




The implications of rapid eco-evolutionary processes for biological control - a review

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Abstract

Novel environmental conditions experienced by introduced species can drive rapid evolution of diverse traits. In turn, rapid evolution, both adaptive and non-adaptive, can influence population size, growth rate, and other important ecological characteristics of populations. In addition, spatial evolutionary processes that arise from a combination of assortative mating between highly dispersive individuals at the expanding edge of populations and altered reproductive rates of those individuals can accelerate expansion speed. Growing experimental evidence shows that the effects of rapid evolution on ecological dynamics can be quite large, and thus it can affect establishment, persistence, and the distribution of populations. We review the experimental and theoretical literature on such eco-evolutionary feedbacks and evaluate the implications of these processes for biological control. Experiments show that evolving populations can establish at higher rates and grow larger than non-evolving populations. However, non-adaptive processes, such as genetic drift and inbreeding depression can also lead to reduced fitness and declines in population size. Spatial evolutionary processes can increase spread rates and change the fitness of individuals at the expansion front. These examples demonstrate the power of eco-evolutionary dynamics and indicate that evolution is likely more important in biocontrol programs than previously realized. We discuss how this knowledge can be used to enhance efficacy of biological control.

Introduction

Rapid evolution or contemporary evolution are terms that have become widely used in the past few decades to refer to evolutionary processes that occur within ecological time scales, that is within decades or centuries (Hendry & Kinison, 1999; Reznick & Ghalambor, 2001). Anthropogenic factors often drive rapid evolutionary processes, with good examples coming from insecticide, herbicide, or antibiotic resistance (Reznick & Ghalambor, 2001). Other lines of evidence for rapid evolution are strongly linked with colonization events where individuals are introduced into a new environment, move onto a new host, or a previously

unoccupied or unsuitable habitat (Reznick & Ghalambor, 2001). In these scenarios, changes in abiotic and biotic ecological conditions, such as the physical environment, host plant, trophic or competitive interactions, have led to directional selection and rapid evolution of diverse traits (Reznick & Ghalambor, 2001). Thus, we know that ecological change can affect evolution, which can be very rapid, and there is growing evidence that evolutionary processes can feed back to affect ecological characteristics of populations (Yoshida et al., 2003; Pelletier et al., 2009; Hendry, 2016). For example, Yoshida et al. (2003) demonstrated that competition for nutrients in green algae (*Chlorella vulgaris* Beijerinck) leads to rapid evolution by increasing the frequency of genotypes that are better competitors, which also happen to be of higher nutritional value to their predators (planktonic rotifers, *Brachioums calyciflorus* Pallas). Evolution in prey feeds back and alters an

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ecological process, the predator–prey cycles in this system (Yoshida et al., 2003). These unidirectional and reciprocal interactions between ecology and evolution are referred to as eco-evolutionary dynamics (Yoshida et al., 2003; Pelletier et al., 2009; Schoener, 2011; Hendry, 2016).

Introductions for biological control, particularly those of classical biocontrol agents that are introduced from the native range of exotic pests into a novel habitat, are likely subject to eco-evolutionary processes. Biocontrol agents experience novel abiotic and biotic conditions in their introduced environments that can include climates that differ from what they are adapted to, altered availability, distribution, genetic composition, defense, or phenology of their hosts or novel predators, parasitoids, and competitors. These novel ecological conditions may impose strong natural selection, which can lead to evolutionary change (Reznick & Ghalambor, 2001). Indeed, an increasing number of studies report rapid evolution in biocontrol agents, for example, by changes in critical daylength for diapause induction (Bean et al., 2012) or increasing development speed and survival when exposed to shorter growing seasons (McEvoy et al., 2012; Szűcs et al., 2012a). Given the sudden and often large changes in environmental conditions upon introduction, the ecology-to-evolution pathway of eco-evolutionary dynamics should be quite prevalent in classical biocontrol systems.

The genetic and phenotypic change in traits in response to selection will alter the fitness of individuals and will thereby change the demographic (ecological) characteristics of populations, such as rates of reproduction, survival, or dispersal, which in turn will affect population dynamics (Pelletier et al., 2009). Thus, evolutionary change can also affect ecological processes (evolution-to-ecology pathway) (Schoener, 2011). These eco-evolutionary processes and feedback loops can have potentially large effects on biological control agents, influencing their establishment, population growth, persistence, efficacy, and spread rates.

From the perspective of species introductions into novel environments, rapid evolutionary change can increase or decrease fitness, and can shape the rate of spread across the environment. Adaptation to a novel environment by definition increases fitness in that environment. As fitness of individuals increase, population growth rate can increase. In situations like biological control and biological invasions, habitat space or resources are generally not limiting shortly after introduction, and thus populations introduced into a suitable environment can grow and spread even without evolution. However, adaptive evolution can increase fitness in novel environments that are not optimal. There is experimental evidence that adaptive

evolution can increase population sizes within a few generations following introduction into a challenging novel environment (Stewart et al., 2017; Szűcs et al., 2017a). As larger populations are more likely to establish and also to persist in novel environments (Lockwood et al., 2005; Szűcs et al., 2014; Blackburn et al., 2015; Szűcs et al., 2017b), adaptive evolution can have both short- and long-term positive effects on colonizing populations. Moreover, in the context of biological control, achieving higher population sizes of biocontrol agents can be beneficial as those should exert higher pressure on the target pests and are more likely to persist over time. However, as control is attained and the target pest becomes scarce, population sizes of even highly adapted biocontrol agents decline, tracking resource availability.

Rapid evolutionary processes can also lead to decreases in fitness. For example, deleterious mutations can be exposed to selection via genetic drift and inbreeding, processes that are common in small introduced populations such as biocontrol agents (Fauvergue et al., 2012). As fitness decreases, population growth rate decreases, and populations shrink, which can feed back to amplify ecological processes that negatively impact biocontrol agents, such as Allee effects or demographic stochasticity. These eco-evolutionary feedback loops can keep populations small or may lead to extinction. Small populations of biocontrol agents then will have lower chance of adaptation to their new environments as they will likely harbor lower genetic diversity than larger populations (Barrett & Schluter, 2008), and their effectiveness can be diminished by sustained small population sizes.

Finally, recent experimental work shows that evolution has the potential to accelerate population expansion rates (Phillips et al., 2006; Williams et al., 2016a; Ochocki & Miller, 2017; Szűcs et al., 2017a; Weiss-Lehman et al., 2017). Multiple traits may evolve in expanding populations, notably dispersal tendencies and growth rates of individuals residing at expansion fronts. At expansion fronts, spatial sorting brings together highly dispersive individuals, which then preferentially mate with each other and the low population densities typical at range edges can relax competition and select for higher reproductive rates (Phillips et al., 2010a; Perkins et al., 2013). Increased dispersal can be beneficial as it could enable biocontrol agents to spread onto new infestations of the target pests faster. Dispersal can also create and then connect metapopulations of agents reducing extinction risk on the landscape level.

These examples highlight some of the ecological and evolutionary processes and their interactions that can affect biocontrol programs. We primarily focus on processes operating in the early stages that can setup

biocontrol programs for success or failure by influencing establishment success, initial population growth, adaptive potential, and dispersal of agents. We discuss (1) mutation, the ultimate source of genetic variation, which, along with standing genetic variation, influences the rate of response to selection; (2) genetic drift and inbreeding depression, genetic processes that can drive non-adaptive evolution in small founding populations; (3) founder effects, which can profoundly influence the ecological characteristics and evolutionary potential of colonizing populations; (4) adaptation, which can increase the fitness of biocontrol agents; and (5) spatial evolutionary processes that may act on dispersal and/or life-history traits of individuals at expansion fronts and can determine the distribution of both the agents and their targets in the introduced range. We then integrate across these topics to provide recommendations for best practices in biological control based on our current knowledge.

Mutation

Mutations occur all the time and are the fundamental source of all genetic variation, including the standing genetic variation among individuals at any given time, and novel variation arising each generation. The effects of mutation on fitness can be positive, negative, or neutral, as discussed further below. Mutations are infrequent, on the order of 10^{-9} or 10^{-8} per nucleotide site per generation in eukaryotes. Given these small values, mutation is generally dismissed as having a weak influence on most populations. We argue, however, that even though mutation rates on a per nucleotide basis are low, mutation can have an impact on evolutionary (and thus ecological) processes much more quickly than is often supposed.

The actual number of mutations that occur each generation can be surprisingly large, as it depends not just upon mutation rate, but mutation rate \times genome and population sizes. For example, the *Drosophila melanogaster* Meigen genome, although small relative to many other organisms, has an estimated size of 180 Mb, or 180 000 000 bases, each of which can mutate each generation. Given this genome size, at a mutation rate ranging from 2.8×10^{-9} (Keightley et al., 2014) to 7.7×10^{-9} (Schridder et al., 2013), each individual should have an average of 0.50–1.38 new mutations at conception. Organisms with larger genomes or higher mutation rates consequently experience more mutations. In a population of two million individuals, that translates to 1–2.8 million new mutations scattered about the genomes of the individuals in the population *each generation*. Thus, even biocontrol agents that are often introduced in small numbers or reproduce asexually (e.g., wasps like *Tetramesa romana*

Walker; Goolsby et al., 2014) can actually acquire substantial standing genetic variation fairly quickly via mutation, and thus can evolve.

The evolutionary and ecological consequences of mutations depend upon whether they are deleterious, neutral, or beneficial, and whether their effects are dominant, additive, or recessive. Most mutations are thought to be neutral or mildly deleterious (Eyre-Walker & Keightley, 2007), but some can be strongly deleterious or lethal. As mutations accumulate over generational time, the number of mildly or strongly deleterious mutations an individual contains also increases until it is balanced by selection against them. Humans, for example, are thought to each harbor the equivalent of 0.6–1.4 lethal deleterious mutations, or ‘lethal equivalents’ in their diploid genomes (Bittles & Neel, 1994; Gao et al., 2015).

Mutations also, of course, can be beneficial. A recent study of *Escherichia coli* Castellani & Chalmers found a rate of beneficial mutation to be as high as 10^{-5} per genome per generation (Perfeito et al., 2007). Although this is still much lower than the per nucleotide site rate of all mutations, it suggests that beneficial mutation can contribute strongly to standing genetic variation, particularly in large populations (because, as shown above, the absolute number of mutations each generation is equal to the mutation rate \times the population size). Whether beneficial mutations tend to be of large or small effect remains an open question (Orr, 2010). Another important consideration is that the fitness effects of mutations can depend upon the environment in which an organism finds itself. Mutations that are neutral in one environment can be deleterious or beneficial in other environments (Latta et al., 2015; Roles et al., 2016).

The evolutionary consequences of mutations depend on whether they are recessive or dominant. For beneficial mutations, the experimental evidence is mixed but is generally consistent with many segregating beneficial mutations not being fully recessive (Orr, 2010), thus making their fixation much more probable than if they were fully recessive. Deleterious mutations that are dominant are removed from the population quickly (and often in the embryonic stage), and thus, in practice, most deleterious mutations segregating in diploid populations will be recessive. This means that outcrossing diploid species that have relatively large population sizes can accumulate recessive deleterious mutations over time exactly because they are recessive and not exposed to selection.

Lynch et al. (1995) showed with a compelling and elegant model that this kind of accumulation of mildly deleterious mutations can increase extinction risk of small populations. They evaluated genetic load of populations

accumulating mutations, where genetic load is the difference in the mean fitness of a population and the fitness of an optimal genotype that does not carry deleterious mutations. Their model started with standing genetic variation (e.g., mutations that had accumulated over time) and then continued with additional spontaneous deleterious mutations, so that genetic load increased over time. They conclude that populations with effective sizes smaller than 100 (or census sizes that are smaller than 1 000) are more susceptible to extinction via ‘mutation meltdown’ over only around 100 generations relative to populations not experiencing deleterious mutations. Clearly, with populations of biocontrol agents often starting at small size, or being maintained first in laboratories at small size, deleterious mutations are likely to play a crucial role in short-term fitness. Thus, such mutations will influence population size and long-term persistence of populations of introduced biocontrol agents, particularly outcrossing diploid species.

Hymenoptera play a large role in biological control of insect pests, and given their unique biology, it is useful to address their genetic load directly. As haplodiploids, males are (typically) haploid, and thus deleterious mutations that might be recessive in the diploid state, are exposed to selection and can be removed from the population. A consequence of this is that haplodiploids tend to have lower genetic load (Henter, 2003). However, even they can experience inbreeding depression, particularly haplodiploids with complementary sex determination, in which homozygous diploid individuals become phenotypically male rather than female (Cook & Crozier, 1995; Zayed & Packer, 2005; Fauvergue et al., 2015).

Mutations, as the ultimate source of genetic variation, are at the origin of the standing genetic variation found in populations of target pests and of potential and actual biocontrol agents. Beneficial variation that facilitates adaptation and deleterious variation that reduces fitness arise not over millennia but quite rapidly over relatively few generations (depending upon mutation rates and population sizes) and can thus rapidly affect population dynamics and success of biocontrol agents.

Genetic drift and inbreeding depression

Genetic drift

Genetic drift is the random change in allele frequencies due to stochastic fluctuations that occur when populations are small. It can lead to increases in frequency of deleterious alleles, and even their fixation, and similarly reduction in frequency of beneficial alleles. Loss of heterozygosity by drift depends upon the population size such that heterozygosity at some time in the future (H_t) is a function of initial

heterozygosity (H_0) minus that initial value divided by the effective population size (N_E), or

$$H_t = H_0 \left(1 - \frac{1}{2N_E} \right).$$

Effective population size is typically much smaller than the census size due to fluctuating population sizes through time, unbalanced sex ratio, and unequal reproductive success, thus loss of heterozygosity via drift may be faster than the census size of a population might indicate. The consequences of reduced heterozygosity (and increased homozygosity) for biological control are discussed further below.

Inbreeding and inbreeding depression

Inbreeding is mating among relatives, and does not by itself change allele frequencies, so does not in itself cause evolution. However, inbreeding does increase homozygosity, and that effect occurs genome wide. When the genome contains recessive deleterious alleles, increased homozygosity will be associated with reduced fitness. This is inbreeding depression. Not all inbreeding leads to inbreeding depression—only when recessive deleterious alleles are present, yet masked by another allele prior to inbreeding, and in the case of complimentary sex determination, when diploid males with low or zero fitness are produced (Vaysade et al., 2014). Furthermore, inbreeding depression can depend very much on environment, with some loci having no deleterious affect even when homozygous in benign environments, but strong deleterious effects in novel or stressful environments (Fox & Reed, 2010).

In practice, inbreeding depression is measured by comparing fitness of inbred individuals to outbred individuals (Figure 1). Most commonly, inbreeding leads to lower fitness: inbreeding depression (Figure 1A). However, sometimes there is no change in fitness with inbreeding, and thus no inbreeding depression (Figure 1B). Ongoing inbreeding or drift can influence inbreeding depression by both fixation and purging of deleterious alleles. Fixation occurs when a population becomes homozygous with deleterious alleles present in all copies of an allele (i.e., it is ‘fixed’). In this case, there will be no difference in fitness between outbred and inbred individuals, and thus no inbreeding depression (Figure 1C), but absolute fitness will be quite low. In contrast, if deleterious alleles are brought together in some individuals via recombination, and those individuals do not reproduce, then the deleterious alleles can be removed from a population all together or purged. Finally, without deleterious alleles, inbreeding will not reduce fitness in organisms without complimentary sex determination, and thus a population can be inbred but have high fitness (Figure 1D). With

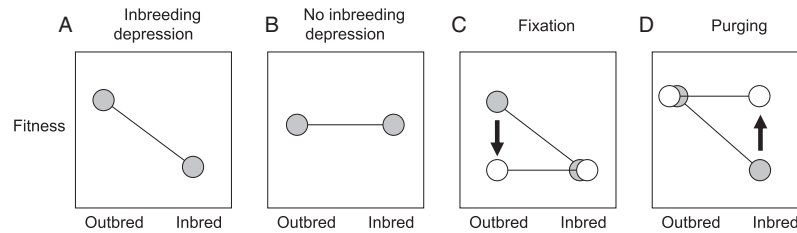


Figure 1 Graphic illustrating how inbreeding is measured and can evolve. (A) Inbreeding depression, measured as the difference in fitness between inbred and outbred individuals. (B) A general case without inbreeding depression. (C) Fixation of deleterious alleles reduces inbreeding depression, but also leads to low fitness overall. (D) Purging of deleterious alleles equivalently reduces inbreeding depression, but instead leads to high fitness overall. Grey points in C and D represent a population's starting situation, white points represent the evolved situation. Modified from Laugier et al. (2016), with permission from the publisher.

complementary sex determination, alleles that are homozygous are not necessarily deleterious, except when they are matched by the same allele, leading to low-fitness diploid males.

Experimental evidence in whiteflies, *Bemisia tabaci* (Gennadius), and red flour beetles, *Tribolium castaneum* (Herbst), has shown that inbreeding can impact establishment success, growth rates, persistence, and adaptive ability (Hufbauer et al., 2013; Szűcs et al., 2017b). For example, both inbred and outbred whitefly populations could establish at the same rate on a natal host (benign environment) but only 5% of inbred populations established on a novel host (challenging environment) in contrast to 55% of outbred populations (Hufbauer et al., 2013). Inbred founders also had lower reproductive rate, and growth was generally lower on the novel than on the natal host (Hufbauer et al., 2013). In red flour beetles, smaller populations and those with lower genetic diversity (inbred) had lower establishment success and persistence over seven generations in a novel environment than larger or higher diversity populations (Szűcs et al., 2017b). Inbreeding severely reduced the chances of adaptation to a novel environment leading to high extinction rates, whereas inbred founders were able to survive and persist in the natal environment that they were originally adapted to (Szűcs et al., 2017b). These experiments highlight how the negative effects of inbreeding may be amplified in novel environments, which is usually what biocontrol agents are exposed to upon introduction.

Implications for biological control

The consequences of genetic drift and inbreeding for biocontrol systems is only just beginning to be understood. Low genetic variation may limit the ability of biocontrol agents to adapt to novel environments. Furthermore, high genetic load can reduce population growth rates directly, slowing build-up of populations of biocontrol agents, and hampering control as well as reducing the availability of

agents for redistribution. One path forward to understanding the relative importance of increased homozygosity is to study the strength of inbreeding depression in biocontrol agents.

In general, inbreeding depression is known to be quite prevalent in wild populations of animals and plants (Crnokrak & Roff, 1999). Island populations especially, which can be small given the constrained size of their habitat, experience strong inbreeding depression (Frankham, 1998). Several groups have studied biocontrol systems with a focus on hymenopterans, many with complementary sex determination. Often those agents are hampered by inbreeding depression (Fauvergue et al., 2015; Bueno et al., 2017; Zaviezo et al., 2018), but not always (Trevisan et al., 2016; Quaglietti et al., 2017). Low fitness in biocontrol agents in introduced populations relative to native ones, as in *Aphidius ervi* (Haliday) (Hufbauer, 2002), might be explained by fixation of deleterious alleles through either drift or inbreeding during the introduction. However, that is a hypothesis that has not yet been tested on the *A. ervi* system or others, to our knowledge. The converse situation, high fitness in introduced populations in a novel range relative to native populations in the native range, might be explained by purging of deleterious alleles. That indeed seems to be the case in *Harmonia axyridis* (Pallas) (Facon et al., 2011; Laugier et al., 2016), a biocontrol agent that has become a notorious invasive species.

Founder effects

Demographic and genetic founder effects—that is, the number and genetic characteristics of founders—can have profound effects on individual fitness, short- and long-term population dynamics, dispersal rates, and the evolutionary potential of introduced populations (Briskie & Mackintosh, 2004; Hufbauer et al., 2013; Szűcs et al., 2014, 2017b). Classical biological control represents a unique case because as a program is being developed and

implemented demographic and genetic founder events can occur repeatedly during the (1) collection of agents in their native ranges, (2) quarantine rearing, and (3) release of agents in the novel range, which we discuss in more detail below. Founder effects in these stages will influence the amount of genetic diversity available for selection to act on, initial population sizes in the field following release, population growth rates and spread, and other ecological processes, such as competitive, predator–prey, or parasite–host interactions that can be mediated by population density.

We know that small founding populations are subject to demographic stochasticity and Allee effects, and both experimental and observational evidence show that establishment success and population growth rates are reduced in smaller compared to larger introduced populations that are better buffered against these ecological processes (Lockwood et al., 2005; Szűcs et al., 2014, 2017b; Blackburn et al., 2015). Fewer individuals in a founding group will also typically harbor less genetic variation and smaller populations are more likely to be subject to genetic drift and inbreeding depression that can increase extinction rates and lower growth rates (Bijlsma et al., 2000; Reed et al., 2002, 2003). These demographic and genetic founder effects are connected, as genetic diversity usually increases with the number of individuals in a founding group (Hufbauer et al., 2013). Moreover, the mismatch between the environment that the individuals are adapted to (e.g., where the biocontrol agents were collected from or reared prior to release) and where they are introduced can also have strong effects on establishment and population growth (Hufbauer et al., 2013; Szűcs et al., 2014, 2017a). Thus, there can be complex interactions between demographic processes, the genetic diversity of founders, and the environment where the introductions take place that will mediate the eco-evolutionary dynamics of newly founded populations.

Collection in the native range

In the early years when classical biocontrol programs started, the general recommendation was to collect potential biological control agents from a wide range of environments from several populations in the native range (Bartlett & Van den Bosch, 1964; DeBach & Rosen, 1991). At that time, little was known of just how quickly evolution may begin to influence ecological processes, but in general, higher genetic diversity was perceived as beneficial because it could enable establishment in different environments and enhance the long-term evolutionary potential of agents (DeBach & Rosen, 1991; Hopper et al., 1993). In theory, this approach could have benefitted biocontrol programs, but it had not been evaluated whether single-

vs. multi-population collections in the native range led to differing outcomes in terms of establishment success, population growth, or impact of the agents after introduction in the exotic range.

In the past decade, regulations have become much stricter, partly due to an increasing number of studies demonstrating that different populations of a species can differ in several biological traits but most importantly also in host specificity (Hopper et al., 1993; Hoffmann et al., 2002; Mathenge et al., 2010). Given that, it is now expected that each genetically and/or geographically distinct population of an agent be tested separately for host specificity (Barratt et al., 2010), which has led to the general practice of screening agents only from a single or very few populations to keep cost down. This practice likely results in reduced genetic diversity and thus evolutionary potential of newly imported agents. On the other hand, an increasing number of studies report of several invasive species having higher genetic diversity in the introduced range than in their native ranges mostly as a result of multiple introductions from different geographic areas followed by admixture (hybridization) in the introduced range (Schierenbeck & Ellstrand, 2009; Uller & Leimu, 2011). This increased genetic diversity was shown to contribute to the evolution of invasiveness, for example, by increasing vegetative colonization ability and phenotypic plasticity in a wetland grass (Lavergne & Molofsky, 2007) and fruit production in ornamental pear trees (Culley & Hardiman, 2009).

During the initial host specificity evaluations, population bottlenecks often occur while rearing techniques are optimized for a new species in a laboratory, which can further reduce genetic variation. Bottlenecks can reduce both allelic diversity and heterozygosity, and although rare alleles are likely to be lost, most of the heterozygosity may be retained especially if the bottleneck is followed by rapid population growth (Nei et al., 1975; Allendorf, 1986). However, a review found that introduced insects show a consistent loss of genetic diversity compared to their native ranges, and that populations originating from a single source tend to have lower genetic diversity than those from multiple locations (Uller & Leimu, 2011). Positive heterozygosity–fitness correlations are commonly found both in animals and plants for life history, morphological, and physiological traits, and were shown to affect individual fitness as well as the demography of populations (Leimu et al., 2006; Chapman et al., 2009). Thus, the genetic variation collected and retained in this initial stage of a biocontrol program can influence population dynamics, growth rates, life history, and other biological traits in later stages. These ecological processes in turn can affect how populations respond to

selection both in the quarantine environment and following release in the exotic range.

Quarantine rearing

Biocontrol agents usually pass through multiple generations in a quarantine to ensure they are healthy, free of parasitoids, and to increase their numbers for field releases. The entire or part of the host specificity testing can also take place in a quarantine. Mortality of agents can be high during transportation to and the initial rearing in a quarantine resulting in small founding population sizes. In small populations genetic load can increase via drift, and mating between related individuals can lead to inbreeding and inbreeding depression, processes that can reduce the survival and fitness of individuals as described above (Charlesworth & Willis, 2009; Fauvergue et al., 2012). In addition, agents can inadvertently adapt to the rearing environment where temperatures tend to be constant, population densities higher than in nature, food abundant, and no opportunities exist for dispersal (Mackauer, 1976; Hopper et al., 1993; Sørensen et al., 2012). Traits evolving in response to these conditions will likely affect the dynamics of populations following release in nature. For example, commercial strains of *H. axyridis*, developed for biological control in Europe failed to establish despite repeated releases (Turgeon et al., 2011). This is likely due to their poor performance at lower temperatures in the wild resulting from adaptation to the laboratory environment and low effective population sizes during rearing (Turgeon et al., 2011).

Introduction in the novel range

We still know little about how best to release biocontrol agents, which is reflected in relatively low establishment rates of 32.6% against insect pests and 63.2% for agents released against invasive weeds (Cock et al., 2016; Schwarzländer et al., 2018). However, we know that on the most fundamental level the demographic and genetic characteristics of founding populations will be crucial in determining not only establishment success but also the fitness and evolutionary potential of populations. Theory mostly considers ecological factors that could mediate establishment success providing recommendations that vary from many small releases to a few large releases depending on environmental variability, the strength of Allee effects, and the distribution of hosts (Grevstad, 1999a; Shea & Possingham, 2000). Experimental field introductions have consistently shown that larger releases of biocontrol agents are more likely to establish and persist (Grevstad, 1999b, 2006; Memmott et al., 1998, 2005). However, there are examples of a single female founding populations (Grevstad, 1999b) and of releases made each with 65 000 individuals failing

(Grevstad et al., 2011). Recent experimental work in the laboratory has shown that several small introductions result in the highest establishment of red flour beetles in a novel environment (Koontz et al., 2018), but having even a few founders pre-adapted to the novel environment was more important for establishment than the introduction scenario (Vahsen et al., 2018).

During the initial introduction of a new agent the number of individuals available for release are usually limited (Grevstad et al., 2011), and even when larger founding groups are released (i.e., 100–1 000) there is usually a large initial drop in population sizes (Mackauer, 1976; Memmott et al., 2005; Fauvergue & Hopper, 2009; Grevstad et al., 2011; Fauvergue et al., 2012). Thus, even large releases can result in small founding populations (Fauvergue et al., 2012), and effective population sizes can be even smaller if the release comes from a large population that was started from a small sample. In conservation biology, the recommended effective population size to preserve evolutionary potential is 500–1 000 individuals (Franklin & Frankham, 1998). Even though there are records of establishment and short-term survival of biocontrol introductions that were founded with very few individuals (Grevstad, 1999b, 2006; Memmott et al., 1998, 2005), the long-term survival and evolutionary potential of those introductions may be compromised. For example, laboratory *D. melanogaster* populations subjected either to a single generation of bottleneck or a combination of bottleneck followed by three generations of inbreeding showed a 25 and 29% reduction in evolutionary potential, respectively, and went extinct earlier compared to outbred populations (Frankham et al., 1999). Similarly, laboratory experiments with flour beetles showed that at all different founding sizes (2, 4, or 32 individuals) introductions that used inbred compared to outbred individuals went extinct at a higher rate and had lower growth rates and reduced evolutionary potential (Szűcs et al., 2017b). Even in outbred populations, the signatures of the most severe bottlenecks were visible seven generations after population founding in the form of reduced growth rates (Szűcs et al., 2017b). Lasting negative effects of population bottlenecks were also found in native and exotic birds in New Zealand that had experienced a bottleneck of less than 150 individuals, which had reduced hatching rates even after 100 generations (Briskie & Mackintosh, 2004).

Even if biocontrol agents are released in environments that closely match the climate of their area of origin there will be several aspects, both biotic and abiotic, of the new environment that will be different. Thus, maintaining adaptive variation should be a priority in biocontrol introductions to ensure agents can evolve in response to changing environmental conditions and to the target species

that are often evolving themselves (Schierenbeck & Ellstrand, 2009; Colautti & Lau, 2015; Dlugosch et al., 2015). Admixture (hybridization/outcrossing) between genetically distinct populations has great potential to increase adaptive genetic variation and fitness of populations as it can restore allelic richness and heterozygosity lost during bottlenecks, and reduce genetic load (Lynch, 1991; Schierenbeck & Ellstrand, 2009; Rius & Darling, 2014; Dlugosch et al., 2015).

Upon admixture fitness of individuals can increase immediately (heterosis), which can impact establishment success and early population dynamics. For example, introductions done using hybrid pheasants had higher establishment success than those using non-hybrids due to transient heterosis (Drake, 2006). Similarly, populations founded with admixed red flour beetle, water strider, cowpea weevil, and whitefly individuals had higher establishment success and/or population growth than non-admixed populations (Ahlothe et al., 2003; Hufbauer et al., 2013; Szűcs et al., 2017b; Wagner et al., 2017). Even if the heterotic effects of outcrossing decrease over time, high population growth rates for a few generations could buffer newly released biocontrol agent populations against demographic and environmental stochasticity, help reduce the severity of founder effects, and increase establishment success.

Implications for biological control introductions

At the core of all the above-described processes are the genetic diversity of founding populations and their interaction with demographic and environmental conditions. Thus, biocontrol programs should focus on managing genetic diversity of the agents, especially during the early stages of a program. For example, candidate biocontrol agents that pass the initial host specificity evaluations should be collected from multiple genetically distinct populations in the native range, even if the independent testing of each population increases the upfront cost of developing a program. This could ensure that even after repeated bottlenecks sufficient genetic variation remains that could enable agents to adapt to novel and changing environments. Adaptation to the rearing environment should also be minimized by keeping culture times short and by creating conditions that mimic the natural environment better. Hopper et al. (1993) recommended that agents should be reared for less than five generations in culture where temperatures fluctuate in a similar range than in the field and where the agents have to search for hosts and mates.

It has been long debated whether distinct populations of the same agent species should be merged before or after release in the field (Lewontin, 1965; Whitten, 1970; Messenger et al., 1976). We recommend keeping genetically

distinct lineages of agents separate during culture to maintain their differences, which could include adaptation to aspects of the environment where they were collected. During rearing hybrids can be created, and their fitness and host specificity can be experimentally evaluated. In case hybrids do not show strong outbreeding depression or altered host specificity then the distinct populations could be released in proximity in the field where natural selection can sort out, which lineage(s) (either pure populations or their hybrids) fit the environment of the target pest best. In the first few generations hybridization might occur, but it is unlikely to wipe out all pure individuals, and thus early in the establishment process either of the pure 'parental' lineages and their hybrids may co-exist for several generations. Over time, the constitution of populations will shift in response to selection, maintaining the genotypes that have highest fitness in the given environments (Figure 2).

Releasing hybrids created in the laboratory along with their pure parental populations might change the course of evolution because hybrids often show heterosis, which can substantially increase early population growth rates. High growth rates may enable hybrids to establish at higher rates and to achieve higher abundances quicker than the parental populations, potentially out crowding the pure populations and also increasing chances of further hybridization (i.e., backcrossing). These processes can lead to a population that quickly becomes largely made up of hybrids. However, in later generations hybrids may not be the best fit as heterosis decreases and mismatches of adaptation to the local environment may get revealed. Thus, considering the potential negative consequences of hybridization giving a head-start to hybrids by creating them prior to release may not be the best approach. Our recommendation above would still allow for hybridization and hybrids to eventually take over a population, but it would provide more opportunities for pure populations to persist if they are a better fit for the new environment.

Adaptation

Adaptation in any species will lead to an increase in some fitness traits, such as reproductive rate or survival, which in turn can increase population growth rates and lead to higher population densities. Higher densities of biocontrol agents should increase their impact on the target pest. In addition, high densities can increase the speed of range expansion via density-dependent dispersal (see 'pushed waves' below), which can lead to faster coverage of the target species' distribution. Adaptive evolution can be rapid enough to influence population sizes within 2–3 generations (Stewart et al., 2017; Szűcs et al., 2017a), and thus in

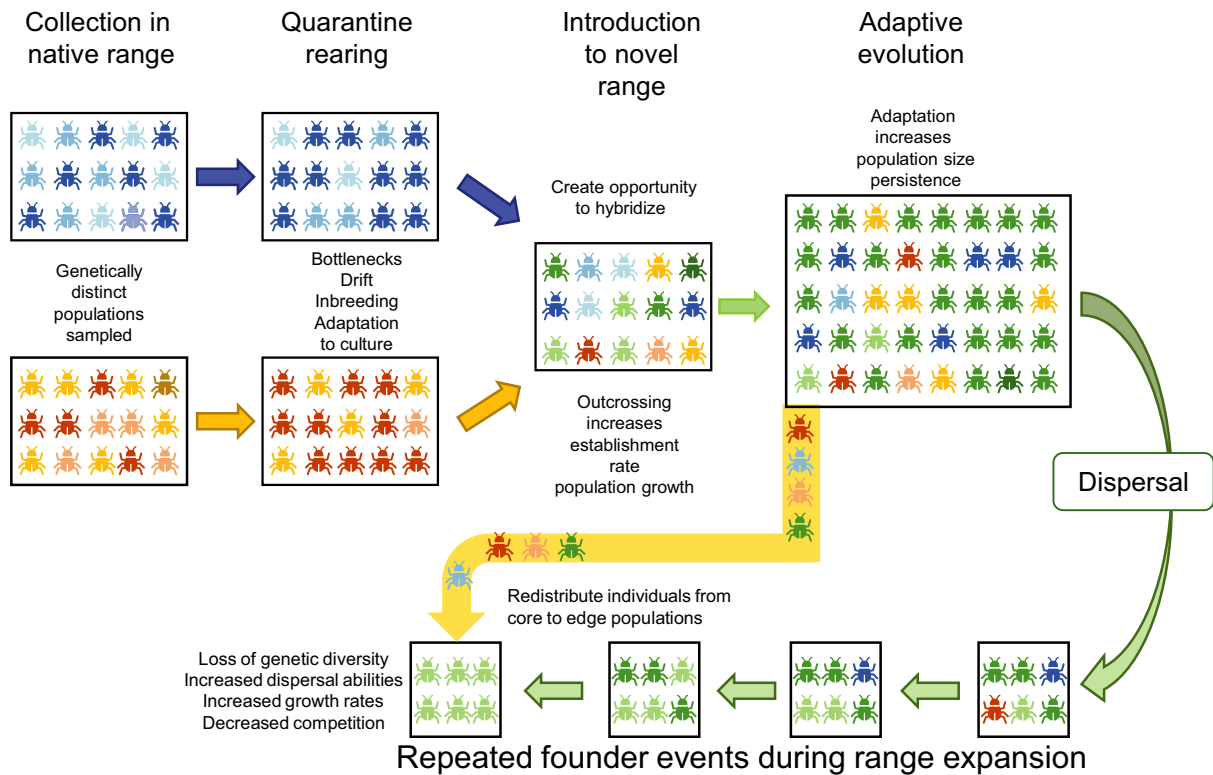


Figure 2 Ecological and evolutionary processes during different stages of a biocontrol program and their effects on the dynamics of biocontrol agent populations. Shades of blue and shades of yellow represent two genetically distinct populations of agents collected in the native range of an invasive species. Different shades within color families represent the genetic variation sampled. These populations, ideally kept separate, will likely experience bottlenecks in the quarantine, which can reduce their genetic variation (shown as a loss of a shade), and small population sizes can lead to inbreeding and/or genetic drift (shown as random shades increasing in frequency). Upon introduction of the agents in the exotic range, if the two genetically distinct populations are released in proximity, this will create opportunities for hybridization, which can result in populations that are a mixture of pure individuals from the two originally collected populations and of hybrids (shades of green) between them. Hybridization can increase establishment rates and population growth and facilitate adaptation; however, adaptation can also reduce genetic variation (loss of a shade). As established agent populations expand their ranges repeated founder events occur, which can result in loss of genetic diversity at the expanding front compared to the population core. Spatial evolutionary processes during dispersal can increase dispersal abilities of individuals, may increase growth rates, and decrease competition. Redistribution of agents may be advised from the core to the edge of populations to restore genetic diversity lost during expansion. See text for details regarding eco-evolutionary processes during each stage.

theory it could influence the dynamics of biocontrol agent populations early on, probably mediating establishment success and growth rates.

Newly released biocontrol agents are unlikely to be perfectly adapted to the novel abiotic and biotic conditions in the introduced range and, thus, multiple traits will be under selection to better match their new environment. Despite expectations that adaptive evolution will increase fitness in introduced populations, convincingly demonstrating adaptive evolution can be difficult (Colautti & Lau, 2015; Bertelsmeier & Keller, 2018). Reciprocal transplant or common garden experiments are necessary to show that phenotypic differences between introduced and

native populations have a genetic basis (Colautti & Lau, 2015; Bertelsmeier & Keller, 2018). In addition, the experiments should ideally span more than one generation and measure traits directly related to fitness, such as survival or reproduction (Colautti & Lau, 2015).

Even though rapid evolution is often claimed in invasive species, adaptive evolution can be demonstrated only in a few cases convincingly (reviewed in Colautti & Lau, 2015). Similar to the invasive species literature, examples from a recent review seem to indicate that post-introduction adaptive evolution is common in biocontrol agents (Wright & Bennett, 2018), but few of the studies listed meet any of the above criteria to actually demonstrate that

adaptation has happened. For example, studies simply documenting reduced genetic diversity (Roehrdanz et al., 2006; Franks et al., 2011; Ma et al., 2013), the retention of genetic diversity (Taylor et al., 2011), or the presence of geographic structure post-introduction (Vorsino et al., 2014) do not by themselves provide evidence of adaptive evolution. Likewise, the assessment of heterosis or inbreeding depression in laboratory crosses (Benvenuto et al., 2012; Szűcs et al., 2012b) or the fact that hybridization of an agent can happen with native species without any measurement on its fitness effects (Havill et al., 2012) are not indicative of adaptation in field populations. Thus, there is little strong evidence for post-introduction adaptation in biocontrol agents in field populations (but see Bean et al., 2012; McEvoy et al., 2012; Szűcs et al., 2012a).

In the following section, we review several studies that illustrated adaptive evolution in response to novel abiotic (climate, photoperiod) and biotic (competition, predation) environments with most examples coming from invasive species rather than biocontrol agents. The paucity of empirical evidence from biocontrol agents suggests that we need more studies that explicitly test whether adaptation has occurred on ecological time scales. Ideally, such research would evaluate how adaptation to a new environment affects fitness and potentially population growth rates. Results from these types of experiments would provide a more direct eco-evolutionary understanding of biological control, including how adaptation influences population size.

Novel abiotic conditions

The physical environment introduced species arrive in or spread into following establishment can differ in multiple characteristics from their native range. Here, we provide examples indicative of adaptations to these novel abiotic conditions. Sotka et al. (2018) used environmental data combined with common garden experiments to show that invasive red seaweed, *Gracilaria vermiculophylla* (Ohmi), populations have evolved higher tolerance to warmer temperatures than populations from the native range. Furthermore, they were able to trace the genetic history of several invasive populations to more accurately identify niche shifts and phenotypic shifts between native and invasive populations to demonstrate local adaptation. Rapid adaptive evolution was also clearly demonstrated in northern populations of the invasive purple loosestrife, *Lythrum salicaria* (L.), which evolved earlier flowering times compared to populations at the southern front (Colautti & Barrett, 2013). The biological control agents *Tyria jacobaeae* (L.) and *Longitarsus jacobaeae* (Waterhouse), both introduced to North America for control of tansy ragwort (*Jacobaea vulgaris* Gaertn.), were released at both low and

high elevations, and rapidly evolved differences in life-history traits in response to the cooler climate and shorter growing seasons at high elevations (McEvoy et al., 2012; Szűcs et al., 2012a). In *L. jacobaeae*, evolution of life-history traits resulted in higher fitness via increased larval densities and winter survival at high elevations. In the case of an agent expanding its range, southern populations of *Diorhabda carinulata* (Desbrochers) had evolved a shorter critical daylength that allowed for diapause induction later in the year (Bean et al., 2012). This shift enabled the beetle to track its target host, invasive tamarisk, further than anticipated and is predicted to allow for 16 additional days of reproductive activity which should dramatically increase population growth rate (Bean et al., 2012).

Novel biotic conditions

Upon introduction, biocontrol agents are exposed not only to novel abiotic conditions but also to a novel biotic environment including altered competitive, predator-prey, or parasitoid-host interactions. Encounters with closely related native species or of genetically distinct populations of its own species can also result in hybridization, and all of the above biotic interactions will likely affect ecological traits as well as the extent and direction of rapid evolutionary responses of introduced populations.

Competition is generally thought of as an ecological process that reduces fitness of individuals and population sizes of competing species (e.g., Gurevitch et al., 2000; Alzate et al., 2017). Recent theory evaluates the effects of competitive interactions on evolutionary process, and finds that when competition reduces population sizes, it slows rates of adaptation and increases extinction risk (Johansson, 2008). However, species can also adapt to competitive environments (Stuart et al., 2014). The theoretical work (Johansson, 2008) has empirical support from experimentally evolving populations of two-spotted spider mites, *Tetranychus urticae* Koch. In that system, competition with another mite species, *Tetranychus evansi* Baker & Pritchard, can reduce population sizes, increase extinction rate, and slow or prohibit adaptation to a novel host, whereas gene flow from non-adapted populations can overcome the negative effects of competition to allow successful adaptation (Alzate et al., 2017).

Biocontrol agents are generally assumed to experience reduced competition for resources upon introduction because they will represent one or only a few of specialized natural enemies that attack the target pest. Competition may also be reduced because the target is a pest, and as such it is likely present at higher densities than in the native range, at least initially prior to control. Thus, one would expect that biocontrol agents would not be subject to intense selective pressure from competition in the early

stages of a new program. However, often several agents are released to control a target host (Cock et al., 2016; Schwarzländer et al., 2018). For example, at least three seed-head feeding weevil species have been released to control invasive yellow starthistle, *Centaurea solstitialis* L., in addition to picture wing flies and a rust pathogen (Gutierrez et al., 2017). Direct competition between niche-overlapping phytophagous insects, such as the three seed-head feeding weevils can have similar consequences for population sizes and adaptation as discussed above. Competition might be stronger in insect biological control as the mean number of agents introduced against insect pests is higher than that for weeds (Cock et al., 2016; Schwarzländer et al., 2018). In the case of introduced parasitoids competition may ensue not only for hosts but for other resources, such as extrafloral nectar, that could impact life span and fecundity of the agents.

Natural enemies can affect eco-evolutionary dynamics of the target species, for example, by reducing population sizes and thus limiting the power of selection in pests relative to drift. However, biocontrol agents themselves will accumulate natural enemies over time (Hawkes, 2007; Paynter et al., 2010), which can reduce efficacy and evolutionary potential.

Finally, hybridization can be thought of as a unique biotic interaction that occurs when introduced species cross with native species or with distinct populations of conspecifics that they encounter in the new range. The short-term positive effects of hybridization are discussed in an earlier section on 'founder effects'. Here, we expand on the longer term ecological and evolutionary consequences of hybridization and its effect on adaptation. Several studies link hybridization to invasiveness, whether through the emergence of transgressive phenotypes or through heterosis (i.e., Keller & Taylor, 2010; van Kleunen et al., 2015; Bock et al., 2018). In a recent study, Shi et al. (2018) found that admixture between populations of purple loosestrife increased fitness even in well-established yet continually expanding invasive populations. Hybridization in the context of biological control can lead to evolution of important life-history traits. Bitume et al. (2017) found that, depending on which species crossed, hybridization could increase fecundity and reduce development time in tamarisk leaf beetles, *Diorhabda* spp., released to control tamarisk. Similarly, Szűcs et al. (2012a) showed that admixture between two distinct populations of the ragwort flea beetle *L. jacobaeae*, released to control invasive *J. vulgaris*, increased fecundity. In that system, hybrid populations have higher population densities and tend to be more effective at controlling target plants than non-hybrid populations in the field (Szűcs et al., 2019). This evidence suggests that

hybridization can change ecological processes, such as population dynamics and herbivore-plant interactions and may increase efficacy of biological control, but whether it facilitates adaptation is not yet known (Szűcs et al., 2012a, 2019; Bitume et al., 2017).

Although adaptation of agents to novel biotic and abiotic conditions could benefit biocontrol programs, there may be concern regarding rapid evolution of host ranges and of potential non-target effects. For weed biocontrol agents, unanticipated non-target effects occurred in <1% of the 457 species released until 2008 (Hinz et al., 2019), and there has been no evidence that the fundamental host range, predicted by host specificity testing, would have evolved in any agents post-release (van Klinken & Edwards, 2002). Non-target effects are more common in biocontrol agents released to control arthropod pests, which largely stem from past programs where generalists were introduced and/or host specificity tests were not required (Hajek et al., 2016). However, there are very few post-release studies (Hajek et al., 2016) and none that we know of that can demonstrate evolution of host range. Currently, specialist parasitoids are the most often used arthropod biocontrol agents (Hajek et al., 2016), and the host ranges of these types of parasitoids seem fairly conserved. For example, six native parasitoid species from four genera could not adapt to increase their rates of parasitism on an invasive species, the brown marmorated stink bug (*Halyomorpha halys* Stål), which remained under 5% over a 9-year sampling period (Dieckhoff et al., 2017). All this evidence indicates that the risks of potential host range evolution are negligible for biocontrol agents.

Eco-evolutionary processes at expanding range edges

Classical biological control is based on the idea that once a biocontrol agent is successfully established in a given area, it will be able to expand its range to follow the distribution of its host and persist at the landscape scale (Eilenberg et al., 2001). Although all biocontrol agents possess species-specific dispersal-related traits that can mediate their rates of dispersal, some general processes have been identified that all species may be subject to during range expansion. During expansion evolutionary processes can alter the fitness, reproductive rates, and dispersal ability of individuals on the front. Rapid evolution of the above traits in turn can feed back to change the ecological characteristics (e.g., growth rates or competitive traits) of edge populations. These eco-evolutionary feedback loops that can occur during range expansion will likely affect the dynamics of introduced populations, such as biocontrol agents, and also species that are expanding their ranges in response to climate change.

Dispersal tendency and life-history evolution

Individuals with the highest dispersal tendencies tend to be the first to arrive to the edge of an expanding front. There, they will preferentially mate with each other and leave many highly dispersing offspring, as density and intraspecific competition are lower on the front. This phenomenon, known as spatial sorting (Shine et al., 2011), creates a directional selection on dispersal, so that individual dispersal tendencies and population expansion rates are expected to increase during an expansion (Phillips et al., 2010a). Even if the initial population is already highly dispersive (as can be selected in agricultural ecosystems, subject to frequent fluctuations in resource distribution at the landscape scale), this directional selection process can further increase dispersal tendencies in edge populations. This pattern was predicted repeatedly with different modeling approaches (e.g., Travis & Dytham, 2002; Hughes et al., 2007; Phillips et al., 2008) and supported by numerous empirical demonstrations of increased dispersal abilities in populations at range edges (natural populations, Cwynar & MacDonald, 1987; Thomas et al., 2001; Hanski et al., 2002; Simmons & Thomas, 2004; Léotard et al., 2009; biological invasions, Phillips et al., 2006; Lombaert et al., 2014). More recently, several independent laboratory experiments have shown that rapid evolution can accelerate range expansions, for example, in ciliate protists (Fronhofer & Altermatt, 2015), insects (Ochocki & Miller, 2017; Szűcs et al., 2017a; Weiss-Lehman et al., 2017), or plants (Williams et al., 2016a).

Besides dispersal ability, life-history traits are also predicted to evolve at the edge of an expansion in response to the relatively low conspecific density that individuals experience (Phillips et al., 2010b; Perkins et al., 2013). The low densities at the edge are expected to select for increased reproductive rates as competition is relaxed (Roff, 1993). In contrast, individuals in the core of the population will generally experience higher density conditions, which should select for higher competitive ability (Charlesworth, 1971). Empirical studies of invasive populations have found indications of evolution of life-history traits in response to low population densities showing that individuals from the front grow faster (Phillips, 2009), mature earlier (Amundsen et al., 2012), or have higher fecundity (Laugier et al., 2013).

Loss of genetic diversity

The expanding edge of a population can be subject to intense genetic drift because of repeated founder events and reduced population size. Neutral genetic diversity is thus predicted to be reduced on the front compared to the core (Excoffier & Ray, 2008; Hallatschek & Nelson, 2008).

In addition, pioneer individuals on the front can spread their genes faster than individuals from the core, as they may enjoy higher reproductive success and contribute more to the expanding front of the population. This can lead to ‘gene surfing’, where rare alleles can spread over wide areas and reach very high frequencies on the front (Klopfstein et al., 2006; McNerny et al., 2009). Theory predicts that gene surfing can also apply to mildly deleterious mutations (Travis et al., 2007), thus creating an ‘expansion load’ if these mutations become fixed (Peischl et al., 2013). Recent analyses of genetic structure in human populations (Peischl et al., 2018) and laboratory experiments on bacterial populations (Bosshard et al., 2017) provided consistent evidence in support of this expansion load hypothesis.

‘Pushed’ and ‘pulled’ expansion

All of the above predictions arise from the interplay of demographic and evolutionary processes operating at low-density populations at the expanding front. This pattern is consistent with the scenario of a population expanding by sending a few pioneer individuals ahead, who manage to reproduce and send a few descendants even further, and so forth. This dynamical process is referred to as a pulled expansion wave, because the expansion of the whole population is ‘pulled’ by the few individuals that are ahead. However, in some cases, expansion is hampered at low density, for instance in the presence of an Allee effect (Roques et al., 2012; Gandhi et al., 2016), or because dispersal is density dependent (Haond et al., 2018). In these cases, the population needs to grow locally before being able to spread and the expansion will be ‘pushed’ from behind by the high-density core. In pushed expansions the edge populations are not characterized by low-density conditions, which means that dispersal and life-history traits would not evolve differently on the front than in the population core, and that neutral genetic diversity would tend to be conserved during expansion. These predictions have been consistently supported by recent theoretical work on the evolution of expanding populations in presence of an Allee effect (Roques et al., 2012; Wittmann et al., 2014), a native competitor (Burton et al., 2010; Roques et al., 2015), or long-distance dispersal (Goodman et al., 2014), and in heterogeneous environments (Williams et al., 2016b). However, experimental or empirical evidence is still lacking to confirm that pushed dynamics are indeed able to neutralize the joint effects of genetic drift and natural selection on expansion fronts.

Implications for biological control: pest–agent interactions in a heterogeneous selective landscape

All field-based examples of the spatial evolutionary processes we just reviewed originated from natural expansions

or invasive populations, with no insight from biological control programs. Long-term monitoring of populations is notoriously lacking in biological control, especially with regard to expansion beyond the introduction area (one exception being the biocontrol agent-turned-invasive *H. axyridis*; see Laugier et al., 2013; Lombaert et al., 2014). Therefore, we can only build on the main theoretical predictions available to anticipate how spatial evolutionary processes can affect pest–agent interactions at a large spatial scale, and how deployment strategies could optimize the outcome of biological control in time and space.

Many life-history traits are predicted to evolve during expansion, and thus the performance of an introduced biocontrol agent may change over time and space. To limit heterogeneity in control over the whole targeted area, initial agent releases should be conducted both in the core and edge of populations of invasive species. After establishment, redistribution of individuals from different areas can also be used to slow or prevent the selection of extreme phenotypes, following the concept of ‘genetic backburn’ (Phillips et al., 2016). For example, individuals from the core could be introduced to the edge to counteract the effects of spatial selection if those are impeding control efficiency. This could also serve to restore genetic variation that may be lost during range expansion and to maintain evolutionary potential.

Second, when the target pest is an invasive species, it has also been experiencing expansion in its new range and evolving accordingly, so that populations from the core and edge of its range may be characterized by different life-history traits. Thus, the efficacy of biocontrol agents may change spatially due to spatial differences in traits of the target, a phenomenon not considered previously as a factor that might mediate control success.

Concluding remarks

Research to better understand the eco-evolutionary processes that mediate the dynamics of populations is likely to be the focus of numerous future studies across multiple fields as rapidly changing environmental conditions caused by climate change, pollution, and habitat destruction impose ever increasing selection pressures on all species. To date, most of our knowledge regarding the immediate or longer term consequences of eco-evolutionary dynamics comes from theoretical work and direct evidence usually from laboratory experiments. Thus, we still know very little how eco-evolutionary interactions may play out in field populations, and how they may impact the fitness and distribution of endemic vs. introduced species or widespread vs. rare species. Biological control introductions can serve to increase our knowledge of the

importance of these processes given the breadth of information available regarding source populations, introduction times and sizes, or redistribution routes, and because the experimental release, manipulations, and movement of agents do not pose ethical challenges, as may be the case with native or invasive species. In turn, we could use this information to help mediate the impact of environmental change on native species and for the benefit of biological control to increase establishment and population growth rates, adaptive abilities, and ultimately the control potential of agents.

With regard to biological control we can already make some recommendations based on the examples reviewed in this paper. All lines of evidence point toward the importance of maintaining genetic diversity during the initial stages of a biological control program, from collection in the native range through mass rearing and release to increase chances of establishment, initial population growth, and persistence. This means that from the start of a program we should strive to sample the genetic diversity of an agent widely in the native range, and to keep losses of diversity at a minimum during rearing. In addition, to alleviate the negative fitness effects of bottlenecks that may have occurred prior to release and to maximize genetic variation available for selection in the new environment outcrossing between genetically distinct populations of agents should be facilitated post-release. Moreover, both the initial introduction and subsequent redistribution of agents should consider the consequences of spatial eco-evolutionary processes. For example, releases should be done both in the core of invasive species infestations as well as at the edges, and ideally the impact of agents quantified in all areas separately to reveal any potential mismatches between traits of an expanding invasive population and a newly established biocontrol agent. Although some gene flow between agent populations residing in the core and edge of the distribution of target species seems desirable from a spatial evolutionary perspective, multiple introductions or redistribution of agents into already established populations can hinder local adaptation and should be done after careful considerations.

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