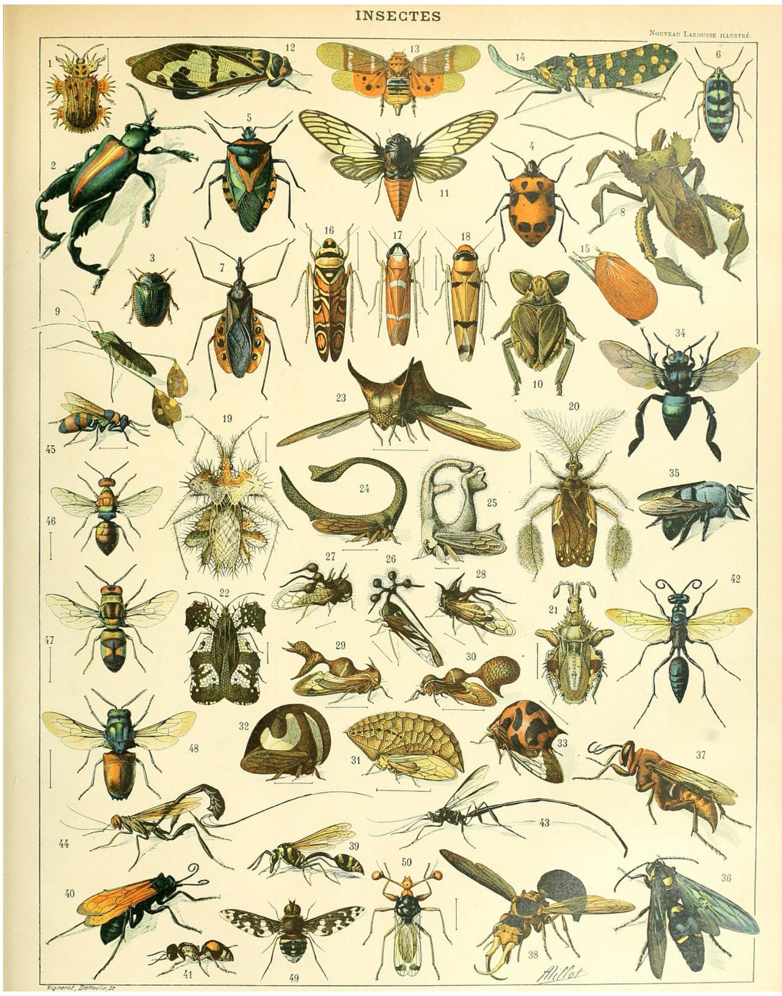
Invasive Insects and Their Genetic Success: Lessons for Conserving Decline Native Populations



Adolphe Millot' Illustrations of insects for Nouveau Larousse illustré

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Abstract

The alarming rate of declining native insect populations is reducing the genetic variation within these populations. This reduces the evolutionary potential of these populations and moreover increases risk on inbreeding depression and effects of genetic drift. A genetic paradox is however created when observing invasive insect populations. These populations experience often bottleneck events, which reduce the population genetic variation severely. Invasive species however are thriving as never before and are therefore an interesting factor to enhance insect conservation. This review focusses on the genetic success of invasive insect populations to give new insights in native insect populations conservation. The results indicate that the answer to this paradox is very complex as multiple ecological and evolutionary processes are at play. An important factor observed is that invasive insect has a higher evolutionary potential as their genome is bigger and has a higher GC content. This causes an increased genetic resource to tap into and moreover the high GC content causes a higher mutation rate increasing genetic diversity as well. Another partially explanation are ecological aspects. The global trade and travel in forming continuous pathways for invasion creating multiple introductions in novel environment of these populations. This enhances the gene flow and therefore the evolutionary potential. Moreover, climate change is an important success factor as well for insect populations. Invasive insect populations are developing at a faster rate in higher temperature environments. This creates an advantage due to global warming. This review indicated the importance of genome sequencing as a conservation tool. The genomes of invasive and native insect populations give conservationist a lot of insight in their evolutionary and ecological processes.

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1. Introduction

1.1 Importance of insect conservation

Human well-being, economies and agriculture are all depending on ecological services where insects play a crucial role. Their role in pollination, nutrient cycling, food webs and more are key factors in maintaining healthy ecosystems. The disruption of these services could impose a real threat to human well-being. (Crespo-Pérez et al., 2020). Moreover, agriculture depends on pollination as it is essential in the process of food production. This pollination is mainly performed by insects, indicating their importance in agriculture (Pardo and Borges, 2020). The economic importance of insects is becoming clearer as well. The annual value of the ecological services provided by insects was estimated at $57 billion U.S. dollars (Losey and Vaughan, 2006).

As we become more aware of the importance of insect conservation, insect populations are globally decreasing rapidly. They are threatened by human-driven environmental changes of habitat loss and fragmentation, climate change and the use of pesticides in agriculture. These factors result in the decrease in population size and the increase in isolation of these populations (Hailay Gebremariam, 2024). The rate of insect population decrease could lead in the next few decades to an extinction of 40% of the worlds insect species (Sánchez-Bayo and Wyckhuys, 2019). The significance of this decline and impact was made clear in the manifesto *Scientists' warning to humanity on insect extinctions* by Cardoso et al. (Cardoso et al., 2020), which indicated the importance of insect conservation in the upcoming decades.

1.2 The genetic paradox

The small populations of native insects due to habitat loss and fragmentation cause a decrease in genetic variation within these populations. This reduces the population fitness by decreasing adaptation ability and increases fixation of deleterious alleles. Moreover, due to the isolation, these populations have increased inbreeding risk and negative effects of genetic drift (Leigh et al., 2019). However, the success of invasive species challenges this principle.

Invasive populations when introduced into novel environments often experience bottleneck events. This reduces the population size and therefore the genetic variation within the population. It is therefore expected that these populations will suffer from the same consequences from low genetic variation (Allendorf and Lundquist, 2003). However, these population are able to adapt, establish and, thrive in these novel environments and even outperforming adapted native insect populations (Gloss et al., 2016).

This raises a paradox for researchers: If low genetic variation is harmful for populations, how are new introduced bottlenecked populations so successfully invasive? (Allendorf and Lundquist, 2003). A lot of research is already performed on finding the answer to this paradox. However, these studies are mostly aimed at targeting invasive species and reduce their harmful acts. In this review we focus on the studies in a different way, as it aimed to enhance conservation of native insect populations by understanding the success of invasive insect populations.

2. Context of invasive insects

2.1 invasive insects: an overview

Human health, economies, agriculture and biodiversity are threatened by invasive insects around the globe. Introduced from an exotic origin, they negatively impact the invaded ecosystem with their successful invasive mechanisms (Sun et al., 2023) These effects can be direct by predation, herbivory and hybridization with native species. Moreover, the effects could also be indirect due to cascading effects of disease transmission and competition (Fortuna et al., 2022).

2.2 pathways and drivers of invasions

The two main drivers of introductions of insect populations are: international trade and global warming. As human populations are increasing, the expectations of invasive insect instructions are increasing as well. The habitat range of populations is in normal conditions determined by their environmental adaptations, interspecific interactions and dispersal barriers. However, these ranges are expanding over the last few decades facilitated by human interactions (Gippet et al., 2019). Moreover, international trade is still increasing and causing international pathways for invasion by insects. The trade in live plants, wood packaging material, logs and more are some of these pathways where insects are transported by accident (Meurisse et al., 2019).

3 The Genetic paradox in invasive species

3.1 Founder effects

The founder population is the first generation of introduced species before becoming invasive. The population sizes are often small and have often therefore a decreased genetic variation within their population. This process is described as the founder effect or are called bottleneck events (Dlugosch and Parker, 2008). Founder effects have often negative effects on population as genetic variation is considered to be the foundation of evolutionary change of a species. It enhances the adaptation ability within a population and therefore increases evolutionary potential (Etterson and Shaw, 2024). The harmful influences of founder effects were observed in the invasion of the Asian honeybee (*A. cerana*) in Australia. The loss of genetic variation was observed at the complementary sex determiner loci. Homozygosity of this locus results in diploid male production. This process reduced the fitness and reproductive success of the population. Moreover, secondary genetic bottlenecks were observed in new small colonies causing a slowed down range expansion due to the founder effect (Hagan et al., 2024).

Founder effects can have positive effects on population fitness as well as observed in the invasive ladybird (*Harmonia axyridis*). If founder effects are not significantly severe, they expose recessive deleterious alleles within populations. The reduction of fitness in an individual due to expression of these recessive deleterious alleles causes the purging of these alleles by natural selection. This enhanced the overall population of the invasive *H. axyridis*. Experiments comparing the native and invasive populations showed that native populations suffered severely from inbreeding depression as the invasive populations did not. The invasive populations have due to this process a reduced genetic load and increased fitness traits as shorter generation times and higher lifetime performance. Therefore, the bottleneck events caused the invasive success of the harlequin ladybird (Facon et al., 2011).

3.2 Challenges to genetic fitness

The loss of genetic variation due to founder effects causes a lot of challenges to invasive insect populations. The overall fitness of the population is decreased by this loss of genetic variation, as they are more vulnerable to diseases, predators and the consequences of the novel habitat conditions (Neaves et al., 2015). Habitat and genetic variation are intertwined with each other as genetic variation drives adaptation to habitat conditions. This poses a real challenge for the founding population as they introduce novel habitat with a decreased genetic variation. Moreover, small populations are more sensitive to inbreeding depression and genetic drift which could catalyse the process to extinction of these populations (Sánchez-Bayo and Wyckhuys, 2019).

3.2.1 Inbreeding depression

Inbreeding is the procreation of two closely related individuals. This increases the homozygosity within populations as chances of sharing the same alleles due to common ancestor are increased. This reduces the population fitness by increase of homozygosity of partially recessive detrimental mutations and the increase in homozygosity of alleles which have heterozygote advantage (overdominance) (Charlesworth and Willis, 2009). Therefore, with each generation the fitness is reduced compared to offspring originating from randomly mated individuals. The reduced fitness of these offsprings caused by inbreeding is defined as inbreeding depression (Hedrick and Kalinowski, 2000). Founder populations are typically suspected to suffer from inbreeding depression, as small population have increased chances on mating between close relatives (Facon et al., 2011). The severity of the impact of inbreeding depression is variable. It is depending on the interaction of genotypes and the environment. Moreover, genetic drift is a factor for reduced fitness as well in small population. This could cause the fixation of deleterious alleles. (Hedrick and Kalinowski, 2000) (Cheptou and Donohue, 2011).
In some rare cases inbreeding is the foundation of the invasive success. The invasive ant species: *Brachyponera chinensis* has a pre-adapted tolerance to inbreeding. The native population of *B. chinensis* exhibits inbreeding and likely purged deleterious and harmful alleles during naturing selection. The studies showed that the introduced populations experienced founder effects and genetic variation was reduced with 30%-40%. However, this did not affect their reproductive system and had therefore minimal fitness cost. Moreover, the pre-adapted trait of inbreeding decreased founder effect severely and resulted in invasive success (Eyer et al., 2018).

3.2.2 Allee effect

The small size and low-density of the founder populations puts them a high risk for extinction and therefore fail to establish. To understand this the Allee effect should be considered. This concept states that each population has a threshold of individuals in a population to be viable This effect could be caused by vary processes as inability to locate mates, inbreeding depression, inability to satiate predators and lack of cooperative feeding (Liebhold and Tobin, 2008).

3.3 Mitigating factors in invasive success

The challenges that invasive species face during introduction can sometimes be mitigated by certain ecological and evolutionary processes. The processes as multiple introductions and hybridization increase the genetic variation within these population and could therefore play a key factor in invasive success.

2.3.4 Multiple introductions

Introduction patterns of invasive species are often more complex than a ‘simple’ introduction across countries or continents. Population studies on insects as the medfly (*Ceratitis capitata*) by (Malacrida et al., 2007), Bronze bug *(Thaumastocoris peregrinus*) by (Nadel et al., 2010), and more showed that their success lies in multiple introductions of small populations. Multiple introductions maintain the genetic variation within population and therefore enhancing the adaptation abilities of these populations.

3.3.2 Hybridization and Admixture

Hybridization and admixture are processes that enhance gene flow within populations. These processes occur when individuals from different populations breed, enhancing the genetic variation of the offspring. This improves the overall fitness of a population by growth rate, fertility and stress tolerance (R. Garnas et al., 2016) . The increased gene flow due to these processes moreover decrease founder effects and inbreeding risk (Beaurepaire et al., 2024).

3.3.3 Reproduction

The loss of genetic variation in invasive species of often reduced by different mating systems. Invasive insects, especially social insects, show a great variation in their breeding systems that can influence the success of invasion. A high breeding rate can increase the population density very rapidly and therefore reduce possible impacts of founder effects. Polyandry and polygyny are good examples or mating systems that increase genetic variation within populations by rapidly increasing in population size. Polyandry is a mating system where a female mates with multiple males during their breeding period and is observed in the invasive spotted lanternfly (*Lycorma delicatula*). (Belouard and Behm, 2023). Polygyny is a mating system where a male mates with multiple queens in the colony. This is a well-established breeding system in the invasive *Vespula germanica, Vespula vulgaris* and *Vespula pensylvanica* and in invasive ants (Eyer and Vargo, 2021).

Insect can also reproduce asexually, which are often considered to have a low genetic variation as they reproduce parthenogenetically. The invasive hemlock woolly adelgid however challenges this assumption as its significant regional cold hardiness was observed. The research suggest that northern populations had adapted trough natural selection acting on pre-existing cold-tolerance traits. This indicates that the invasive success of this asexual insects lies in the adaptation ability due to genetic variation within the population (Lombardo and Elkinton, 2017) .

4 Establishment and Adaptation

4.1 Genetic mechanisms of establishment

Invasive species need to establish in their new environment after introduction. The establishment is influenced by a combination of ecological and evolutionary processes. Ecological factors as habitat suitability and resource availability interact with the adaptation ability of the invasive species (R. Garnas et al., 2016). The evolutionary processes are driven by natural selection that change traits to enhance survival and reproduction. This is for example well studies in *Drosophila* species. These populations have shown quick adaptation to temperature, altered food availability or competition with native species. Moreover, research of the silverleaf whitefly (*Bemisia tabaci*) indicated evolution of new traits as improved reproduction, or resistance to predators, pathogens, or pesticides (Hill et al., 2016).

4.2 Adaptation

The invasive insect success lies in their quick and effective adaptation ability. They exhibit rapid evolutionary responses to their new environment giving rise to their successful invasion in novel environments (Lee, 2002). The importance of adaptation ability is observed in the *T. solanivora,* one of the most successful invasive species agricultural pests across the Northern Andean region. This invasive insect has one of the strongest declines in genetic variation due to bottleneck events. It was therefore expected due to loss of heterozygosity that this population has a reduced population fitness. This example indicates how biological invasion relies often on a combination of retained adaptive traits, ecological compatibility, and reduced environmental constraints. These factors reduce the effects of genetic bottlenecks and enable the species to establish in novel environments (Puillandre et al., 2008).

4.2.1 Phenotypic plasticity

Phenotypic plasticity is an important factor in adaptation for invasive species, without altering the genetic variation. It is the ability to produce different phenotypes from a single genotype in response to changing environmental conditions. The *Drosophilia suzukii* is a great example of this. Their invasive success is due to their high phenotypic plasticity in wing size and develop time in response to their environment (Etterson and Shaw, 2024) . However, disadvantages of phenotypic plasticity in invasive species obsereved as well in the emerald ash borer (*Agrilus planipenis*). This invasive insect loses their cold tolerance in response to warmer environments. This decreases the survival abilities during cold events in the winter. This indicates the importance of the collaboration between environmental condition and adaptation (Sobek-Swant et al., 2012) .

4.2.2 Genetic variation

The paradox of invasive biology lies in genetic variation, as genetic variation is the foundation of adaptation and provides for insects' significant evolutionary advantages. It enables for example in herbivore insects the adaptation to diverse environments and challenges. The host-plant interaction is in these insect population very important, as the plant chemical and defense mechanisms are changing continuously as well. The resolving of these challenges lies in the genetic variation in these population, which allows them to adapt quickly and effective (Gassmann et al., 2009).

The success of invasive relies in their genetics as they evolve more rapidly than non-invasive species. Their genetics cause their invasive mechanisms as rapid adaptation to their host food, migratory and spreading ability, and their adaptation to pesticides. This shows the importance of their genetics in their success of invasion. The invasive insects show that they have a significant larger genome compared to non-invasive species. This shows that they have a higher genetic variance and therefore a higher adaptation ability. Moreover, this study shows that the GC content of invasive species was significantly lower compared to non-invasive species. The low GC content indicate a less stable DNA, which results in a higher mutation rate, rapid transcription and replication. This results in faster genome evolution, fast growth and reproduction. This could be a factor in the ability to outperform a non-invasive species. The genetic success of invasive species becomes also clearer in research on the TEs, repetitive DNA sequences, and gene nucleotide diversity which are greater in invasive insect species. These are all mechanisms that enhance the evolutionary ability of insects (Sun et al., 2023)

Another example of the influence of genetic variation during invasion is observed in the highly invasive Argentine ant (*Linepithema humile*). The decreased genetic variation due to founder effects is mostly harmful for populations as adaptation ability and fitness is decreased. However, the Argentine ant contradicts this statement. This highly invasive species success lies in the reduction of genetic variation. Studies showed that this species experienced bottleneck events during introduction in California causing a significant reduction in genetic variation compared to the native Argentina ant. This caused a decrease in intraspecific aggression and therefore the formation of so called 'super colonies'. Moreover, if intraspecific aggression was observed between populations in California, it resembled the same degree of intraspecific aggression and genetic variability in the native population in Argentina. Thus, the results of founder effects caused a significant increase in population size and density as the colonies where not competitive to each other (Tsutsui et al., 2000).

5 Spread and migration

5.1 Bridgehead effect

The successful invasive population can accelerate their success by a process called the bridgehead effect. This describes the process where a successful invasive population serves as a source for further invasions. For instance, if the population is adapted to the local environment, the survival and reproduction potential is increased. This is a stable source for populations to spread further. This gives rise to secondary introductions and accelerates the rate of invasion. (Bertelsmeier and Keller, 2018). The significance of the bridgehead effect is indicated in a study on invasive ant populations. This study showed that a significant proportion (75.7% in the U.S.) of alien ant species originated from invaded ranges and not native ranges (Bertelsmeier et al., 2018).

5.2 Climate change

A crucial environmental factor on insect populations is temperature. Researchers found that invasive insects have a higher lower developmental threshold (LDTs), indicating that invasive insects need higher temperatures to initiate development. However, invasive species often have a lower sum of effective temperature (SETs), indicating a faster development once above the temperature threshold. Thus, invasive insects have faster development if temperature is higher creating an advantage and disadvantage depending on the regional climate. Climate change is therefore an important factor in these findings. As the temperatures rise around the globe, the invasive potential of invasive insects is increased (Jarošík et al., 2015) .

6 Conclusions and Discussion

6.1 The success behind invasive mechanisms

The solution to the genetic paradox stated in the introduction of this review has a complex answer, as there a lot of ecological and evolutionary processes involved for a successful invasion. This review however indicated that a crucial part for invasive success lies in the genetic variation of invasive insects. The role of the part is in every invasion different, as shown that every invasion is unique in their own way. Another key factor observed for successful invasion is human interactions. The invasive pathways, climate change and habitat change are all human induced factors that have shown to be a crucial factor for invasive success.

6.2 Environmental conditions

The genetic paradox is partly explained by the human-driven environmental changes. They are a significant factor in shaping the dynamics of insect populations. It is a major factor in invasion success while simultaneously contributing to the decline of native insect populations.

6.2.1 Dispersal pathways

Habitat fragmentation is one of the key factors in the decline of native insect populations as it increases isolation of populations. This causes a decreased fitness within populations by a decline in genetic variation. The isolation causes therefore an increased dispersal barrier, whereas dispersal barriers of invasive insects are reduced by international trade. The international trade is one of the key factors of new introductions of invasive species around the world. It creates pathways of invasive routes that are only increasing in the next decades. Moreover, these pathways are suspected to be used a lot creating multiple introductions of the same species overtime. This causes an increased gene flow for invasive populations and reduces the effects of genetic drift and inbreeding depression (Schrieber and Lachmuth, 2017).
The overall observation is that native species rapidly decrease due to isolation. This decreases gene flow and increases therefore the effects of genetic drift and the risk on inbreeding depression. Whereas invasive species have increased pathways due to international trade which decreases isolation. Moreover, it increases gene flow due to multiple introductions enhancing genetic variation (Gompert et al., 2014).

6.2.2 Climate change

Climate change is another important factor for invasive and native populations. Isolated native insect populations experience a low genetic variation due to decreased population by habitat loss and isolation by habitat fragmentation. Changing habitats due to climate change is therefore another catalysator population decrease as these population lost their adaptation abilities. Whereas climate change is causing a reduction of dispersal barriers for invasive populations as they have higher lower developmental threshold. Moreover, invasive species have a lower sum of effective temperature. This indicates that global warming is enhancing development in invasive insects.

6.3 Evolutionary processes

6.3.1 Founder effects

The founder effects mostly have deleterious effects on population as evolutionary potential is decreased of a population. The ability to adapt is highly needed in population and especially in invasive species as they need to rapidly adapt to novel environments. The founder effects however do not always have negative effects as observed in *H. axyridis* and *L. humile*.

The definition of founder effects is a reduced genetic variation within a population compared to the native population (Kivisild, 2013) . This can be applied to the native population as their genetic variation is reduced by habitat loss and fragmentation. The fragmentation moreover causes the same circumstances as invasive populations experience as gene flow is reduced. The changing habitats is also an important factor in this problem. Native species are expected to be specialized in their environmental and have therefore an advantage on invasive species. However, these habitats are changing rapidly by climate change, habitat loss and other factors. This habitat transformation causes a problem for native specialist populations as they need to adapt rapidly to their changing environment. This however is limited due to the fragmentation of habitat (Rippel et al., 2021). Native species and invasive species experience therefore the same founder effects as they have a reduced genetic variation and need to overcome challenges of novel habitat.

6.3.2 Genetic variation

Genetic variation reflects the adaptation ability of a population against environmental challenges. The level and rate of genetic adaptation therefore determine how fast and easy adaptation occurs. The evolutionary potential in invasive species was found to be higher compared to native species due to their enhanced genetic variation driven by different evolutionary processes. The bigger genome size of invasive insect population is therefore a crucial factor for invasive success. This enables a higher adaptation and therefore increased fitness within these populations. Moreover, the invasive insects DNA has a higher GC content, which indicates a less stable DNA, and it is due to this more sensitive for mutations.

6.4 Future directions

The insights in ecological and evolutionary processes on the invasive success give rise to multiple possible conservation strategies of native insect populations. The importance of gene flow was indicated when looking at the success of multiple introductions for invasive species. This increases genetic variation and therefore the evolutionary potential, it moreover decreases the risk on inbreeding and genetic drift. A possible good solution is found in the Netherlands, called an: “Ecoduct”. This is a green passage connecting two natural habitats. This would create a passage for insects to migrate and increasing gene flow between populations (Van Bohemen, 2002). Genome sequencing of native and invasive insect population is an important tool for conservation as well. The DNA of these populations gives as shown in this research a lot of insights in the evolutionary potential and processes. This could help conservationist to develop effect strategies of conservation.

7 Literature

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