 'escape from enemy' hypothesis holds that transplanting a species from its native habitat separates it from natural enemies such as soil pathogens and parasites. Callaway *et al.* (2004) showed that soil microbes in the home range of spotted knapweed (*Centaurea maculosa*) native to Europe have stronger inhibitory effects on the plant's growth than those found in the weed's North American habitat. By considerably sterilizing the European soil, these researchers increased plant biomass as compared to that of weed transplanted to Montana, USA, where the soil received the same treatment. Prenter *et al.* (2004) gave empirical support confirming that invader populations are not only infested with significantly fewer parasites than native populations, but also

that the transmission of parasites from invading to native species can occur, thus enhancing invasion success.

In an attempt to explain the success of some invasive species, Blossey and Notzold (1995) proposed the hypothesis known as EICA (evolution increased competitive ability) which postulated that invasions of introduced exotic species occur after evolutionary changes due to the escape from enemies. The evolutionary loss of defense enables resource to be directed toward growth, fecundity and other traits improving performance. The hypothesis would also explain the lag period between the time of introduction and the invasion that presents some exotic species. This hypothesis is still a source of debate. Tests in favor of the hypothesis have been inconclusive (Handley *et al.*, 2008).

However, it must be considered that aliens may not always experience enemy release, and this mechanism may not always result in greater plant performance (Chun *et al.*, 2010). Agrawal *et al.* (2005) stated that escape from one group of enemies does not necessarily imply escape from others. 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. Given the complexity of process that underlie biological invasions, Colautti *et al.* (2004) argued against a simple relationship between enemy release and the vigor, abundance or impact of non indigenous species.

#### *Allelopathy*

An other hypothesis to explain the success of some exotic plant species to invade, was proposed by Callaway and Aschehoug (2000). They proposed that some invaders possess biochemical compounds that function as powerful allelopathic agents,

providing them with an advantage in the process of invading. According to Hierro *et al.* (2005) the novel weapons hypothesis argues that exotics exude allelochemicals that are relatively ineffective against well-adapted neighbors in communities of origin, but highly inhibitory to naive plants in recipient communities.

Caulerpenyne and catechin are two of the compounds that function as a weapon to invade new territories. Caulerpenyne (metabolite synthesized by *Caulerpa racemosa* var. *cylindracea*) is a potential allelochemical present in this invasive Mediterranean seaweed. Caulerpenyne showed a phytotoxic effect over the native seagrass *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 seagrasses.

Catechin (a natural phenol antioxidant plant secondary metabolite) is a compound exuded by the roots of the spotted knapweed *Centaurea maculosa*, native of Europe where it is relatively uncommon. The species was introduced in North America, where it is among the most destructive and successful invasive plant species. There is evidence that *C. maculosa* is more allelopathic to North American native species than con-generic European native species. The invasive success of this species may be related to its stronger allelopathic effects of catechin on native North American species than on related European species (He *et al.*, 2009).

#### *Darwin's naturalization hypothesis*

Darwin proposed in *The Origin of Species* (1859) that introduced plants are less likely to invade and become naturalized in areas with closely related native species, due to competition with the

con-generic native species. Furthermore, introduced species are more likely to be attacked by native herbivores and pathogens that could use them as host.

A different and opposite explanation (also considered in Darwin, 1859) and termed 'pre-adaptation hypothesis' indicate that introduced species with native con-generic 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 as the one of Rejmanek (1996), while others reject it and, in some cases support the pre-adaptation hypothesis (Duncan and Williams, 2002). In an attempt to find which hypothesis is a better explanation for invasion, Ricciardi and Mottiar (2006) using data on fish introductions, 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 in-

creasing 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 introduced community that no local species utilize (Hierro *et al.*, 2005).

Elton (1958) 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-rich areas should use limiting resources more completely, leaving fewer open niches for invaders. On the other hand, in areas of low species richness, niches are filled less completely; therefore, they are thought to have a reduced ability to repel invasions by exotics. 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 on the effects of species richness on invasibility were mixed (Levine and D'Antonio, 1999; Hierro *et al.*, 2005; Ricotta *et al.*, 2010).

#### *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 are observed that are not as genetically poor as expected, partially explaining their successful invasion (Frankham, 2005). Occasionally, hybridization provides introduced populations with more genetic variation than

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); and 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 (Perez *et al.*, 2008). Among them are:

**Hybridization.** Unlike mutation, hybridization provides genetic variation in hundreds or thousands of genes in a single generation, making it possible for large and rapid adaptive transitions to occur.

**Genome and gene duplication.** The duplication of genes and genomes does not directly increase genetic variation (with the exception of allotetraploidy), but it does allow the possibility of its increase without the constraint of natural selection.

**Endosymbiosis.** This involves the fusion of the entire genomes of two organisms; it overlaps with horizontal gene transfer, the introduction of genes or parts of genes.

**Transposition.** These small packages of DNA can splice into other sequences and provide fortuitous opportunities for evolutionary innovations.

**Somatic mutations and mitotic recombinations.** These are an important source of genetic variations in species that mainly reproduce asexually by fragmentation.

**Small regulatory RNAs** (miRNAs, siRNAs, and piRNAs) that can exert regula-

tion by affecting chromatin structure either at the transcriptional level (epigenetic regulation) or post-transcriptionally, affecting mRNA stability or translation.

#### Purge

Biological invaders suffer one obvious disadvantage. The low number of introduced organisms at the beginning of the invasion and the so-called population bottlenecks will reduce genetic diversity and increase inbreeding, which can lead to inbreeding depression and in some introductions to the extinction of the invader. As 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).

The literature abounds with a diversity of explanations for purging, but there seem to be few consistent trends to aid predictions of how this might affect a population (Leberg and Firmin, 2008). Facon *et al.* (2011) by using a worldwide invader native to Asia, the harlequin ladybird (*Harmonia axyridis*), evaluate 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 established itself in North America, but had also rapidly become an invasive pest on a world-wide 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 the invasions world wide. This result was associated with a population bottleneck, which was of the appropriate level for purging to occur. Facon *et al.* (2011) demonstrate that replicate introduced populations experi-

ence almost none of the inbreeding depression suffered by native populations. Thus, rather than posing a barrier to invasion as it is often assumed, bottlenecks, 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 independent 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 eukaryotes, Denver *et al.* (2004) have suggested that cellular stress responses might provoke hypermutation in the roundworm *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.

#### Phenotypic plasticity

This 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).

The genetic and epigenetic bases of plasticity remain largely unexplored. If the term epigenetic inheritance is used comprehensively to include mitotic inheritance, then some of the mechanisms underlying phenotypic plasticity may be based on epigenesis. But if the term refers exclusively to meiotic epigenetic inheritance, then epigenetics do not overlap phenotypic plasticity, as plasticity is a genotype-specific, environmentally-induced, and a non-heritable change of the phenotype (Oliver Bossdorf, Helmholtz Centre for Environmental Research, Halle, Germany, personal communication). In this paper the term is restricted to the inheritance of epigenetic variation across generations.

Funk (2008), in a rather interesting approach, compared the plasticity in response to variation in light and nutrient availability in five phylogenetically related pairs of native and invasive species occurring in a nutrient-poor habitat, and confirmed the general paradigm that invasive species display high trait plasticity. Davison *et al.* (2011) found that invasive species are more plastic in a variety of traits, but that native, non-invasive species respond just as well, if not better, when resources are limited. These findings have interesting implications for predicting responses to global change.

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 (Bradshaw and Holzapfel, 2006).

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 generation. 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.

Dyer *et al.* (2010) gave an example of TGP for early flowering in *Aegilops triuncialis*, a phenological response that reduced drought stress in this annual grass invader. These authors showed that maternal responses to soil conditions led to greater stress tolerance in seedlings in the form of greater photosynthetic efficiency. According to them, the period of expansion during invasions can be divided into demographic and evolutionary processes. In the first, the spread to high-resource environments is strongly influenced by the dynamics of dispersal, nutrient availability, disturbance, and propagule pressure. In the second, further population expansion is constrained by both biotic and abiotic factors, evolutionary changes and new adaptive phenotypes, then becoming necessary before further expansion into stressful habitats.

#### Epigenetic changes

The term epigenetics refers to a set of molecular processes, including DNA methylation, histone modification, and RNA interference, that can alter gene function and ultimately the phenotype, without changes in DNA sequences (Bossdorf *et al.*, 2010). The best described of these mechanisms is the methylation of DNA on cytosine bases, most often at CpG sites, that plays an important role in the epigenetic regulation of genomic imprinting, suppression of transposons and other parasitic sequences of DNA, and the inactivation of the X chromosome (Laurent *et al.*, 2010). Addition

and removal of DNA methylation can be highly dynamic, but the means by which the methyl mark is removed in animals is unclear (Xu *et al.*, 2011). Cytosine methylation is also strongly associated with the modification of histones and the condensation of chromatin, and is an important factor in the regulation of gene expression (Bossdorf *et al.*, 2010).

Recent research has shown that in many species there is a natural variation in epigenetic modifications, very similar to that found in DNA sequences, and that at least some of this variation is inheritable and independent of genetic variation, thus making it potentially subject to evolution by natural selection (Grant-Downton and Dickinson, 2006; 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, without any genetic change, particularly when populations are small and lack genetic variability, as is 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.

An example of epigenetic adaptation is illustrated in a study by Adam *et al.* (2008) on resistance by *E. coli* to ampicillin that acts by inhibiting cell wall synthesis. Evidence of epigenetic inheritance in multicellular organisms also exists, its occurrence being more common in plants and fungi, probably because soma and germline are not segregated in these groups, and developmentally induced epigenetic variations occurring in somatic cells are readily transferred to the gametes when these somatic cells assume germ line functions (Jablonka and Raz, 2009). But Crews *et al.* (2007) also demonstrated that inheritable epigenetic varia-

tion can affect even animal behavior. As 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.

The genome and other inheritable structures represent a 'memory' of past environments, but the entire process of epigenesis provides an opportunity to 'respond' to both present and 'predicted' future environments, as well as to gather new information and add some of it to the memory via genetic assimilation (Balon, 2002).

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).

Ho (2009) proposed that the intrinsic dynamic structure of the epigenetic system is the source of non-random variations that direct evolutionary change in the face of new environmental challenges. When a population of organisms experiments a new environment or adopts a new behavior, the following sequence of events might take place:

- a) A novel response arises, if not in all of the population, in a large number of individuals experiencing the new environment.
- b) This response is canalized in successive generations by epigenetic mechanisms independent of natural selection.
- c) After a number of generations, the response may become 'genetically assimilated' in that it may be observed even in the absence of the stimulus.

#### Assembling the Puzzle of Invasions

There is evidence that gene expression is affected by environmental influenc-

es, 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 of proteins. The information flows in a one-way direction and there is no reverse flow information. The reductionist view that organisms can be understood using properties of their genes and nothing else must also be critically assessed.

From the moment that small groups of individuals are introduced and become incorporated into a receptor environment, complex interactions between the environment, genetic, and epigenetic mechanisms arise to either thwart or foster the invasion.

Clearly, a single explanatory factor for invasions is not expected to emerge from the numerous studies. However, in some cases a single factor seems to be of greatest importance, as vegetative reproduction in *Caulerpa taxifolia*; parental care of offspring in *Oreochromis mossambicus*; enemy release; propagule pressure as in the Cuban brown lizard (*Anolis sagrei*) in Florida, USA; phenotypic plasticity in populations of brown trout (*Salmo trutta*) introduced into the Argentinean Patagonia; or epigenetic adaptation on resistance by *E. coli* to ampicillin. Bioinvasions seem to be a matter of more than one of the mechanisms already analyzed.

Although research on epigenetic mechanisms is still in its infancy, based in the limited existing knowledge it is possible to envision the great importance of epigenetic changes in bioinvasions. Epigenetic mechanisms are based on the fact that natural variation in epigenetic modifications is very similar to that found in DNA sequences, and that at least some of this variation is heritable and independent of genetic variation, thus making it potentially subject to evolution by

natural selection (Grant-Downton and Dickinson, 2006; Jablonka and Raz, 2009; Bossdorf *et al.*, 2010). Adaptation, as indicated by Jablonka and Raz (2009), can take place very rapidly through selection of epigenetic variants, without any genetic change, particularly when populations are small and lack genetic variability, as is the case of bioinvasions. When environmental conditions change, these epigenetic variants are often induced into several individuals in the population, many of them acquiring similar modifications at the same time.

Finally, the Allee effect must be mentioned (Allee, 1931). That is, the *per capita* birth rate declination at low densities can dramatically affect the dynamics of biological invasions (Taylor and Hastings, 2005). Several factors are known to cause this effect in low-density populations, but the most prevalent cause of Allee dynamics is the failure of mates to locate each other at low population densities (Yamanaka and Liebholt, 2009).

Allee effects cause longer lag times, slower spread and decreased establishment likelihood of invasive species. Expected spatial ranges, distributions and patterns of species may be altered when an Allee effect is present (Taylor and Hastings, 2005; Tobin *et al.*, 2009).

Actually, conservation biologists may attempt to minimize the Allee effect so that extinction is less likely, while invasion biologists should consider it as a benefit in limiting the establishment success or the spread of an invading species. Efforts to reduce the density of populations below an Allee threshold can be an effective strategy in efforts to manage invasive pests. In particular, culling is a commonly used tactic in efforts to manage population densities of native and non-native pest species alike (Tobin *et al.*, 2011).

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