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Toward the Development of Novel Long-Term Pest Control Strategies Based on Insect Ecological and Evolutionary Dynamics

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1. Introduction

Most of the organisms that have negative impacts on agroecosystems and human health, namely bacteria, arthropods, fungi and weeds, share distinctive traits: short generation times, numerous offspring, and therefore large population sizes. These characteristics allow these organisms to change so fast that control of their population growth is difficult to achieve. However, species with these traits, viewed in an ecological context, are subjected to different selective pressures that impede unlimited growth. For instance, as insects are currently the most devastating group within agroecosystems, producing grave economic losses, farmers have resorted to the use of insecticides—whether natural, synthetic, or expressed in genetically modified organisms—as the main control method used to deal with this problem. While the use of insecticides can aid in the short-term control of insect pests these control methods present six fundamental problems that are environmentally irreversible: 1) the pest evolution of insecticide resistance; 2) eradication of non-target species; 3) elimination of ecological interactions; 4) modifications of the biogeochemical cycles; 5) environmental pollution; and 6) impact on human health. Currently, a great deal of knowledge about ecological and evolutionary processes and dynamics is becoming available; this can help to explain the issues mentioned above. In this chapter, we will analyze these processes to subsequently propose alternatives for a long-term integral pest management system.

1.1 Understanding insect pest populations

Insects represent almost 60% of the total species diversity existent in the planet (Strong *et al.*, 1984; Purvis & Hector, 2000; Gibbs, 2001). It is estimated that 26% of all extant living organisms on Earth (361,000 species) are phytophagous insects, while 31% (430,000 species) are saprophagous or predators (Stong *et al.*, 1984). Insect populations are mostly characterized by presenting early reproduction, small body size, undergoing just one

reproductive event in their lifetime (i.e., semelparity), having small progeny, and allocating substantial resources to reproduction (Borror *et al.*, 1992). In general, they lack paternal care (Daly *et al.*, 1978) and individuals produce a great amount of descendants to maintain the stability of the population size (Huffaker *et al.*, 1984). Populations of insects are generally discrete, which means that generations do not overlap (Begon *et al.*, 1996).

The size of insect populations is regulated when intrinsic or environmental forces modify their capacity for survival, reproduction, or migration (Berryman, 1973). Predation, competition, and resource availability (e.g., habitat, food) are factors that regulate populations (Price, 1984). If these factors pose a limitation when a certain population density and growth rate is attained, then they are acknowledged as density-dependent processes (Varley *et al.*, 1973; Price, 1984). On the other hand, external factors such as the weather or the soil type can control the population size independently of population density (i.e., density-independent; Price, 1984). Thus, Huffaker *et al.* (1984) mention that insect populations are basically regulated by the ecological relationships they sustain, being predation and parasitism the most relevant interactions. Taking this into consideration, when natural enemies of an insect species are eliminated, its populations may undergo an accelerated increase, such that it becomes a pest. Any organism that causes economic losses by affecting crops and/or domestic animals or human health is considered a pest (Speight *et al.*, 1999). As a general rule, a species needs to have numerous individuals to be regarded as such. Moreover, pests generally emerge as a consequence of human activities (Uvarov, 1964), given the fact that in the wild these species tend to occur in low densities, although their numbers drastically increase when favorable environmental conditions arise (Dominguez, 1992). Other authors define a pest as a species that causes an economic loss to humans by damaging their food, house, or dress. In nature, there are no such things as pests; therefore, this concept does not have a strict biological meaning—it is derived from human values related to health, economics, and aesthetics (Leyva & Ibarra, 1992).

Pests arise for three main reasons (Uvarov, 1964; Leyva & Ibarra, 1992; Speight *et al.*, 1999):

Increased resources: Human activities provide insect species with the best resources: These are unlimited. A good example comes from the huge extensions of mono-crops, which supply a great amount of food.

Elimination of natural enemies by control methods: Many parasites, parasitoids, and predators control the growth of phytophagous insect populations and limit their distribution.

Introduction of exotic species: When a species is introduced to a new region, it can multiply rapidly due to the lack of natural enemies.

1.2 Recent trends in insect-control methods

Throughout history, human societies have battled pests, sometimes losing against them and thus confronting dramatic losses (Losey & Vaughan, 2006). Yet, we do not have a complete record of these events, as knowledge regarding plagues was somewhat unspecific before better tools (e.g., microscopes) allowed us to characterize them. In addition, scientific interest was less attentive to normal agricultural complications. From the late nineteenth to the early twentieth century, crop protection specialists relied on knowledge of pest biology and cultural practices to produce multitactical control strategies (Gaines, 1957). This

approach changed in the early 1940s, when the use of organosynthetic insecticides supplanted virtually all other tactics and became the dominant approach to insect pest control. This period (from the late 1940s through the mid-1960s) was called “the dark age of pest control” (Newsom, 1980), because specialists began to focus on testing chemicals to the detriment of studying pest biology and non-insecticidal control methods. By the late 1950s, however, warnings about the risks of the preponderance of insecticides in pest control began to arise. Reports coming from the workers of cropping areas in North and South America (Dout & Smith, 1971) and Europe (MacPhee & MacLellan, 1971) described early signs of the consequences of insecticides, but did not have much impact, given that pesticides seemed very successful at a relatively low cost, providing long-season crop protection against pests and complementing the benefits of fertilizers and other agricultural production practices. During the decade of the 1960s, the application of insecticides reached its highest exploitation, and the negative consequences became evident in the agricultural yield. Given this problem, in the 1970s, different alternatives were adopted that focused on combining chemical methods with other strategies, for instance, considering biological and traditional agricultural knowledge.

Integrated pest management (IPM) is a concept that arises from the difficulties presented by the unsystematic use of insecticides. IPM has a long history and a broad scope, including the use of chemical insecticides in combination with improved cultural and biologically based techniques with a focus on achieving the most permanent, satisfactory, and economical insect control possible (Kogan, 1998). Yet, although conceived as a strategy friendlier to the environment, even the most successful contemporary IPM programs have been implemented with little consideration for ecosystemic processes. While species and population ecology have been the foundations of those programs because populations are the biological units in which species exist (Geier, 1966; Kogan, 1998), little attention has been paid to understanding the characteristics, processes, and dynamics at all ecosystemic levels (Gliessman, 1990). This information is essential for a scientific analysis of agroecosystems (Risser, 1986). Different definitions of IPM proposed in the last decades tried to incorporate these concepts; some were discussed and adopted in international committees (Kogan, 1998) with varying degrees of success. For instance, the management of rice pests in Southeast Asia was proposed to be based mainly on the restoration of natural controls through the removal of broad-spectrum insecticides (Kenmore, 1996). Furthermore, Kogan (1988) proposed that the four basic hierarchical ecological scales— individual, populations, communities and ecosystems—should serve as the template for IPM integration. This framework will be further discussed within this contribution, as the notion is compatible with our proposal.

Lastly, at the present time, excitement about genetic engineering dominates the literature and global management strategies; nevertheless, nothing will have been learned from past experiences if genetic engineering prevails over all of the other technologies that are also blossoming (Kogan, 1998). Like in the “dark ages,” we do not have enough knowledge about the risks that genetic engineered crops could pose for wild plant populations (e.g. through gene flow; Ellstrand, 2003; Andersson & de Vicente, 2010; Dyer *et al.*, 2009), non-target organisms (Dale *et al.*, 2002; Hilbeck & Schmith, 2006), and human health (Schubert, 2002; Finamore *et al.*, 2008; Spiroux de Vendomois *et al.*, 2009).

Despite the control strategy used, the pest evolutionary arms race continues, and the ongoing development of insect resistance to insecticides has become a serious problem. Moreover, other factors linked to human populations have complicated the problem. For instance, policy strategies concerning these practices should be guided firstly by strict scientific knowledge.

1.3 Economic, ecological, and evolutionary costs of insecticide use

Historically, with the advent of agriculture, the human social structure changed and the establishment and growth of human societies began as a result, this practice lies at the very core of human cultures. Agriculture is an activity that clearly benefits from environmental services, since these provide primary sources essential to farming such as soil, biogeochemical cycles, and ecological interactions (e.g., pollinators, predators, nitrogen fixing bacteria). By altering the environmental services that sustain agriculture, we would be jeopardizing not only valuable biological diversity and ecological processes, but also a series of economic, social, and cultural components in a way that the calculation of the costs would involve many different levels. Nevertheless, an important question to ask in a broader sense, not just in the context of agriculture is as follows: How much is an environmental service worth? Some works have revolved around this issue and estimated that the costs of losing even one ecological service rises up to billions of dollars (Losey & Vaughan, 2006, 2008; Pimentel 1992, 2005).

At first glance, the use of pesticides may appear to be an advantageous and low-priced pest control option; nevertheless, major environmental complications follow this practice, finally resulting in economic, ecological, and evolutionary costs. As summarized in Figure 1, the alteration of ecological dynamics has short-term (ecological) and long-term (evolutionary) consequences that may or may not be reversible according to the magnitude of the damage. All of the biome processes at different levels—namely the individual, population, community, and the biome itself—are affected by the drastic conditions insecticides impose when applied irresponsibly. This practice affects the evolutionary processes in agroecosystems and jeopardizes the environmental sustainability necessary for future generations to survive, sometimes altering biological processes that are irreplaceable. Within lower ecological levels, insecticides compromise the life span, growth, reproductive potential, and behavior of individuals, thus reducing their fitness, and with time, modifying the evolution of life history traits. At the population level, increases in the mortality rate and alteration of the age structure could lead to the reduction of genetic and phenotypic diversity, decreasing the fitness of surviving individuals and increasing the potential for species extinction. At higher ecological levels, the affections inflicted by insecticides must not only be considered according to their ecological and evolutionary consequences, but also evaluated in relation to the ecological services that are being affected, since they are mostly provided by a complex of species through network interactions. Indiscriminate insecticide use damages the services that ecosystems inherently provide through their proper functioning, and insects, being one of the most diverse and successful animal groups, are involved in performing important ecological tasks such as pollination, pest control, suppression of weeds and exotic herbivorous species, decomposition, and soil improvement (Losey & Vaughan 2006, 2008).

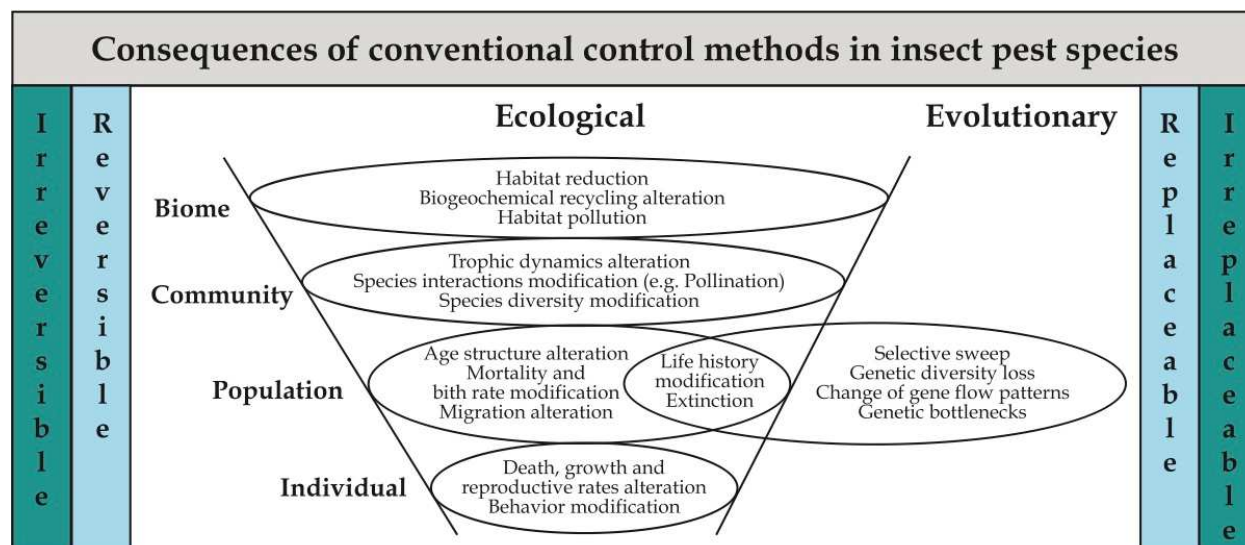


Fig. 1. Ecological and evolutionary consequences of insecticide control methods. Ecological consequences are shown at different ecosystemic levels, while evolutionary consequences occur only at the population level. Consequences can be irreversible or reversible and affect replaceable or irreplaceable environmental services.

When altered, ecological communities could suffer from an alteration of trophic dynamics and interactions, as well as a modification of species richness, diversity, and abundance; this could ultimately end interspecific relationships that could have been occurring for millions of years, affecting biodiversity irreversibly. Perhaps one of the most relevant concerns in this matter is the adverse effect of broad-spectrum insecticides on non-target organisms, especially if these contribute to an ecological service. For example, in all ecosystems, natural predators and parasites regulate the growth of herbivorous populations that could develop into potential pests. Pests can grow uncontrollably if their natural enemies are destroyed, or even if pesticides alter their predators' searching and attacking behaviors. This alteration of interactions can cause increases in pests of the same species, or even promote the appearance of new pest species (Metcalf, 1980; Van den Berg *et al.*, 1998; Mochizuki, 2003; Devine & Furlong, 2007). When this happens, additional and often more costly pesticide treatments are needed to avoid losing the crop; thus, it is possible to replace this "free" natural pest-control service, but this becomes highly expensive and environmentally hostile. Pimentel (1992) estimated that about half of the control of pest species is due to natural enemies, and that pesticides give an additional control of 10%; the main percentage is due to host-plant resistance and other limiting factors present in the agroecosystem. Losey and Vaughan (2006) estimated that if no natural predators were functioning to control native insect pests in the United States, the damages could reach \$20.92 billion dollars each year. Insect pollinator species are also affected unintentionally but gravely by the use of insecticides. This is a serious matter, considering that this process is vital to plant reproduction and species preservation, and that it is a service that is not replaceable by any human technology. This problem affects not only crops, but also their wild relatives, by modifying the composition of native as well as non-native pollinators. Moreover, the lack of effective pollination reduces crop yields and the quality of the agronomical products, and can also cause the loss of the entire crop. Furthermore, it can affect the next sowing season, since seeds cannot be collected. In the United States, native pollinators may be responsible for yielding almost \$3.07 billion dollars a year by allowing the successful production of fruits and vegetables (Losey & Vaughan, 2006).

Insects are not the only populations affected by the use of pesticides. Other organisms, such as birds and mammals, are directly or indirectly impacted by open exposure or the consumption of contaminated nourishment, respectively (Pimentel, 1992).

As insecticides pollute the environment, the habitat where living organisms can dwell is reduced. Insecticides may be toxic to soil microorganisms that are fundamental in maintaining the structure and function of ecosystems by enabling vital processes to take place (e.g., biogeochemical recycling, nitrogen fixation, organic matter disintegration; Atlas & Bartha, 1987; Brock & Madigan, 1988), this is why soil community alterations cannot be taken lightly. Moreover, since insecticides are often sprayed without sufficient care, they can reach neighboring crop fields and wild communities, and can even find their way into ground and surface water by soil erosion and water runoff (e.g., aldicarb, alachlor, and atrazine; Osteen & Szmedra, 1989; Relyea, 2005), finally disturbing aquatic ecosystems and contaminating potable water.

The consequences of insecticide usage are evidently costly. Simply, while the agricultural products are fixed in the markets and depend on private interests, the price of the crops freely fluctuates in the global markets. This inequity causes problems that will not be addressed in this chapter but that reveal the economic dimensions the loss of environmental services could have as a consequence of indiscriminate insecticide use; these could perhaps be considered “pest evolutionary arms race collateral effects.” Studies about the environmental services jeopardized by current pest control methods and their economic costs are greatly needed. More reliable data documenting the involvement of insects in environmental services must be published to allow the generation of mathematical models and consequently the accurate estimation of the value of these services. Ideally, these efforts should be undertaken worldwide to guide each country’s policy strategies regarding such practices, for example, through risk assessment studies.

2. Ecology of insect populations and life histories

More than 50 years ago, Cole (1954) published one of the first works pointing out the relevance of organisms’ life history to the management of pest species. Later, almost forty seven years after Cole, Nylin (2001), indicated the necessity of studying pests’ life history traits to control them, and to prevent as much as possible the development of potentially dangerous species. In this chapter, we assert that Cole and Nylin’s ideas are still valid; however, in our view, trying to eliminate or at least control a species with a complex life history is almost impossible. Under current control methods, including IPM, it is unfeasible to control the population sizes of species with great reproductive potential, growth rate, and dispersal ability. It is obvious that current trends regarding pest management should be modified. To achieve this goal, the first step should be revealing life history parameters that will potentially increase the population size and distribution range of a species. Pest management strategies should be adjusted to species’ life histories, so that mortality and birth rates or immigration and emigration rates can be estimated and projected.

2.1 Life history traits of insect pest species

Let us imagine the characteristics a crop-devastating insect should have. Females should be extremely fertile, being able to leave a large number of eggs, which would constitute the

next generation population. For example, let us picture a highly fertile female who can leave 70 to 100 eggs per laying and the number of laying events in her lifetime is, on average, three. Moreover, let us imagine that this female belongs to a species presenting a number of generations higher than one per year; let us say there could be up to three generations in a year. Furthermore, let us assume that the devastation potential of this species is not limited by space because it can migrate very long distances, e.g., hundreds of kilometers in just one day. Additionally, let us say that these organisms are polyphagous, being able to consume different plant types, not just the ones that humans cultivate but their wild relatives as well. Finally, let's imagine that these super-organisms have the capacity of inhabiting places that present very variable conditions, where they can perfectly survive, develop, and reproduce. If such an organism existed, it should be named *Schistocerca gregaria* and it would belong to the order Orthoptera. This locust species is one of the most devastating worldwide, not only nowadays but throughout agricultural history. Considering the information described above, we could obtain a simple population growth projection for a few years in a scenario lacking natural predators and providing unlimited resources. After one year, just from the mating of one female with one male, 900 new individuals would join the population in the next generation. If these 900 individuals presented a 1:1 sex ratio, the next year it would be 400,000 individuals, and five years after that the number of individuals would reach 3.5×10^{13} individuals. Although these numbers appear to be unreal, they represent very well the potential a single couple of locusts could have in an agroecosystem when no restrictions are imposed. Even when most of the individuals can be eradicated by conventional control methods, the infestation can reemerge in just a few generations with a higher population density. Unfortunately, the control methods do not have an impact on the traits that contribute to the demographic success of insect populations. *Schistocerca gregaria* is not the only species with these life history characteristics. All pest species possess at least one trait endowing them with high reproductive rates and survival success. Regarding the number of generations per time unit, aphids are exceptionally capable of originating new individuals. The species *Aphis glycines*, for instance, can produce 18 generations per year in soybean fields. Moreover, all individuals of this species, when present in monocultures, are parthenogenic females (thus, they do not need males to reproduce).

Some pest species display great dispersal ability. Some control measures are focused on avoiding or at least revealing the migratory routes of these species (Riley & Reynolds, 1983; Farrow & Daly, 1987; Riley & Reynolds, 1990; Pedgley, 1993; Chapman *et al.*, 2010). *Oedalus senegalensis* is a pest species that can migrate up to 350 km in just one night (Cheke, 1990). This insect can infest and destroy crops in huge areas of western Africa in just a few days, given its outstanding dispersal skill. Orthoptera species and other insect groups that present incomplete metamorphosis can immediately devastate large crop extensions. In the case of insects with complete metamorphosis, the damage normally occurs in the next season, since individuals at the adult stage are the ones with dispersal ability, while those at the larval stage—i.e., the next generation—eat the crops. It has been observed that recent African infestations have been related to the migration routes of *S. exempta*. Moreover, the diamondback moth, *Plutella xylostella*, can perform transoceanic migrations, thus being able to continuously travel up to 3000 km over a course of days (Talekar & Shelton, 1993). During its larval stage, this insect feeds nearly exclusively on cruciferous plants and due to its dispersal potential, it is possible to find it in almost every cruciferous crop field around the

world. Most of the migrations carried by insects are aided by wind currents (convergent winds in Africa), which allow the insects to invest a minimum of energy in flight (Chapman *et al.*, 2010).

Other species of insects, although they lack flight capacity, are able to colonize new agroecosystems. The orthopteran *Sphenarium purpurascens* can disperse more than 10 km annually throughout crop fields and wild environments, mostly due to its capacity to feed on greater than 50 different plant species (Cano-Santana & Oyama, 1994). Two decades ago, this grasshopper had a narrow distribution in central Mexico; at present, however, it inhabits locations hundreds of kilometers beyond its original range. *S. purpurascens*, like many other insect species, displays pronounced diversity regarding its life history traits when inhabiting crop fields as opposed to wild ecosystems. Its populations can actually change their life history traits in just a few generations (Cerritos, 2002).

2.2 Adjustable life histories: Phenotypic plasticity or swift changes in allele frequencies?

Let us now imagine a potentially crop-devastating species able to regulate its life history traits depending on environmental conditions, the resources available, and its own population density. If this species, when inhabiting locations with suitable environmental conditions and unlimited resources, could give birth to more than one generation per year and produce a huge amount of eggs each breeding, as well as being able to migrate long distances, it could be an extremely serious pest. *Locusta migratoria* is one locust species able to exhibit polyphenism, which is a biological mechanism characterized by the ability to adjust life history traits according to environmental or demographic factors (Simpson *et al.*, 2005). This kind of phenotypic plasticity has been documented in orthopterans, specifically from the Acrididae family. More than 15 locust species that are known to damage agroecosystems display polyphenism in their morphological, physiological, and behavioral traits (Song, 2005). Crop-devastating insects like *S. gregaria*, *L. migratoria*, and *L. pardalina*, for instance, possess the ability to assemble huge congregations of individuals that can migrate long distances and therefore have the potential to cause global infestations. These swarms can generally reach more than 250 million individuals (Simpson *et al.*, 2005).

The origin of this kind of plasticity was first explained, at least for *L. migratoria*, by the existence of two genotypes within their populations: one that favored the establishment of congregations and consequently infestations, and another that promoted solitary behaviors. Recently, however, it has been demonstrated that regardless of the genotype, this species has the ability to form huge groups of individuals anywhere in the world (Chapuis *et al.*, 2008). Locusts are not the only insects with phenotypic plasticity. Lepidopterans like *Polygonia c-album* and *Pararge aegeria* can modify their diapause in response to latitudinal variation and photoperiod and the heteropteran *Eurygaster integriceps*, a serious wheat and barley pest in Iran, can modify its generation time and fecundity as a result of temperature changes (Iranipour *et al.*, 2010).

Given the previous examples, it has become evident that to achieve successful pest management strategies, it is urgent to understand and unveil the genetic bases that underlie life history traits, especially those exhibited by insect pests. These traits appear to be subjected to strong selective pressures, such that in only a few generations, new genotypes

increase their frequencies and eventually become genetically distinct from the ancestral populations. Few studies have been performed in this context; nevertheless, a pioneering work comparing pest and non-pest populations of the beetle *Epilachna nipponica* offers some insight. The results show that pest populations exhibit a continuous ovoposition rate, shorter immature stages, and bigger female body size. Let us now picture a species that is not only very plastic phenotypically, but also extremely diverse genotypically (Shirai & Morimoto, 1997). What could we do to control such a species? What can we do to control *S. gregaria* or *L. migratoria*?

3. Evolution of insect pest populations

One or more genes determine almost all life history traits. The modification of these genes would probably involve the modification of one of such life history characteristics. The frequency change of the different alleles of these genes and the evolutionary forces that shape their distribution form the subject matter of a field called Population Genetics. For pest species, knowledge about their genetic structure is relevant to learning how certain traits become fixed within their populations. The genetic diversity of insect populations is a result of the huge population sizes that increase the probability of mutational events. All the genetic variants (i.e., genotypes) stored in populations are consequential when selective pressures, like insecticides, occur; for instance, one genotype might be resistant to a given insecticide and will therefore increase its frequency in a few generations, thereby performing a process called “resistance evolution.”

Unfortunately, for chronological reasons, Darwin never observed the effects caused by insecticides on inheritable traits; however, if he could have seen them, what he may have concluded is that strong selective pressures could modify populations in just a few generations. Darwin thought of evolution as a gradual process, but perhaps by observing the insect species subjected to insecticides, even he would have concluded that evolution could be very fast, occurring in sudden “jumps.”

3.1 Effective population sizes in a pest management context

Quantification of past and present population size can provide insight into the success of an invasive population, the amount of effort required to eradicate or suppress that population, and the effectiveness of a control strategy. Habitat structure, geographic extent, mobility, size of the individual, the cryptic or elusive nature of the species, and population distribution, however, often hamper quantifying population size by direct census (Rollins *et al.*, 2006). Genetic data can be used to calculate current effective population size (the number of individuals in a population that contribute offspring to the next generation, or N_e ; Wright, 1931), estimate minimum population size, and detect evidence of population expansion or decline (Rollins *et al.*, 2006). Due to the importance of performing conservation efforts focused on endangered species, we currently have access to a lot of examples that apply this concept. From them, we could ask: How difficult is it to achieve the local or global extinction of a species? Frankly, when humans have managed to drive a species to extinction, it has not been easy even when this species, in contrast to insects, was several orders of magnitude smaller and thus simpler to extinguish, for instance because its population size or effective population size was comparatively much lower. Pest control methods as applied today

appear to be low-success practices when viewed through a population genetics, phylogeographic, and conservation genetics perspective.

Let us think of a hypothetical pest species that is affecting a given crop field. We then decide to locally eliminate it using direct methods, which will kill most of the individuals, producing a genetic bottleneck. The first alleles that will disappear from the population are the ones present at low frequencies (Hauser *et al.* 2002). After $4N_e$ generations (N_e being the effective population size), more alleles will be lost, which means that the loss of alleles will depend on the effective population size. However, is this the right path to effective pest control? To answer this question, we need to know: 1) how the loss of genetic diversity increases the susceptibility of a population toward extinction, and 2) how much genetic diversity is needed for a species to maintain its adaptability in response to environmental changes. These problems can both be addressed through estimation of the effective population size and the genetic diversity of the species.

In the case of insect species, they are a good model for understanding the evolutionary processes influenced by natural selection. On a neutral theory scenario, we can have an elephant population with few individuals and an insect population with numerous individuals, and both will have the same mutation rate. With the passage of time, it is evident that some evolutionary forces will act in this comparison. In insect populations, the generation time is smaller, the recombination rate is faster, and the selective pressures are bigger; since the genetic drift is dependent on the effective population size in elephant populations, genetic drift is the most important evolutionary force because of the low number of individuals, whereas in insect populations, other evolutionary forces are stronger. In the context of pest management, molecular techniques that estimate genetic diversity and identify sudden population contractions (i.e., bottlenecks), due for example to the survival of resistant individuals after the selection pressure imposed by insecticide application, can provide feedback on the effectiveness of control programs and are especially useful in situations where direct population size assessment is difficult (e.g., Hampton *et al.* 2004). If we are able to analyze these characteristics in a pest species, then we will be closer to designing better long-term control strategies.

3.2 Genetic structure and gene flow in pest populations

Local elimination of pest populations is not a solution. It is like thinking that removing the cockroaches from one apartment of an infested building would be a long-term eradication solution. Thus, the control strategy should be directed to the whole population. Information concerning the number of populations present in a given place (i.e., a building), along with the degree of connectivity between them, is vital to constructing sound management and control policies for pest populations (Rollins *et al.*, 2006). Genetic structure can be described as the distribution of genetic variation resulting from migration, selection, mutation, genetic drift, and related factors. In other words, it is a measure that will reveal the level of connectivity between populations. If this measure is significantly high, then the populations are evolving together (and thus are highly connected); inversely, if it is low, each population could be considered as an independent evolutionary unit (and the populations are poorly connected). In situations where population subdivision is unclear or boundaries are cryptic, incorrect estimation of the number of populations may bias assessment of population dynamics (Taylor, 1997). For example, Robertson and Gemmell (2004), in a study on

eradicating rat pests from the Guadeloupe archipelago, concluded that populations were sufficiently isolated to be sequentially eradicated without a high risk of reintroduction; however, in a later work using genetic data for the same species, Abdelkrim *et al.* (2005) identified groups of islands that would require simultaneous eradication due to high levels of gene flow.

What would happen if we applied any control method to a population that exhibits a constant migration rate with neighboring populations? Since the population is not confined, new individuals from other populations could arrive, colonizing the area once more. If this is the case, then the overall genetic diversity of the species might be preserved in populations that are not being directly subjected to the control method. Thus, no matter how strenuous the effort to control a pest population in a particular locality is, new individuals will colonize it if their migration potential allows it. Then, it is important to determine not only the effective population size, but also the geographic area that a single population inhabits, as well as the overall species. This knowledge will aid in making more effective decisions when applying a control method, as well as contributing to a more fruitful investment in pest management.

Effective control of invasive populations may largely depend on the ability to identify their source. In many situations, the point of origin is unclear, or there may be multiple sources of an invasive population. Simple models assume that rates of movement are independent of landscape structure and use constant movement rates whatever the landscape mosaic in question (Goodwin & Fahrig, 2002), assuming that dispersal is random (Conradt *et al.*, 2001; Hunter, 2002). Because direct measurements of dispersal are typically difficult to obtain, indirect measures using population genetics may be employed (Pritchard *et al.*, 2000; Piry *et al.*, 2004). The study of gene flow can be even more informative: such an approach can be employed as a method of delimiting dispersal potential in species in which males are more likely to disperse than females (Hunter, 2002). Traditionally, sex-biased dispersal has been detected by comparing the level of population structure of bi-parentally inherited genes to those inherited from one parent only (e.g., mitochondrial genes).

Assessment of the dispersal potential may influence decisions on how to manage invasive populations. Species that experience restricted dispersal may be better candidates for control than those that disperse widely (Rollins *et al.*, 2006). A variety of methods have been developed to assign an individual to a population of origin or to exclude it from putative source populations (Wilson & Rannala, 2003; Piry *et al.*, 2004; Guillot *et al.* 2005; Rollins *et al.*, 2006).

3.3 Landscape genetics as an approach to understanding pest genetic diversity

The recent improvements in molecular genetic tools, combined with existing or new statistical tools (e.g., geo-statistics, maximum likelihood, and Bayesian approaches) and powerful computers has led to the emergence of the field of landscape genetics, which is an amalgamation of molecular population genetics and landscape ecology (Turner *et al.*, 2001). This discipline aims to provide information about the interaction between landscape features and microevolutionary processes such as gene flow, genetic drift, and selection. Landscape genetics can resolve population substructure across different geographical scales at fine taxonomic levels (Smouse & Peakall, 1999). Understanding gene flow is also

fundamental for ascertaining factors that enable or prevent local adaptation, and for describing dynamics that facilitate the spread of new, beneficial mutations (Sork *et al.*, 1999; Reed & Frankham, 2001). However, the aim of managers is to determine what constitutes a natural break within or between populations, the ratio of habitat (i.e., edge to interior; Chen *et al.*, 1995; Radeloff *et al.*, 2000), the isolation of habitat fragments (Collinge, 2000), subpopulation area (Kruess & Tscharntke, 2000), subpopulation quality (Hunter *et al.*, 1996; Kuussaari *et al.*, 2000; Hanski & Singer, 2001), subpopulation diversity (Gathmann *et al.*, 1994; Varchola & Dunn, 2001), and microclimate or ecological niche (Braman *et al.*, 2000). All of these phenomena contribute to determining the abundance and richness of insects on particular landscapes (Hunter, 2002). Lenormand *et al.* (1999) found a decrease in pesticide resistance with increasing distance from the treated zone by studying pesticide resistance in the mosquito *Culex pipiens*. This cline can be interpreted as a consequence of local adaptation when migration and selection act as antagonistic forces (Manel *et al.*, 2003). Landscape genetics is uniquely suited to exploring mechanisms of speciation in a complex resistance landscape, where parts of a population may experience sufficiently reduced gene flow such that drift or selection along locally steep selection gradients could lead to new species (Balkenhol *et al.*, 2009). Finally, adaptive landscape genetics explicitly deals with spatial genetic variation under selection, and can be used to study the adaptive and evolutionary potential of populations (Holderegger *et al.*, 2006, 2008; Balkenhol *et al.*, 2009).

Recently some scholars incorporated temporal changes in landscape structure (Solbreck, 1995; Onstad *et al.*, 2001), genetic change in insect populations (Singer & Thomas, 1996; Ronce & Kirkpatrick, 2001), and differential responses of predators and prey (Kruess & Tscharntke, 1994; With *et al.*, 2002) into their understanding of the spatial ecology of insects (Hunter, 2002). Roderick and Navajas (2003) suggested that identifying the origin of specific genotypes in an invasive pest population might assist in the identification of natural enemies in the native range, thus facilitating the design of effective biological control programs (Rollins *et al.*, 2006).

In the case of genetically modified crops that present insect protection features, to the extent that greater host availability increases pest adaptation to a particular host plant (Kelly & Southwood, 1999), widespread planting of transgenic insecticidal crops should favor resistance evolution (Gassmann *et al.*, 2009). Certainly, the selection pressure placed on pest populations to evolve resistance is more intense in this kind of crops because the pressure they impose is persistent instead of dependent on manual application. Resistance management of pests in insecticidal cropping systems has relied on the high dose/refuge strategy (Taylor & Georghiou, 1979; Gould, 1998). The refuge consists of growing non-transgenic host plants in close proximity to insecticidal crops. The refuge plants are expected to harbor and enable the reproduction of a large number of toxin-susceptible individuals, which will mate with any resistant individuals that emerge from the insecticidal crop, diminishing the resistance to the transgenic crop in the next generation (Gassmann *et al.*, 2009). However, the available data suggest that, in at least some cases, genetic variation serving to evolve resistance is present in the field. Numerous insect strains have responded to laboratory selection by evolving greater resistance to *Bacillus thuringiensis* Berliner (Bt) toxins (Tabashnik, 1994; Ferré & van Rie, 2002; Gassmann *et al.*, 2009), and this is suggestive of the evolutionary potential of pests to evolve resistance to transgenic Bt crops (Gassmann *et al.*, 2009). More importantly, analysis of field populations has revealed the presence of major resistance alleles for resistance to Bt crops in populations of pink bollworm

Pectinophora gossypiella (Tabashnik *et al.*, 2005), tobacco budworm *Heliothis virescens* (Gould *et al.*, 1997), the corn earworm *Helicoverpa zea* (Burd *et al.*, 2003), and the old-world bollworm *Helicoverpa armigera* (Downes, 2007; Wu *et al.*, 2006; Gassmann *et al.*, 2009).

3.4 Phylogenetic patterns

Phenotypic traits are influenced by their evolutionary history and the evolutionary forces in their actual environment. Phylogenetic patterns can reveal the effects of history in character evolution, which is relevant to understanding pest species and the ability to control them. On one hand, the history of pest relatives is essential, since many aspects that we may not know about the species in question may be shared with some of its relatives; thus, valuable information could be obtained through their study. Another key aspect that can help us determine how to fight a pest depends on the plant being cultivated, because the location inhabited by its wild relatives can provide a lot of information. These sites contain the natural enemies of the pests that attack plants, but also are home to a greater number of organisms adapted to plant defenses, and therefore monoculture in these places could be counterproductive, since the density and diversity of plants often support the defense mechanism. Additionally, most cultivars are genetically uniform; thus, natural predators can be much fiercer with these plants and the mechanisms to combat them much less effective. In many cases, gene flow between cultivated plants and their wild relatives can put their genetic diversity at risk and make wild plants more susceptible to herbivores, causing irreversible environmental damage (Ellstrand, 2003; Andersson & de Vicente, 2010).

4. Understanding the ecology and evolution of insect pest species and their crops as a basis for pest control

Which are the best methods of reducing insect pest populations in agroecosystems? For a long time, this question has been answered in terms of economic gain, and therefore control methods have been applied following this inclination. However, it is evident now that this question needs answers, and consequently actions, based on ecological and evolutionary knowledge of pest species.

Chemical and biological control methods, beyond doubt, have temporally diminished the damages caused by insect pests. The beneficial outcomes that these kinds of methods have accomplished in terms of agricultural production are considerable, but unfortunately, transient and extremely unaffordable from a biological perspective. These methods do not take into consideration the costs of locally or generally extinguishing a predatory species, of polluting the water or soil or of changing some life history traits of a pest species. The most suitable control methods should be those that, before being put into action, consider the pest species' ecological and evolutionary traits. Ecological attributes such as migration, reproductive or mortality rates, dispersion, or population growth regulatory processes (e.g., by predators or parasites) are key components in the understanding of species' short-term dynamics. Likewise, revealing the evolutionary attributes of a species such as the genetic diversity within and among populations, the gene flow between populations, the genetic structuration, and the effective population size could illuminate how fast the resistance to a given control method could evolve and how broadly, in a geographic sense, this method should be applied.

Figure 2 presents the ecological and evolutionary trait thresholds that a pest species could hypothetically display in contrast to a non-pest species. We propose that from them, it is possible to formulate better strategies to reduce, control, or eradicate pest species. This representation suggests a pest species regulation model through the application of evolutionary and ecological knowledge. Each species may have a certain surface within a multiple axis system. Each axis represents a trait, and by connecting the axes, an area is generated inside a multivariate space. Hypothetically, with colored circles, risk thresholds are represented. By quantifying each trait for a determined species, we could draw a corresponding area inside the model in a way that we could observe its shape and compare it to the proposed thresholds. The species with more devastating potential would occupy a maximum area inside the vectorial system (dotted blue line), while a species that is placed below the green circle probably will not represent a pest problem at that moment. Depending on the size and shape of the surface formed inside the system, different long-term control strategies could be proposed.

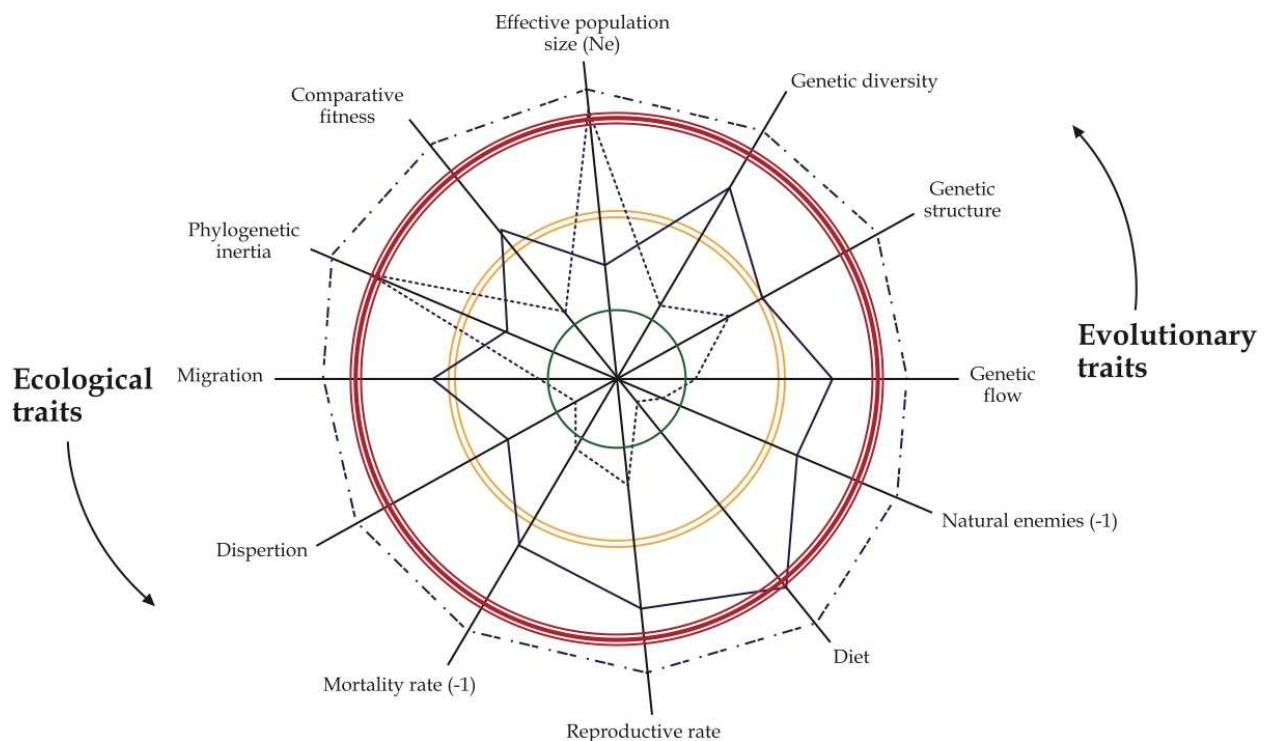


Fig. 2. Hypothetical representation of the ecological and evolutionary assessment suggested for pest control management. Each edge of the graphic represents a trait; when all of the edge's values are connected, a polygon is formed which will represent the potential of a species to become a pest. Hypothetical pest species display very different life histories and population genetics traits than non-pest species. Each of the solid line circles represents a hypothetical threshold of the damage that a species could cause; thus, the red circle illustrates a maximal threshold expected for a pest species, while the green circle will conform to a non-pest species. Polygons represent the trends for three different species: a lethal pest species (blue polygon), a moderate pest species (solid line black polygon), and an incipient pest species (dotted line).

4.1 Short-term pest control strategies: From insecticides to transgenic plants

Let us imagine an insect species that possesses all the ecological and evolutionary characteristics to become a pest, not on a short-term basis but over thousands of generations. Let us picture, then, that systematically, for decades, the same control method has been applied that has, immediately but temporarily, minimized the problems caused by the pest. Within a few generations, these insect populations will resurge even more devastatingly than before, in such a way that more complex and stronger control methods will be needed. Even though the methods used so far have proven to be inadequate, let us assume their application is continued, maybe in different presentations like a liquid or a bacterial gene that codes for a crystal-forming protein inserted into a crop plant, but leading to the same consequences. Over time, the selection pressures imposed by these methods could prompt the species' rapid adaptation and resistance evolution, thus hindering a long-term solution by these means.

The control methods predominantly used today are chemical and biological, followed by the growing development of genetically modified plants that, in some instances, could be regarded as chemical control. Numerous works have revealed that after the application of chemical agents, pest species can rapidly develop resistance and reemerge. Actually, over the last two decades, several insect populations have evolved resistance to some insecticides (Farnham, 1973; Robb, 1989; Liu & Scott, 1995; Jensen, 2000; Siqueira *et al.*, 2000). Georghiou (1990), in his classic work, reported that by 1990, around 500 species were resistant to at least one insecticide. Diverse locust species exhibit insecticide resistance through different biochemical mechanisms that reduce the lethal effect (He & Zhu, 2004; MacCuaig, 2008; Yang *et al.*, 2008). As for the utilization of genetically modified plants, some insects have acquired resistance to them, specifically to the protein codified by the transgene CryIA isolated from *Bacillus thuringiensis* (Kaiser-Alexnat *et al.*, 2005; Moser, 2007; Wolfgang, 2007). In Europe, at least four potentially devastating insects have acquired resistance: the pink bollworm *Pectinophora gossypiella* (Tabashnik *et al.*, 2005), the tobacco budworm *Heliothis virescens* (Gould *et al.*, 1997), the corn earworm *Helicoverpa zea* (Burd, 2003), and the old-world bollworm *Helicoverpa armigera* (Downes, 2007). All of the chemical agents provoke an intense selective process in the populations of insects, subsequently diminishing their population size. Nevertheless, some of the individuals of the population can be resistant and tolerate the above-mentioned compounds, thereby increasing the insect population size and diminishing the plant population size (Elrich & Raven, 1964).

Chemical control methods increase the selective pressures without being able to successfully eradicate the pest. An insect pest species with high genetic diversity and a large population size will have the potential to swiftly change its gene frequencies, thus increasing the number of resistant genotypes in just a few generations. Some chemical agents are particularly prone to promoting resistance, since with a single point mutation, the insect can block the pathway of the molecule used as insecticide.

Insecticides, Bt crops, and biological control methods, unfortunately, are not specific to the insect they are meant to control. Consequently, several non-target species are eliminated when these practices are applied, including natural enemies and endemic species (Lockwood & DeBrey, 1990; IUCN, 1996; Hoekstra, 1998; Lockwood, 1998; Stewart, 1998; Lockwood & Sergeev, 2000; Fashing *et al.*, 2010). For instance, Stewart (1998) revealed that when applying insecticides to control *Locusta pardalina* in crop fields, diverse endemic grasshopper species from South Africa were eliminated.

Besides their direct and immediate effects, insecticides also produce indirect and lasting effects. Lahr (1998) commented that organophosphate residues from insecticides applied to control *Schistocerca gregaria* were stored in water bodies, thus affecting numerous species. Recently, Fashing *et al.* (2010) analyzed the impact of insecticides used to control *S. gregaria* on African mammal species, since they feed on this locust species routinely. They analyzed the ecological implications of this particular mammal diet, because locust assimilated and stored the insecticide, which in turn affected the abundance of mammal species.

Let us assume that each of the non-target species could be represented in Figure 2, inside the group of non-pest species. The ecological and evolutionary trends that these species could display would be very different from the ones belonging to a pest species that has all the traits to demographically counteract the pressure imposed by control methods. Several non-target species have probably already been eliminated, locally or definitively, and regrettably without any available record.

Several works have analyzed the effects that biological control methods could have at an ecological level, particularly because of the lack of knowledge regarding the consequences of the artificial interactions that they impose (Louda, 1990; Thomas & Willis, 1993; Godfray, 1994; Jhonson & Stiling, 1998; McEvoy, 1999), for instance, by jeopardizing established natural interactions (e.g., competition or predation). In some cases, biological control methods fail to eradicate pest species, while in others, they promote the emergence of new pest species that parasite or prey on native species (Louda, 1990; Thomas & Willis, 1993; Godfray, 1994; Jhonson & Stiling, 1998; McEvoy, 1999). Regarding genetically modified crops with *Cry* transgenes, they are supposed to be species specific; however, there is a lack of scientific studies that support this notion, since they have not been carried out with species from the same genus or even with populations from the same pest species.

Finally, let us imagine for a moment that for many decades, there have been alternative methods able to minimize pest damages without producing so many collateral effects. And let us think these methods have been applied worldwide with favorable results. Now, what we cannot imagine is why these methods have not been used extensively in agroecosystems. Is it only an issue of lack of imagination?

4.2 Species-specific control methods that do not generate resistance

One method that does not cause resistance and could be species specific is mechanical elimination. This method refers to the removal of insects manually or by means of different kinds of tools (Faure, 1944; Van Huis, 1996; Abate *et al.*, 2000; Cerritos & Cano-Santana, 2008; Cerritos, 2009; Cerritos, 2011). This method has proven to be the most effective in controlling conspicuous insects such as locust, hemipterous and larvae. However, its practice in agricultural fields is very limited. Lockwood (1998) discusses that the main disadvantages of this method are its cost, since it could be very expensive, and that it is time-consuming, especially when the removal is undertaken manually. Nevertheless, it is a strategy that does not cause collateral effects on the environment. Lockwood (1998) mentions that because it is an extremely selective method, it does not represent a menace to non-target species. Furthermore, from an evolutionary point of view, it would be very hard for insects to develop resistance to manual removal.

The mechanical capture of pest species in some places is a common practice, especially in third world countries where insect consumption still prevails. However, although this strategy can reduce the population sizes of insect species, it is not considered a technological control system.

Although costly and labor intensive, mechanical removal is a potentially profitable method from the ecological, economic, and social perspectives. If we could compare between the chemical, biological, and mechanical methods in terms of resource investment and outcomes, we would probably find contrasting results. For instance, *S. gregaria*, a widely distributed and abundant species, caused economic losses of over 2.5 billion dollars in only the past 5 years in Africa, while around 400 million dollars were invested in chemical and biological control without success (FAO, 2008). The ecological and social damages of insecticide deployment were not evaluated in this case. Now, let us evaluate the input and profit for this example if the mechanical method could have been used. Considering that 10 million tons of edible insects could be harvested in each African country that this species inhabits, an investment of 10 million dollars would be needed, but the economic, ecological, and health gain would be immeasurable (Cerritos *et al.*, in preparation). Another example worth mentioning occurs in America, specifically in the United States, where several native grasshopper species ingest 25% of crop foliage in 17 states each year (Hewitt & Onsager, 1983). The cost of these losses has been estimated at 1 billion dollars per year (Pfadt & Hardy, 1987). To control these species, broad-spectrum insecticides have been the method of choice; in only two years (1986–88), around 5 million liters of Malathion worth 75 million dollars were used (NGMB, 1995). By implementing the mechanical method, the potential gain of the harvest could be 1 to 5 million tons annually with an investment not higher than 5 million dollars. Although in the United States, culturally, insect consumption has not been a common practice like in other countries, all that biomass could be used as livestock food. These two examples confirm the need for new and more suitable control methods to eradicate exotic pest species and maintain local or endemic pest species at low population sizes.

In Mexico, a country where insect consumption (i.e., entomophagy) is a very common practice, several grasshopper species are consumed as food. Not only is the grasshopper *Sphenarium purpurascens* one of the most significant pest species, but it is also the insect most consumed in Mexico (Cerritos & Cano-Santana, 2008). Nowadays, in just one village, hundreds of tons of this insect are produced yearly in alfalfa and corn crops, where it is especially considered a pest. The economic profit of grasshopper harvesting would be, on average, 5,000 dollars per family per year, without adding the savings related to not purchasing insecticides or investing in biological control (Cerritos & Cano-Santana 2008). The *S. purpurascens* biomass estimate that could be obtained by mechanical removal maintaining its population sizes at a level that minimizes crop damage is in the thousands of tons. The distribution and abundance of this grasshopper was estimated through demographic models, rendering the potential biomass quantity calculated per year to be almost 700,000 tons of grasshoppers in around 1 million hectares. The economic profit of this biomass extraction would exceed 50 million dollars, while the nutrimental contribution would yield 50 million rations, each with 20 grams of protein content (Cerritos *et al.*, in preparation). Beyond doubt, even when they may seem unconventional, these kinds of strategies could be applied around the world, taking advantage of native locust and grasshopper species and even considering them as a sort of mini-livestock.

If we place species like *S. gregaria* or *S. purpurascens* in our model presented in Figure 2, it is evident that both insects would be outside the higher threshold (solid line red circle), since their ecological and evolutionary traits are consistent with the characteristics displayed by highly devastating pest species. Let us review the case of *S. purpurascens* in more depth. This grasshopper, in spite of its lack of wings, has an exceptional dispersal capacity (Castellanos, 2001). It can feed on a broad diversity of plant species, from weeds to crops (Cano-Santana, 1992). The amount of natural predators and parasitoids in the environment do not seem to regulate its population size (Cerritos, 2002). Finally, the number of eggs per female and the survival rate at each stage are very high (Cerritos & Cano-Santana, 2008). From an evolutionary perspective, recent analyses have demonstrated that, at least in Central Mexico where this grasshopper dwells, several populations exhibit genetic structuration, with private genotypes and high genetic diversity (Cueva del Castillo, in preparation). When all these properties are considered, it becomes evident why chemical and biological control methods extensively applied in crop fields have been unsuccessful in controlling this pest and have caused diverse collateral ecological and social problems. Some reports reveal an increase in genetic diseases linked with insecticide application, mainly Malathion (Cerritos & Cano-Santana, 2008). Additionally, there is evidence of soil and water pollution and of the local elimination of several species (Cerritos, 2002). The strategy that could be most adequate for the control of *S. purpurascens* populations would be mechanical removal combined with other practices that do not cause collateral effects.

What happens to all pest species that are not suitable for human consumption? Up until now, we have directly linked the mechanical method to the use of insects as food, and it would seem that only edible insects could be subjected to this control method. We think this is hardly the case. We are aware that nowadays, there are not a lot of human practices that involve the exploitation of insect resources; however, since mechanical removal provides a huge amount of biomass, surely something useful and beneficial could be done with it. For instance, in Mexico, since pre-Hispanic times, several insect species have been used; perhaps the most well-known example is the hemipterous larvae *Dactylopius coccus*, an *Opuntia* spp. parasite that is the primary source of a red pigment used in the textile industry. In other instances, if not suitable for human consumption, they could perhaps be used to feed livestock.

4.3 Crop-oriented alternatives

4.3.1 Small-scale polyculture. The *milpa*, *chacra*, *nainu*, and *conuco*, among others, are traditional agroecological systems implemented by indigenous peoples from many different cultures, climates, and places in the world. These systems can be regarded as “small or medium scale polycultures” (Chávez-Servia *et al.*, 2004). While their methods vary depending to the agroecosystem of each place, all of them have active strategies for insect control, and these strategies do not allow harmful organisms to reproduce immensely, but tolerate some level of infection to avoid losing the entire crop affected (Morales & Perfecto 2000). These strategies also allow for the long-term use of soil, for example, by crop rotation and by letting the land rest. In these circumstances, insect pests simply do not find resources and cannot grow in that area or stay in it permanently, so no resistance is generated, nor is there an accumulation of chemical products in the soil (Blanco & García, 2006). In addition, in these systems, one immediate control measure can be growing different crops at the same time in the same field to help reduce infections and enhance economic effects through the profit of attaining food from both crops (Muñoz, 2003).

Some strategies use agrochemicals on seeds before planting them to prevent initial infection; others involve acting collectively in applying insecticides or known enemies of the pest in a large area, thereby preventing the pest from passing from one field to another, unprotected, parcel. Different strategies are used for controlling insect pests that infest seeds during storage, for example placement of the containers near smoke, use of powdered lime (Calcium carbonate) or application of commercial insecticides (Moreno *et al.*, 2005).

4.3.2 Large-scale polyculture. The structure and forms of large-scale mixed farming schemes are quite variable. Many rely on the same strategies described above and are carried out under the same structures, but with a modified scale. The nutrient recycling between different crops requires a little more involvement of applied sciences, and the management of the synchronic cultivation of fruit, vegetables, woody species, and fungi requires more knowledge (Altieri, 1995). In many cases, the issues regarding pest management are based on geographical and chemical barriers that impede the movement of pests, often with the help of local biological control (e.g., insects that are beneficial to crops because they defend them, like some ants species in legume crops, where the latter defend the plant against predators while nitrogen-fixing bacteria in the root system help to conserve the fertility of the soil).

5. Conclusions and future research

This chapter highlighted the need to develop new management strategies to permanently control various insect pests that attack agricultural systems. It is imperative that such proposals take into account the ecological and evolutionary properties of each insect species that can potentially become an agricultural pest. By understanding a species' genetic structure, we can assess its long-term potential to adapt and become a resistant, more devastating, and more invasive pest. On the other hand, by identifying certain life history traits, we can predict the abundance and potential distribution area of a species. From this knowledge, better control methods could be designed. An efficient long- and short-term method would be one that could avoid or minimize side effects in individuals, populations, communities, and biomes, including: 1) the evolution of pest resistance; 2) eradication of non-target species, including the pest species' natural predators; 3) elimination of relevant ecological interactions through the modification of the species' distribution and abundance; 4) modifications to the biogeochemical cycles; 5) environmental pollution; and 6) impacts on human health.

Unfortunately, at present, most commonly used methods have a high cost and high impact, not only from an economical perspective, but also from an ecological, evolutionary, and even social point of view. The deployment of chemical insecticides, including their endogenous production in genetically modified plants, as well as biological control methods, is definitely not fully compatible with our proposal. To expect an insecticide to work for the long-term is to go against the whole theory of evolution and some ecological precepts. Insecticides and biological control act as selective pressures on insect populations, causing the genotypes that can withstand these selective forces to eventually increase their frequencies in populations.

Based on several case studies, we think that the mechanical control method can be employed in relation to some insect pest species, especially those that may have an added economic value like most of the Orthoptera. Grasshoppers are the most devastating insects, not only at present but throughout history; in some countries, however, entomophagy of

this group is customary. For these insects as well as some others (Coleoptera, Hemiptera, Lepidoptera), our conclusion would be not to provoke ecological disequilibria by eliminating them with insecticides or biological control; rather, it would be to mechanically remove them and use their biomass. It is clear that in some instances, the method proposed here cannot be fully functional. In a hypothetical species that is native, emergent, and non-edible, inhabiting within the same range of endemic and specific predators, with life history traits nothing like the ones that characterize a devastating species, perhaps strategies like biological control and insecticides can work as control methods. Ultimately, the fundamental step that should be taken before applying any control method, whether mechanical, chemical, or biological, is to take into consideration the ecological and evolutionary trends that a pest exhibits; only at this point can an appropriate and informed strategy can be put in place.

Our work has underlined the consequences of pest control methods when the ecological and evolutionary traits of the species are not subjected to prior analysis. In the worst scenarios, they could alter environmental processes irreversibly. No pest control methods have been applied so far that have taken into consideration the short- and long-term effects they may pose over environmental services. These practices ultimately generate economic costs that are neither easily affordable nor quantifiable. Understanding how much an environmental service costs could set the path for better decisions regarding suitable and informed pest management. It is imperative to evaluate environmental services such as those arising as a result of ecological interactions such as predation and mutualism (e.g. pollination), the cost of environmental pollution, and the costs for biogeochemical changes. If the cost of eradicating a pest species using insecticides is several million dollars per year, what would be the cost for the environmental service provided by a pest-specific predator, parasite, or parasitoid species?

At present, one of the most controversial methods is the application of chemicals using genetically modified crops as a vehicle for the endogenous production of insecticides. Besides the above-mentioned consequences of the use of conventional chemical control methods, this new method presents major problems at the genetic level, for instance, the gene flow of transgenes to conventional crop populations. This effect can be irreversible and affect the evolution and viability of plant species, especially in regions where transgenic crops are in contact with their wild relatives. Several studies have shown that gene flow from transgenic to wild plants has already occurred. For example, Wegier *et al.* (2011) confirmed the presence of transgenes in wild cotton plants in Mexico, which is the center of origin of this species. In this case, the evolutionary costs of this introgression should be evaluated, while a general question should be addressed: What would be the economic cost of losing the populations that gave rise to different crops used in agriculture today?

Right now, our team is developing a computational platform to formalize our proposal regarding the use of ecological and evolutionary properties to control pest species. This formalization requires an extensive database of each of the pest species and an efficient statistical methodology that enables us to correlate all the variables. In an upcoming study, our team will propose some strategies for some of the most devastating Orthoptera species in certain regions of Mexico. For the moment, we are reviewing all the knowledge available for *S. purpurascens* (a species with a high potential for local crop devastation) and *S. gregaria* (a species with a global distribution); with these data, we will perform a multivariate analysis. From a graphical perspective (see Figure 2), a given area will be generated with a

specific form within a multivectorial system. The analytic model we propose here can lead to future long-term pest management strategies, based on ecological and evolutionary knowledge, thus preventing or at least minimizing the negative repercussions of current pest-management strategies.

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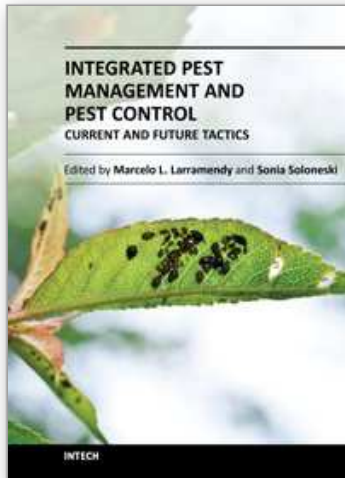
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