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SYNTHESIS

The biology of small, introduced populations, with special reference to biological control

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Abstract

Populations are introduced into novel environments in different contexts, one being the biological control of pests. Despite intense efforts, less than half introduced biological control agents establish. Among the possible approaches to improve biological control, one is to better understand the processes that underpin introductions and contribute to ecological and evolutionary success. In this perspective, we first review the demographic and genetic processes at play in small populations, be they stochastic or deterministic. We discuss the theoretical outcomes of these different processes with respect to individual fitness, population growth rate, and establishment probability. Predicted outcomes differ subtly in some cases, but enough so that the evaluating results of introductions have the potential to reveal which processes play important roles in introduced populations. Second, we attempt to link the theory we have discussed with empirical data from biological control introductions. A main result is that there are few available data, but we nonetheless report on an increasing number of well-designed, theory-driven, experimental approaches. Combining demography and genetics from both theoretical and empirical perspectives highlights novel and exciting avenues for research on the biology of small, introduced populations, and great potential for improving both our understanding and practice of biological control.

Introduction

Understanding the processes that occur when a population is introduced into a novel environment is a prerequisite for the management of invasions as well as the improvement of conservation and biological control (e.g. Sarrazin and Barbault 1996; Freckleton 2000; Roderick and Navajas 2003; Liebhold and Tobin 2008; Tobin et al. 2011). The aim of this article is to review the critical demographic and genetic processes that act in small populations, be they deterministic or stochastic. We focus in particular on biological control.

Recently, much research has concentrated on processes prevailing in the founding of inadvertently introduced populations that have become invasive in their novel ranges. While many insights have been gained, the accidental nature of those introductions limits inferences, and also does not pertain in all cases to introductions performed for conservation or for biological control. Classical biological control relies on the intentional introduction of exotic species for the long-term control of invasive pests (Eilenberg et al. 2001). It is essentially a planned biological invasion, with biogeographic, demographic, and genetic processes similar to those operating in other types of introduction (Fig. 1). But as deliberate events, they render possible (i) observation of mechanisms at work at very small population size during the establishment stage, (ii) experimental manipulation of initial conditions, and (iii) conclusion that a population has indeed failed to establish after being introduced. Hence, classical biological control provides an unparalleled situation to study the biology of introduced populations (e.g. Grevstad 1999a; Marsico et al. 2010).

One major determinant explaining the success of small, introduced populations, be they for biological control or not, is the total number of individuals introduced. The term propagule pressure refers to a combination of

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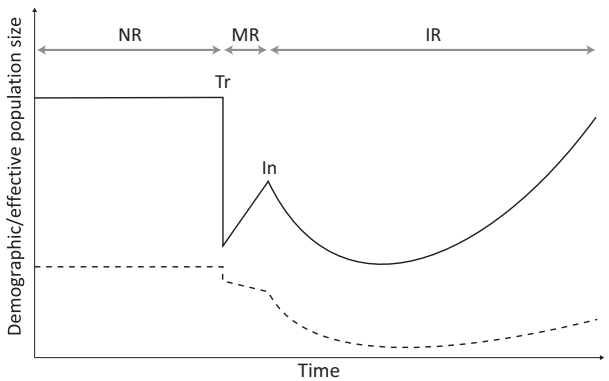

Figure 1 Introductions are characterized by major demographic and genetic disequilibria during transit (Tr) from their native range (NR) and when introduced (In) into the introduced range (IR). The bottleneck in demographic population size (solid line) may be buffered by an episode of mass rearing (MR) in the case of biological control. However, a decrease in population size is often observed after introductions, during the establishment stage. The effective population size (*N*e, dashed line) decreases, as a result of sampling in the native population, and genetic drift during mass rearing as well as after introduction. In the absence of additional inputs of genetic material, the effective population size will lag behind demographic size and remain low even after the population has established and starts to grow.

propagule size (the number of individuals in each introduction event) and propagule number (the number of different introductions). Meta-analyses and reviews on the fate of introduced or reintroduced populations in different taxa are congruent in their conclusion that increased propagule pressure yields increased probability of population establishment (Lockwood et al. 2005; Simberloff 2009). Propagule pressure is by far the most pervasive explanatory variable in the success of founding populations of biological control agents (Table 1; Beirne 1975; Hopper and Roush 1993), invasive species (Green 1997; Forsyth and Duncan 2001; Kolar and Lodge 2001; Colautti et al. 2006; Duggan et al. 2006; Hayes and Barry 2008), or species being reintroduced into a region for biological conservation (Griffith et al. 1989; Fischer and Lindenmayer 2000; Deredec and Courchamp 2007). The effect of propagule pressure is therefore so general and relevant that it can serve as a cornerstone paradigm to approach the biology of introduced populations.

Both demographic and genetic processes may underpin the widespread effect of propagule pressure on introduction success (Fig. 1). Demographic processes include both stochastic processes such as demographic and environmental stochasticity and deterministic processes such as Allee effects; genetic processes include drift, inbreeding depression, selection, and gene flow, which also combine both stochastic and deterministic components. For a number of different reasons, determining which process has the strongest influence on introduced populations is a real challenge. First, the low establishment rates of small populations can be the result of any one of the above mechanisms, making it difficult to determine which is acting in any given case. Second, research on population dynamics and on population and evolutionary genetics is in the domains of distinct scientific communities that interact relatively seldom. Third, and as a possible consequence of the first two, heated debates have arisen, for example on whether or not small populations are driven to extinction by stochastic events and demographic processes before genetic factors impact them (Lande 1988; Spielman et al. 2004). Together, these issues have impeded the development of a general theoretical framework for the biology of introduced populations.

In this article, we review and synthesize the different demographic and genetic processes that can occur in small, introduced populations. There is no standard definition of what a small population is, but we here assume that 1–10 individuals is a very small initial population size, and 10–100 is a small initial population size. In addition to reviewing the existing theory, we highlight the sets of testable predictions that can enable us to better discriminate among the different underlying processes, and we evaluate the evidence for these mechanisms with a focus on the literature on classical biological control. Our hope is to unveil gaps in our understanding of biological control and contribute to its improvement, but also to deepen our fundamental understanding of the biology of introduced populations. Hence, although we focus on biological control, we hope to stimulate the interest of invasion biologists, conservation biologists, and other population biologists studying small or bottlenecked populations.

Demographic and environmental stochasticity

Theory

Demographic stochasticity refers to the deviance between the observed number of individuals and the expected number derived from average vital rates like survival, fecundity, or sex ratio. Demographic stochasticity arises for two main reasons. First, vital rates are averaged over multiple individuals and thus are real numbers, while populations are collections of discrete individuals. Hence, population growth *in natura* follows integer arithmetic, which can result in a significant shift from predicted values. This shift occurs because the fate of any one individual is not buffered by that of others. Second, demographic stochasticity arises because variation in population size is probabilistic and thus includes a nonpredictable, random component. In the absence of complete knowledge of individual characteristics and histories, individual fates are modeled as independent realizations of the same chance events of mortality and reproduction (McArthur and Wilson 1967;

Table 1. A synopsis of the published literature related to propagule pressure and biological control. Studies that were based on single observations are not reported in this table. The effect of propagule size and propagule number is reported as positive (+), negative (−), nonsignificant (0), or unclear (?). Whenever the information is available, we indicate whether the stochastic, demographic, or genetic component of propagule pressure was more explicitly investigated.

References	Response variable	Propagule size	Propagule number	Stochasticity	Demography	Genetics
Experimental studies						
Campbell 1976	Persistence after 3 months	+				
Memmott et al. 1998	Persistence after 1 year	+			■	
Grevstad 1999a	Persistence after 3 years	+		■	■	
	Growth rate	+				
Dray 2001	Persistence after 7 years	?	?	■	?	
De Clerck-Floate et al. 2005	Persistence after 2 years	0				
Memmott et al. 2005	Persistence after 6 years	+		■		
	Growth rate	0				
Fauvergue et al. 2007	Persistence after 3 years	0			■	
	Reproductive rate	−				
	Sex ratio	0				
De Clerck-Floate et al. 2009	Persistence after 2 years	0			■	
Fauvergue and Hopper 2009	Persistence after three generations	0			■	?
	Density	+				
	Female mating rate	0				
	Sex ratio	0				
	Reproductive rate	− & +				
Review/meta-analyses						
Beirne 1975	Establishment success	+	?	?	?	■
Simberloff 1989	Establishment success	0			■	?
Cameron et al. 1993	Establishment success	+	+			
Hopper et al. 1993	Establishment success	+	+	■	■	
Stiling 1993	Successful host control	0 & +				
Theoretical models						
Stouthamer et al. 1992	Sex ratio	+				■
	Growth rate	+				
Hopper et al. 1993	Establishment success	+			■	
Grevstad 1999a,b	Establishment success	+	+	■	■	
Shea and Possingham 2000	Establishment success	+	+ & −	■	■	
Zayed and Packer 2005	Extinction risk	+				■

Roughgarden 1975; Engen et al. 1998). The smaller the population, the lower the number of realizations, and thus, the further result can stray from the expectation. As such, the impact of demographic stochasticity is stronger in small populations (May 1973; Lande 1988, 1993; Lande et al. 2003). Figure 2A,C represents simulations of population growth rates in the presence of demographic stochasticity. In these populations, the expected discrete-time growth rate is 1.0 (i.e. constant expected population size). When initial population size is 100, stochastic population fluctuations are restricted within 40% of this value. In contrast, when initial population size is 10, population fluctuations can reach 200%, which results in several extinction events (dashed lines).

Parasitoid wasps with a local mating structure provide an interesting illustration of demographic stochasticity. In these species, game theory predicts extremely female-biased sex ratio, especially when the offspring of a single foundress female develop together on the same site. On the basis of real-number arithmetic, Hamilton's (1967) local mate competition model predicts an optimal proportion of males of zero, which is generally interpreted as 'just enough males to mate all the females in the brood'. When individuals are assumed more realistically as integers, the optimal sex ratio for single foundress situations becomes the reciprocal of clutch size (Green et al. 1982). Nevertheless, when optimal sex allocation combines with male mortality during immature stages, an expected consequence of demographic stochasticity is the increased occurrence of all-female broods with decreasing clutch size (Heimpel 1994), with a possible decrease in fitness if mating occurs on the site where wasps have developed. A number of laboratory and field studies support this expectation (Hardy et al. 1998; Kapranas et al. 2011).

Environmental stochasticity refers to temporal fluctuations in the average vital rates of populations. Environmental stochasticity reflects variation in the abiotic (climate,

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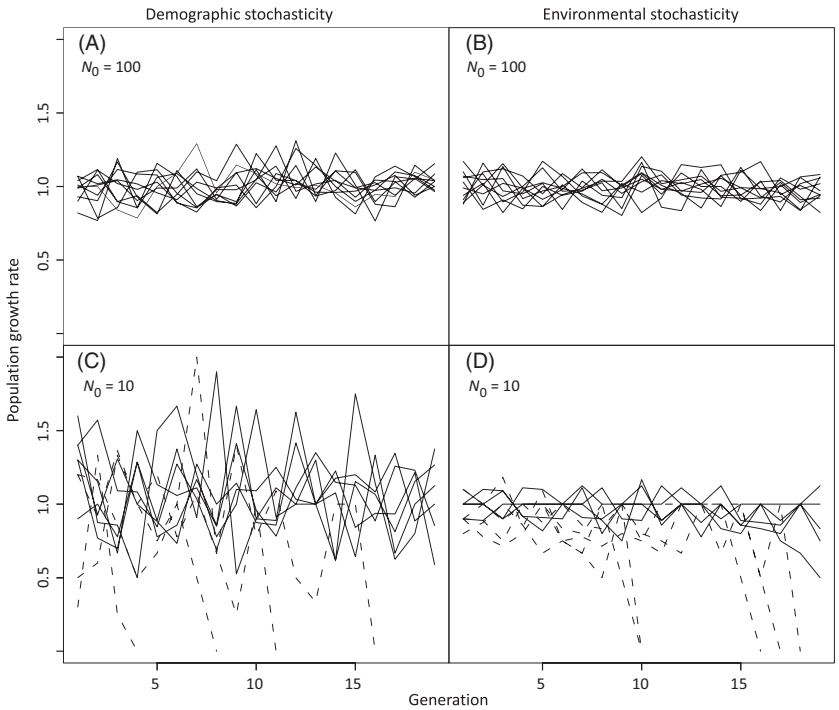

Figure 2 Discrete-time simulations of stochastic population dynamics (random birth–death processes with average fecundity = 100 and average survival probability = 0.01). Trajectories that lead to extinction are represented with dashed lines. N_0: initial population size. (A, C) Demographic stochasticity. Population fluctuations and extinction risk are increased for small populations. (B, D) Environmental stochasticity ($\leq$ 10% random variation of vital parameters at each generation). Population fluctuations are similar for small and large populations, but extinction risk is increased in small populations if populations with less than one individual are considered extinct (pseudo-extinctions).

anthropic perturbations) or biotic conditions (density of prey, predators, competitors, or parasites) that cannot be captured by deterministic dynamics, and as such excludes any predictable pattern like long-term trends in habitat reduction, prey-predator cycles, or density-dependent feedback (Lande 1988; Lande et al. 1998, 2003). Figure 2B,D represents the simulations of population growth rates in the presence of environmental stochasticity. As before, in these populations, the expected discrete-time growth rate is 1.0, and thus, population size is expected to be constant. Environmental stochasticity is set to 10% random variation in average vital rates at each generation. Unlike demographic stochasticity, the impact of environmental stochasticity is independent of population size, that is, the relative amplitude of population fluctuations is the same in small or large populations (Fig. 2B,D). However, environmental stochasticity can interact with demographic stochasticity to increase the extinction rate in small populations, where a random reduction in population growth rate can drive population size down to where the effects of demographic stochasticity come into play (Grevstad 1999b; Drake 2004). This is what we observe in our numerical simulations. In these simulations, demographic stochasticity is included in its minimal form, as we used integer arithmetic to calculate the number of individuals at each generation and we set an extinction threshold at one individual. Therefore, the observation of more extinction events (dashed lines) in the small populations than in the large populations reflects the interaction between the two levels of stochasticity (Fig. 2D).

Several features of stochastic population dynamics are likely to impact the establishment success of introduced populations of biological control agents. In particular, a major consequence of stochasticity is that extinction is possible (and sometimes likely) even when population growth rate is positive, and the population would persist indefinitely under deterministic dynamics (Lewontin and Cohen 1969; Lande 1998; Lande et al. 2003). In the presence of demographic stochasticity only, the relative amplitude of population fluctuations, which reflects inter-individual variance in reproductive success, decreases as population size increases (Figs 2A,C and 3A). Therefore, probability of extinction decreases quickly as population size increases (Fig. 3A). Only very small populations are at high extinction risk, while large populations are essentially buffered against the effects of demographic stochasticity. In the case of environmental stochasticity, however, extinction risk is permanently increased for all population sizes (Fig. 3B).

The probability of establishment reaches a maximum value that is below one, and the actual value will depend on the severity of the environmental fluctuations (Fig. 3B). A consequence of such ongoing risk of extinction is that long-term persistence is impossible in highly perturbed habitats unless multiple introductions are distributed in space to create a functional metapopulation. Therefore, the susceptibility of introduction sites to environmental perturbations and the possibility of population reservoirs should be carefully considered in biological control introduction programs (Grevstad et al. in press).

Stochastic processes do not preclude theoretical projections of population trajectories. Population viability analysis (PVA) is a quantitative assessment of extinction risk based on a model of population dynamics that incorporates both demographic and environmental stochasticity (Shaffer 1981). PVA has been used widely in conservation biology to identify critically endangered populations or to determine which management actions are likely to be most effective in improving population viability and reducing extinction risk (sensitivity analysis; McCarthy et al. 1995; Caswell 2001). A main feature of PVA is the definition of minimum viable population sizes and minimum habitat areas (Shaffer 1983; Armbruster and Lande 1993; Wiegand et al. 1998), both of which are likely influence the establishment success of biological control organisms. Although PVA is characterized by several biases that tend to underestimate extinction risk (Coulson et al. 2001), near-term predictions can be reliable enough to select the size, number, and spatial distribution of introductions, thus avoiding many of the negative effects of stochasticity and improving establishment success.

Evidence

Detailed data on variance in population size in the context of biological control are scarce, which limits the power to quantify the intensity of stochastic processes during establishment phase. Most censuses are restricted to a couple of years after introduction, and populations are often only referred to as established or extinct, without quantitative surveys of population sizes. Experimental introductions are a noticeable exception: Several studies report evidence for the influence of demographic stochasticity from positive correlations between number of individual released and population growth rate (Grevstad 1999a) or establishment probability (Memmott et al. 1998; Grevstad 1999a; Memmott et al. 2005; but see Fauvergue et al. 2007 for a counter-example). However, such conclusions are weak because, as raised in the introduction and Fig. 2, a positive relationship between propagule pressure and population growth could be due to multiple different processes. Convincing evidence for the influence of demographic stochasticity would be based on the analysis of the amplitude of population fluctuations and its effect on establishment probability for different initial population sizes. To our knowledge, such experiments are still in their beginnings in mesocosms (E. Vercken, F. Vincent, L. Mailleret, N. Ris, E. Tabone and X. Fauvergue, unpublished data) and have never been performed in the field, which highlights a significant gap in our understanding of demographic stochasticity. In contrast, experimental evidence for the influence of environmental stochasticity appears more conclusive. For instance, Grevstad (1999a) and Memmott et al. (2005) report strong variation in growth rate between sites and years following the experimental introductions, even for similar population sizes. In these two studies, environmental stochasticity seems to play a major role in establishment success, either because the rate of catastrophic events was high (about 30% of release sites destructed within the 5 years of study; Memmott et al. 2005), or because variance in population growth rate was not explained by population size (Grevstad 1999a).

These experimental results are complimented by indirect evidence derived from the analysis of biological control operations in the field. Weak evidence for demographic stochasticity is found in the positive correlations between the number of individuals released and establishment success, as was the case for releases of different parasitoid species against *Bemisia tabaci* in Texas (Gould et al. 2008). Alternatively, a positive correlation between the number of introductions and establishment success would support a role of environmental stochasticity on population dynamics during early introduction, as was found in release programs against St John's Wort in Canada (Mason and Huber 2002) or cassava green mite in Africa (Neuenschwander et al. 2003), for which the correlation with the total number of individuals was non-significant. In a review of biological control releases carried out in Oregon, USA against invasive weeds, Grevstad et al. (in press) also provides good evidence that environmental stochasticity is a major determinant of their establishment success. She finds no relationship between the number of individuals released and establishment success over the range of release sizes used in the included biological control efforts, but in contrast, she shows a clear positive relationship between the number of different releases and eventual establishment success. A meta-analysis of about 250 worldwide introductions of parasitoids against Lepidoptera provides evidence for both environmental and demographic stochasticity (Hopper and Roush 1993). The study reveals a positive effect of the number of releases on establishment probability for the superfamily Chalcidoidea and a positive effect of the number of individuals per release for all three (super)families (Chalcidoidea, Ichneumonoidea, and Tachinidae) of

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parasitoids (Hopper and Roush 1993). The number of individuals released in these programs ranged typically between 100 and 1000, which is above what one usually considers as a safety threshold against demographic stochasticity (Burgman et al. 1993; Lande 1998). However, a strong initial decrease in numbers has been observed repeatedly during experimental introductions (Memmott et al. 1998, 2005; Grevstad 1999a; Fauvergue and Hopper 2009 see also Fig. 1); thus, even large releases may in effect lead to small founding populations. In addition, parasitoid insects are characterized by life history strategies that result in large inter-individual variance in reproductive success, which reduces the number of individuals effectively participating to population growth (Kokko and Ebenhard 1996). Both these factors are likely to increase the sensitivity of introduced populations of biological control agents (particularly parasitoids) to demographic stochasticity.

Allee effect

Theory

A demographic Allee effect is defined as a decrease in *per capita* population growth rate when population becomes small, population size referring to either the total number of individuals or the density (Courchamp et al. 1999, 2008; Stephens et al. 1999). In contrast to environmental and demographic stochasticity and genetic processes, it is considered a purely deterministic process with no variation among individuals or among generations except that produced by population size. Fundamentally, the Allee effect is a form of positive density-dependence at small population size. Theoretical models of Allee effects have been reviewed by Dennis (1989), Boukal and Berec (2002), Courchamp et al. (2008), and X. Fauvergue, in press.

A demographic Allee effect is always caused by one or more component Allee effects, that is, a decrease in one or several components of fitness with a decrease in population size (Fig. 3C; Stephens et al. 1999; Berec et al. 2007). Many fitness components are depressed at small population size because of beneficial interactions between conspecific individuals. The most often cited component Allee effect is failure to find mates (or to be pollinated) at low density (McCarthy 1997; Gascoigne et al. 2009; X. Fauvergue, in press) as shown in the endangered butterfly *Melitaea cinxia* (Kuussaari et al. 1998), the invading moth *Lymantria dispar* (Tobin et al. in press), or the invading grass *Spartina alterniflora* (Davis et al. 2004). Other traits related to reproduction or survival also can be affected at low population size (Berec et al. 2007). Species that cooperate in rearing young (African wild dog), thermoregulation (marmots), habitat amelioration (drosophila), or to defend themselves against predators (meerkats) may all suffer from small group size (Clutton-Brock et al. 1999; Courchamp and Macdonald 2001; Stephens et al. 2002; Wertheim et al. 2002).

Consequences of the Allee effect for population dynamics depend on its strength. When population growth rates remains positive even in the smallest populations, Allee effects are said to be weak, while when population growth rates becomes negative below a given population size (the Allee threshold), Allee effects are said to be strong. In the case of weak Allee effects, small populations are expected to grow (in the absence of other deterministic or stochastic processes) until eventually reaching the carrying capacity of the environment. In the case of strong Allee effects, the Allee threshold produces an unstable demographic equilibrium: any population below this threshold experiences what has been called 'an extinction vortex' (Caughley 1994) where each decrease in population size results in a further decrease in population growth rate, inevitably leading to extinction.

Consequences of Allee effects can be dramatic for introduced populations. When considered independently of other processes, a weak Allee effect slows population growth but does not affect population establishment. In contrast, a strong Allee effect results in a critical initial population size, below which the population does not establish (Fig. 3C). This has been demonstrated by a number of theoretical models developed in the context of invasion biology and extensively reviewed in Taylor and Hastings (2005). In the context of biological control, the pioneer model developed by Hopper and Roush (1993) analyzed the consequences of a component (mate finding) Allee effect on the establishment success. In their model, changes in male and female densities were determined by a system of partial differential equations as a result of diffusion, births and deaths, and sex allocation. The probability that a female mated depended on male density and the ability of males to find females (mate detection distance). Hopper and Roush (1993) demonstrated that failure to find mates at low density results in a critical propagule size under which a population does not establish. The critical size decreased with increased mate detection distance and population net reproductive rate, and increased with distance dispersed from a release point. Hence, with an Allee effect, the establishment success of introduced populations depends on the combination of propagule size and species-specific life history or behavioral traits that underpins the Allee effect. Hopper and Roush (1993) also demonstrate that an Allee effect can produce a lag period during which introduced populations grow and spread very little and may therefore remain undetectable. Because such lags are often attributed to evolutionary processes (Facon et al. 2006), this modeling result is important.

Grevstad (1999b) also modeled a mate-finding component Allee effect in the context of biological control, using

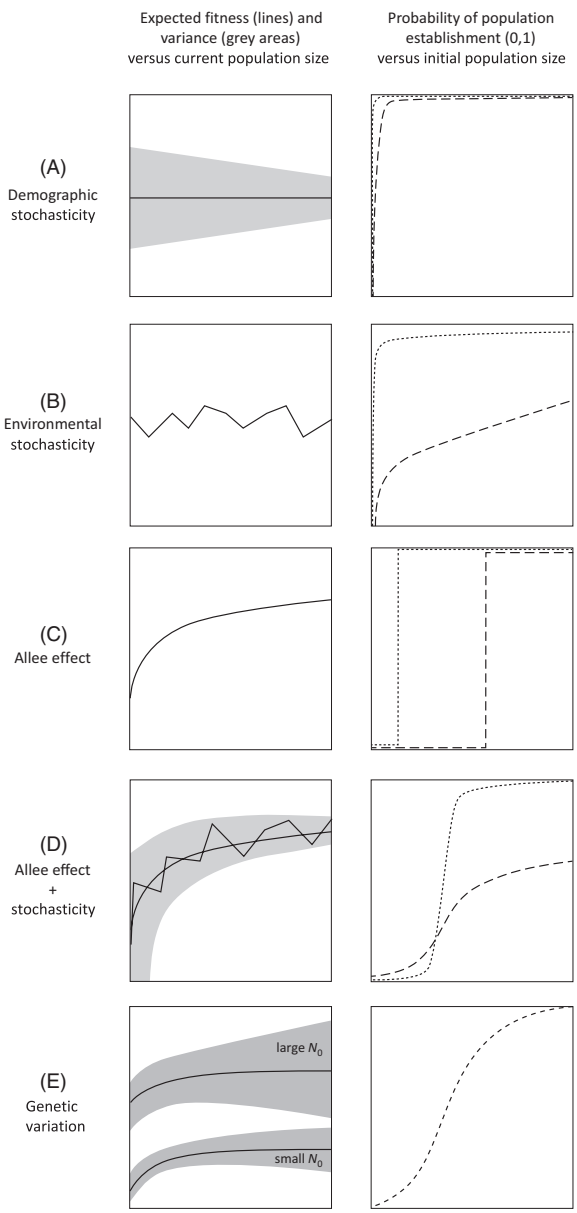

Figure 3 General overview of theoretical predictions resulting from stochasticity, Allee effect, and genetics processes in small, introduced populations. Left panels: individual fitness versus current population size (census or density) a few generations after introduction, during the establishment stage. The gray surface represents variance in fitness. Right panels: Establishment probability versus initial population size (number of founders). Different lines represent differences in the strength of each process. (A, B) Environmental and demographic stochasticity. The small dash illustrates low stochasticity and the long dash illustrates high stochasticity. (C) Allee effect. The small dash shows the Allee threshold at small population size and the long dash shows it at larger population size. (D) Allee effect and stochasticity. The short dash shows demographic stochasticity only. The long dash shows demographic and environmental stochasticity. (E) Hypothesized influence of genetic variation under a scenario with inbreeding depression and no purging of genetic load.

computer simulations to combine the Allee effect with stochasticity (Grevstad 1999b). In her model, the Allee effect produced a positive relationship between establishment probability and initial population size (Fig. 3D). In agreement with Hopper and Roush (1993), the strength of the relationship depended on the magnitude of the mate-finding Allee effect (Grevstad 1999b). These findings have been echoed with models developed in contexts other than biological control (Berec et al. 2001; Drake and Lodge 2006) and now form a cornerstone of theory regarding small populations.

Evidence

Despite the theoretical underpinnings, strong evidence that Allee effects operate in introduced populations is remarkably scarce (Table 1). Although not in the context of biological control, experimental introductions of the planthopper *Delphacodes scolochloa* on prairie potholes reveal a demographic Allee effect and a subsequent higher establishment rate at larger propagule size (Cronin 2009). In the context of biological control, experimental introductions of chrysomelid beetles in North America for the control of the purple loosestrife provide the only striking result (Grevstad 1999a). In the two species released, growth rate increased with increasing initial population size. A putative cause of low growth rate in small founding populations was the difficulty of males and females to find one another (Grevstad 1998, 1999a). In contrast, experimental introductions of psyllid herbivores in New Zealand and of parasitoid wasps in France provided no evidence of Allee effects (Memmott et al. 2005; Fauvergue et al. 2007).

Weak evidence for Allee effects in biological control introductions comes from meta-analyses of establishment success (Table 1). In their meta-analysis of parasitoid introductions, Hopper and Roush (1993) found that the number of individuals per release (propagule size) was the most significant for Ichneumonoidea and Tachinidae, and the total number released (propagule pressure) best explained the establishment for Chalcidoidea. They concluded that Allee effect was the most important process explaining the success of introduced parasitoids. Similar results have been obtained with different data sets (Beirne 1975). Such meta-analyses are of considerable value given the large number of species they include, and the patterns they reveal. However, their conclusions are inevitably weakened by the fact that confounding variables are not controlled. For instance, as noted above, distinguishing between Allee effects and demographic stochasticity is difficult with such data, as both can give rise to the same pattern (Fig. 3). Similarly, the number of parasitoids introduced may be correlated with the number collected in the area of origin (Fig. 2 of Hopper and Roush 1993), so that genetic variation is

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substantially higher for large releases than for small and that could also lead to the observed patterns. Indeed, two experiments specifically designed to test Hopper and Roush's (1993) hypothesis show an absence of mate-finding and demographic Allee effects (Fauvergue et al. 2007; Fauvergue and Hopper 2009).

Genetics

Theory

Much theoretical work on the genetics of small introduced populations focuses on founder-effect speciation and includes the classic works of Mayr (1942) and Carson (1968). While there is no model formally predicting the establishment probability of small, introduced populations as a function of genetic parameters, there are models regarding how bottlenecks in population size influence genetic diversity (Nei et al. 1975; Allendorf 1986). Furthermore, empirical studies demonstrate that founding groups with greater genetic variation are more successful than those with less variation (Newman and Pilson 1997; Kephart 2004; Vergeer et al. 2005). Thus, the level of genetic variation harbored by small, introduced populations is of key importance in understanding how these populations function (Fig. 3E).

The main mechanism determining the levels of variation in small and/or bottlenecked populations (be they introduced or not) is genetic drift. Genetic drift refers to stochastic changes in allele frequencies, which can ultimately lead to loss or fixation of alleles (Fig. 4; Wright 1969). Nei et al. (1975) modeled how bottlenecks in population size intensify genetic drift and in turn affect genetic variation in introduced populations. They reveal that allelic diversity and heterozygosity respond differently. Allelic diversity is sensitive to bottlenecks, as rare alleles can be easily lost as population size declines (Allendorf 1986). In contrast, heterozygosity is more robust, particularly when population growth after a bottleneck is rapid. For example, Nei et al. (1975) modeled a bottleneck in population size of 10 individuals in a population with an initial heterozygosity of approximately 14%. Homozygosity increased because of genetic drift, but when the subsequent growth rate was high ($r = 1$), the populations retained a heterozygosity of approximately 13% (Nei et al. 1975). In contrast, the number of alleles per locus was decreased to less than 1/3 of the pre-bottleneck allelic diversity when simulated under similar conditions (Table 2 of Nei et al. 1975). For both heterozygosity and allelic diversity, the return to prebottleneck levels of variation via mutation takes many generations (see, e.g. Fig. 1 from Nei et al. 1975).

Another important process that reduces genetic variation in small populations is inbreeding (Charlesworth and Willis 2009). As population size declines, mates can become limiting, and the chance of mating between relatives (i.e. inbreeding) increases. This process is sometimes referred to as panmictic inbreeding. With panmictic inbreeding, consanguineous crosses occur, even if mating is random, as a direct consequence of increased relatedness in small populations. Panmictic inbreeding contrasts with systematic inbreeding, where consanguineous matings occur independently of population size (Malécot 1969; Glémin 2003). Inbreeding, like drift, also increases the homozygosity rate across the genome. However, inbreeding reduces homozygosity quicker and more drastically than does genetic drift.

Owing to both genetic drift and inbreeding, small, introduced populations will tend to have low genetic diversity (Fig. 3E). This has at least two main consequences. First, because the rate of response to selection is proportional to genetic variation in fitness (i.e. Fisher's fundamental theorem; Fisher 1930), introduced populations with low diversity will be less able to adapt to their new environment (Fig. 4A,B,E,F). Hence, lower fitness is expected in small, introduced populations (Fig. 3E). Second, when deleterious recessive alleles are brought together in a homozygous state by either drift or inbreeding, they are expressed and thus exposed to natural selection (Fig. 4A–C). This diminishes fitness in individuals that are homozygous for deleterious recessive alleles, as well as the mean fitness of the population (Fig. 3E). When owing to consanguineous mating, this process is referred to as inbreeding depression (defined as the reduced fitness of offspring as a result of breeding of related individuals). Not all inbreeding leads to inbreeding depression; it does so only if deleterious recessive mutations are exposed to selection in the homozygous state (Fig. 4).

One way of understanding inbreeding depression is through the concept of genetic load. Genetic load is the reduction in a population's mean fitness when compared with the mean fitness that would be found in a theoretical population that has not accumulated deleterious alleles. Thus, the higher the genetic load in the source populations, the stronger the expected inbreeding depression in the introduced population (Fig. 4A–D *versus* E–G).

In contrast, increased homozygosity can have unexpected positive effects when the recessive deleterious alleles that are exposed to selection are purged (e.g. individuals harboring them either die or do not successfully reproduce; Fig. 4B–D). This is called 'purging of genetic load', and it increases the mean fitness of the population. Purging is particularly likely for alleles that are strongly deleterious (Fig. 4B–D), while those with small effects are more likely to accumulate in a population and decrease its average fitness (Higgins and Lynch 2001; Glémin 2003). Whether or not deleterious alleles will be purged also depends upon population size, and the degree of inbreeding. If inbreeding is common, theory shows that less-strongly deleterious alleles also can be purged (Fig. 4B,D; Glémin 2003).

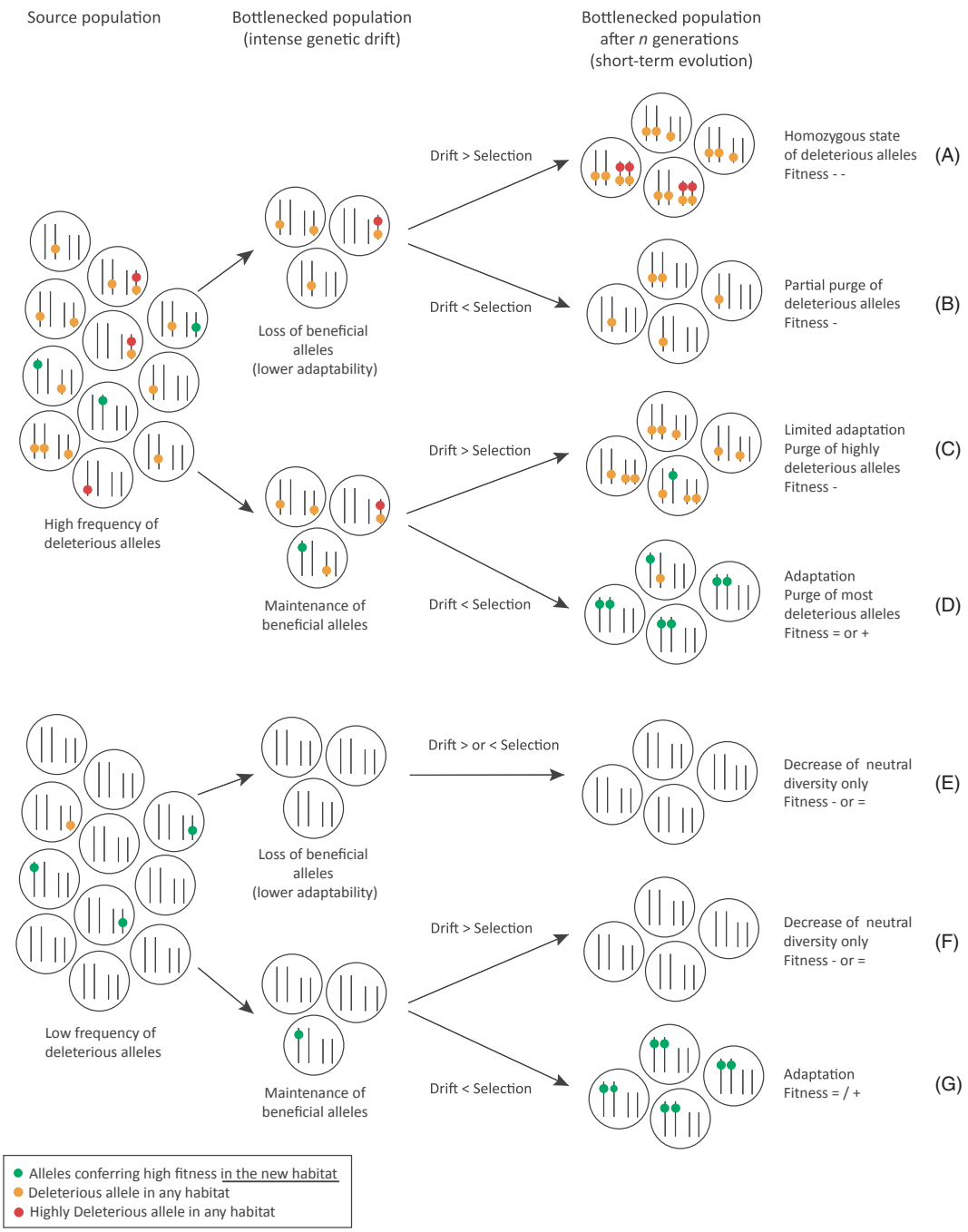

Figure 4 A synopsis of major evolutionary processes at play in small, introduced populations. Genetic modifications occur under the effects of inbreeding, drift, and selection. An individual is represented by a circle and is composed of two pairs of homologous chromosomes carrying three types of alleles (highly deleterious alleles in red, moderately deleterious alleles in yellow, alleles conferring high fitness in the new habitat in green) among a set of neutral alleles not represented but present all along the chromosome. For practical reasons, populations are represented with only a few individuals but the considered ranges of sizes are >1000 for the source populations, and between 10 and 100 for the introduced ones. Only a selection of possible situations among the expected gradient of impact on fitness are shown.

The model of Perez-Figueroa et al. (2009) shows that even highly bottlenecked populations of ten individuals can respond to selection with a purging of load. The evolution of the genetic load is also environment-dependent, as alleles that are deleterious in one environment can be beneficial in another (Cheptou and Donohue 2011).

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Introduction into a novel environment typically exposes a founding population to new selective pressures. The introduced populations may be able to respond to these selective pressures if their diversity is not depleted in alleles conferring reasonably high fitness in the new environment (Fig. 4C,D,G). If natural selection is strong enough relative to genetic drift, the frequencies of beneficial alleles can increase during the establishment process, leading to adaptation (Fig. 4D,G).

The extent to which genetic drift, inbreeding, and selection combine to either decrease or increase mean fitness of small populations, can also be influenced by other processes. Notably, gene flow (or a lack thereof) can result in different outcomes depending upon the context (Slatkin 1987). Recent theoretical work performed in the context of conservation biology, in which the modeled systems consist of small partially isolated populations (rather than newly founded ones), shows that highly isolated populations can adapt to their local environment when population sizes are relatively high (hundreds of individuals) but suffer from inbreeding depression when population size is low (tens of individuals; Lopez et al. 2009). When gene flow does occur, it can either positively or negatively impact the population mean fitness. Increases in fitness occur when the input of new genetic variation buffers the effects of genetic drift, but decreases occur when it disrupts adaptation to local conditions (Alleaume-Benharira et al. 2006; Lopez et al. 2009).

Overall, small, introduced populations are likely to harbor less genetic variation than in their region of origin. However, given the complex interactions among genetic processes and the large range of possible situations (Fig. 4), simple and general predictions regarding the consequences of reduced variation are difficult to make. It may nonetheless be feasible to identify some common trends (i) among taxa frequently used in biological control and sharing common genetic features and (ii) among biological control situations sharing common methods (rearing techniques, number of released individuals, repeated releases, etc.).

Evidence

Evolution at neutral loci or at characters presumably under strong genetic control has been repeatedly observed in biological control agents (reviewed in Hopper and Roush 1993; Roderick and Navajas 2003; Hufbauer and Roderick 2005). However, the underlying processes (genetic drift, inbreeding, natural selection, gene flow) are generally unknown, as are their consequences for fitness.

One first observation from the available data is that the loss of genetic diversity after bottlenecks is detectable but rarely drastic. There is evidence that allelic diversity is typically decreased in the introduced ranges of biological control agents, relative to their native ranges, even when propagule size was large (Baker et al. 2003; Hufbauer et al. 2004; Lloyd et al. 2005; Franks et al. 2011). As predicted by theory, heterozygosity is less sensitive (Allendorf 1986). In each of the four cases cited, heterozygosity did not differ significantly between the native and introduced ranges. Moreover, even after an extreme bottleneck, some heterozygosity can be retained (Nei et al. 1975). For instance, the laboratory colony of a mirid bug, which was to be released on water hyacinth in South Africa, experienced a bottleneck that reduced it to a single gravid female. Individuals from the colony that grew from that single female were released in 1996 and subsequently reproduced rapidly and spread (Taylor et al. 2011). Naturalized populations harbor variation in neutral loci (though comparisons with native range populations are not available; Taylor et al. 2011). Hence, even in the face of strong bottlenecks, the loss of genetic diversity may not be severe enough to cause severe fitness decrease in populations of biological control agents.

There may be cases where quarantined populations of natural enemies went extinct or performed poorly after release because of negative consequences of reduced genetic variation, but unfortunately, there is little documentation of such events and essentially none where genetics are known to be the cause of the decline. We nonetheless can report on two examples where drift and/or inbreeding depression appear likely to have reduced performance of biological control agents following introductions. In a comparative approach studying parasitoids in their native and introduced ranges, Hufbauer (2002) discovered that introduced parasitoids were less able to overcome aphid resistance mechanisms, suggesting at least some detrimental processes associated with introduction. Interestingly, the agent is nonetheless considered to be successful. The only experimental approach suggesting the occurrence of a genetic process affecting negatively the establishment of populations comes from an experiment initially designed to study Allee effects in the aphid parasitoid *Aphelinus asychis* during its introduction in the USA (Fauvergue and Hopper 2009). Mate-finding probability was unaffected by population density, suggesting the absence of mate-finding Allee effect, and population growth rate increased with decreasing density, suggesting negative density-dependence. However, for a given density, growth rate was lower in populations that were initially smaller (as shown in Fig. 3E), and this effect persisted over three generations after introduction, suggesting that genetic processes could have played a role (Fauvergue and Hopper 2009).

Evidence of a positive effect of small population size in biological control, via purging of genetic load, has been recently provided by experiments on the ladybird *Harmonia axyridis*. This ladybird beetle was released into North America multiple times before successful establishment and population growth. After populations in eastern North

America exploded, they proceeded to invade literally around the world (Lombaert et al. 2010). In this system, native populations express strong inbreeding depression while introduced populations do not (Facon et al. 2011). It appears likely that deleterious alleles associated with inbreeding depression were purged during repeated bottlenecks associated with biological control introductions (combined with independent invasion events).

Evidence for a simple response to natural selection in populations of biological control agents is even scarcer. Hopper et al. (1993) summarized the evidence for changes in phenotypic traits that appear likely to be adaptive in the release habitats (expansion of host ranges, changes in temperature threshold for adult emergence, etc.). However, the studies cited in Hopper et al. (1993) remain quite speculative. More convincing evidence comes from the parasitoids released for control of weevils in New Zealand (Phillips et al. 2008). The parasitoid, *Microctonus hyperodae*, reproduces via apomictic parthenogenesis, and no males have ever been observed either in its native South American range or in New Zealand. One hundred and forty-one parthenogenetic lines were introduced. They varied in morphological and molecular traits (proteins) and could be grouped into two distinct biotypes. The change in biotype frequency was tracked over 10 years and was consistent with a response to directional selection toward the biotype that appeared to be better suited to the environment (Phillips et al. 2008). Two more recent studies also demonstrate strong evidence for local adaptation in two biological control agent of plants in the NW of North America (McEvoy et al. in press, M. Scűcs, U. Schaffner, W. J. Price, and M. Schwarzländer, unpublished data), both of which have adapted to a shift in climate.

Combined processes

Stochasticity and Allee effects

Interactions between stochasticity and Allee effects have been investigated with different modeling approaches. A common finding is that the combination of these two processes results in a continuous transition between extinction and establishment as inoculum size increases (Fig. 3D; Grevstad 1999b; Dennis 2002; Liebhold and Bascompte 2003). In the presence of stochasticity, the Allee threshold becomes an inflexion point in the probability of escaping extinction: Adding or removing a few individuals around this point will disproportionately enhance or reduce this probability (Dennis 2002). Moreover, as stochasticity increases, especially environmental stochasticity, establishment probability is lowered over the whole range of initial population size, and the relationship between population size and establishment probability becomes smoother, so that variation around the Allee threshold has less critical consequences for population dynamics (Fig. 3D; Grevstad 1999b).

Another interesting conclusion from these models is that stochasticity has opposite effects on the probability of extinction depending upon whether the population is below or above the Allee threshold. When below the threshold, without stochasticity, extinction will always occur. However, stochastic effects can increase population growth rate by chance so that the population can escape from the demographic zone where extinction is most likely. Inversely, for a population above the Allee threshold, stochastic effects can decrease population size down to a level where it is highly vulnerable to Allee effects (Grevstad 1999b; Liebhold and Bascompte 2003). An important consequence of the latter effect is that even in cases where populations establish successfully from very few individuals, Allee effects cannot be ruled out entirely (Cameron et al. 1993; Stiling 1993). Alternatively, when an Allee effect is known to occur, it is advisable to release substantially more individuals than the Allee threshold, in anticipation of possible stochastic population reductions.

Population models have been used explicitly in the context of biological control to predict the optimum strategy, that is, the combination of number of releases and number of individuals per release that maximizes the total number of established populations (Grevstad 1999b; see also Freckleton 2000; Shea and Possingham 2000). In the presence of environmental stochasticity only, releasing a small number of individuals in many different locations is the most efficient strategy. When Allee effects are present, however, the optimal release strategy depends on population parameters and the level of environmental variability. If establishment probability strongly depends on propagule size (i.e. if Allee effects are drastic) and environmental variance is low, a few large releases maximizes the establishment rate (Shea and Possingham 2000). Alternatively, if Allee effects are moderate but environmental variability is high, an intermediate number of smaller releases will be optimal (Grevstad 1999b). At present, as the detection of Allee effects in biological control agents still is in its early development, such theoretical guidelines for optimizing field introductions have not been tested empirically.

Stochasticity and genetics

In most populations, individuals differ, notably because of genetic differences, so that their expected demographic parameters are not the same. Ignoring this source of heterogeneity between individuals typically results in over-estimation of demographic stochasticity in population dynamics (Fox and Kendall 2002). On the other hand, inter-individual variance in reproductive success, i.e., demographic stochasticity, reduces the effective population

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size, which enhances the process of random genetic drift (Kokko and Ebenhard 1996; Hartl and Clark 2007), and in addition genetic drift and selection shift genotype frequencies between generations. If different genotypes are characterized by different demographic parameters, such changes will result in temporal fluctuations in average demographic parameters, which would resemble environmental stochasticity. Thus, a significant part of demographic or environmental stochasticity is tightly linked with genetic heterogeneity between individuals and vice versa, and disentangling the relative influence of each process can be difficult.

An interesting example of this is found in the analyses of experimental populations of the egg parasitoid *Trichogramma chilonis*, a biological control agent of the sugarcane stem borer *Chilo saccariphagus*. In these populations, demographic stochasticity and extinction risk differ by geographic strain (E. Vercken, F. Vincent, L. Mailleret, N. Ris, E. Tabone and X. Fauvergue, unpublished data). These differences are not attributed to different levels of genetic diversity within strains but rather to true (genetic) variation in demographic stochasticity. Hence, demographic and genetic components of propagule pressure may interact in how they influence the dynamics of these introduced populations. Furthermore, at its core, demographic stochasticity is inextricably linked with genetics, because in sexual organisms, a fundamental component of what is traditionally considered demographic stochasticity, variation in sex ratio, is in fact attributed to a clear genetic trait: sex.

Allee effect and genetics

Research on Allee effects and genetics intersects in two distinct manners. The first point of intersection is with regard to how they are studied. Similarly to component Allee effects, some genetic processes can generate positive density-dependence and for this reason have been referred to as 'genetic Allee effects' (Fischer and Lindenmayer 2000; Berec et al. 2007; Courchamp et al. 2008). The second point of intersection is attributed to a true interaction between Allee effects and genetics, as Allee effects themselves are underpinned by traits that can evolve (Kanarek and Webb 2010). A reduction in fitness at low population size represents strong selection for less sensitivity to population size.

The concept of a genetic Allee effect is referred to anecdotally in the literature and has not been formalized. However, as it unites ideas from genetics and demography, it may have heuristic value. As described in the genetics section, decreased population size erodes genetic diversity (Ellstrand and Elam 1993; Frankham 1995a,b), which may in turn result reduce fitness (Reed 2005). A genetic Allee effect is defined by Courchamp et al. (2008) as a decrease in components of fitness with the decreased genetic diversity that accompanies decreased population size. Genetic Allee effects may be relevant in small, introduced populations because the effective population size is expected to be depressed for longer than the census size or density (Fig. 1). Hence, introductions should reveal genetic Allee effects more than ecological Allee effects.

The second way in which Allee effects intersect with genetics concerns the evolution of traits that underpin component Allee effects (Courchamp et al. 2008; Kanarek and Webb 2010). There are two major evolutionary routes for species faced with Allee effects. One is to evolve spatial aggregations so that local population size or densities are maintained high enough to avoid substantial decreases in fitness. The selfish herd theory for animal aggregations, as well as cooperative breeding and sociality, may therefore be envisaged as evolutionary products of the Allee effect (Stephens and Sutherland 1999). The Allee effect may still be there; it is just avoided by an increase in group size. The second potential route is the evolution of traits underlying component Allee effects. As examples, (i) mates may evolve mate-finding mechanisms such as long-range sex pheromones and movement so efficient that mating success becomes almost insensitive to population density (Hissmann 1990; Kindvall et al. 1998; Fauvergue et al. 2008); (ii) plants may alternate selfing and outcrossing according to mate availability (Cheptou 2004); (iii) haplodiploid organisms may produce precise offspring sex ratios to ensure that their progeny will be mated whatever the abundance of conspecifics or the variations in population sex ratio (Verner 1965; Taylor and Sauer 1980; Hardy 1992). Although these examples are congruent with the hypothesis that traits underlying component Allee effect are subject to adaptive evolution, they are not strong evidence.

For hymenopteran parasitoids, single-locus complementary sex determination (sl-CSD) opens an avenue of research that could combine both genetic Allee effects and the evolution of mechanisms underlying them. Similarly to S-alleles in plants, this mode of sex determination yields unfit homozygous individuals (unviable or sterile diploid males, Cook 1993; Cook and Crozier 1995; Heimpel and de Boer 2008). Sl-CSD may therefore be considered to be a component genetic Allee effect, with the consequence that low propagule size may prevent the success of some biological control introductions (Stouthamer et al. 1992; Zayed and Packer 2005; Hedrick et al. 2006). In these systems, the evolution of particular genomic properties (high mutation rates at loci involved in sex determination), mate recognition, and dispersal abilities (Ode et al. 1995; Metzger et al. 2010; Ruf et al. 2011) are convincing illustrations of how natural selection could shape the Allee effect.

Processes specific to biological control agents

Although biological control introductions can be used as a powerful tool to investigate the general processes affecting the biology of small populations, they display several unique characteristics that may affect their outcome. At first glance, it is difficult to find intrinsic characteristics specific to the types of organisms used as biological control agents as they consist of a vast range of phytophagous, predator, parasitoid, and pathogenic organisms and cover most of the possible genetic architecture and positions in the trophic chains. However, in terms of proportions, biological control agents probably consist of a large majority of organisms at high trophic levels (predators of phytophagous insects and parasitoids), when compared to either species in general or to common invaders (DAISIE database: http://www.europe-aliens.org/index.jsp). Another bias specific to biological control is how specialized modern biological control agents tend to be. For example, parasitoids rely on insect hosts to complete their development, and many phytophagous insects are also highly specialized and live intimately with their hosts. Thus, co-evolutionary processes may be particularly important in the context of biological control (Holt and Hochberg 1997; Jervis 1997).

The importance of hymenopteran parasitoids in biological control also distinguishes biological control organisms from others because they are sexual haplodiploid organisms, an otherwise relatively infrequent mode of reproduction. Deleterious alleles are expressed in haploid males whatever the population size, and thus, their frequency should be reduced relative to diploid organisms. Hence, haplodiploid species are expected to have a much lower genetic load than diploids (Bruckner 1978; Henter 2003), a feature that may improve their success at low population size. Another common property of hymenopteran parasitoids is their tight association with endosymbionts, such as the well-known *Wolbachia*. The occurrence of endosymbiont infections substantially complicates predictions for small populations. Indeed, a large body of literature has shown that they can cause reproductive isolation within and among populations and can manipulate a number of individual traits (sex ratio, behavior, overall fitness, etc.) in a wide variety of ways (e.g. see reviews in Haine 2008; and Engelstaedter and Hurst 2009) and examples in biocontrol agents in (Huigens, 2004 or Vasquez et al. 2011). In some ways, endosymbionts can be viewed as genetic characters in the population, but with a somewhat unpredictable heritability (Moran et al. 2008). This unpredictability is also likely to generate variance in individual fitness and population demographic parameters, hence generating demographic stochasticity in the population dynamics.

Biological control agents are most frequently introduced in agricultural landscapes. Agro-ecosystems are often simplified ecosystems, with few native species and a low complexity of trophic networks, which makes them highly susceptible to invasion by exotic pests or pathogens (Shea and Chesson 2002; Perrings 2011). As such, agro-ecosystems should also be susceptible to invasion by biological control agents, that is, establishment success should be higher in such environments where the low number of resident species leaves wide niche opportunities for potential invaders (Shea and Chesson 2002). However, more specific analyses of landscape ecology in agricultural systems reveal that higher trophic levels, especially predators and parasitoids, are especially sensitive to habitat fragmentation and connectivity (Kruess and Tscharntke 1994, 2000; Hunter 2002). Indeed, to maintain a viable population of predators or parasitoids, the population of preys must be sufficiently large. In fragmented habitats, populations of higher trophic levels have limited carrying capacity, and thus remain vulnerable to extinction in the long term (Kruess and Tscharntke 1994, 2000). Therefore, although agro-ecosystems are favorable to invasion by pests, they may be resistant to some extent to the long-term persistence of biological control agents. This highlights three points that are rarely discussed in biological control: (i) contrary to what is expected for most biological invasions by phytophagous pests, the primary establishment step of biological control agents may not be the main determinant of long-term persistence; (ii) if they frequently go extinct after initial establishment (which should be the case as management practices aim at maintaining the 'prey' populations at the lowest possible level), then such biological control agent populations are probably evolving in metapopulation systems with high extinction probability in each fragmented populations; (iii) while often viewed entirely separately, classical and conservation biological control may actually share a lot of common features, and classical biological control may greatly benefit from landscape management designed for conservation biological control.

Discussion and conclusions

Propagule pressure and establishment: a step ahead

We have reviewed the variety of processes that can occur in small, introduced populations: demographic stochasticity, environmental stochasticity, Allee effects, genetic drift, inbreeding, selection, and adaptation. Each process can, with few exceptions, generate a positive relationship between initial population size and establishment probability (Fig. 2). Thus, the widespread observation that small, introduced populations are prone to extinction proves nothing about which of the underlying processes might be acting and thus should be interpreted with caution.

At present, evidence for the positive effect of propagule pressure on establishment appears strong (Hopper and

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Roush 1993; Lockwood et al. 2005; Simberloff 2009). Meta-analyses have played a major role in the development of hypotheses for key mechanisms affecting introduced populations. The field would be moved further, however, if future analyses of historical data tested specific hypotheses concerning the processes, as at this point, additional evidence for a positive effect of propagule pressure on establishment would be somewhat redundant. For instance, assessing the relative contribution of different components of propagule pressure to discriminate among demographic and genetic processes should provide novel insights into the biology of small, introduced populations (see, for example, Grevstad et al. in press). Biocat, a database gathering biological control introductions of insect parasitoids and predators (Greathead and Greathead 1992), is under revision by the International Organization of Biological Control (IOBC) and should soon be available to implement such novel approaches (J. Brodeur, personal communication). Biological control of weeds may also provide interesting historical data, all the more as these data are still underused. In addition, because our general claim is that basic processes acting in bottlenecked populations are not specific to biological control agents, we advocate that meta-analyses merging historical data on biological control introductions and reintroductions for biological conservation could provide the significant progress beyond the state of art.

Theory: toward a combination of genetics and demography

From a theoretical perspective, our review reveals a clear divide between demographic and genetic approaches to understanding the consequences of small population sizes and the founding of new populations. On the demographic side, the focus has been on factors influencing establishment. Over the last 15 years, models investigating the consequences of Allee effects and stochasticity for the establishment of introduced populations have flourished. Some have approached invasion processes generally (see Taylor and Hastings 2005 for a review) while others have focused specifically on biological control introductions (Hopper and Roush 1993; Grevstad 1999b; Shea and Possingham 2000) or the management of invading organisms (Liebhold and Bascompte 2003; Tobin et al. 2011; Blackwood et al. 2012). These models generally focus on a few parameters that can be manipulated and/or measured such as population size, dispersal, mate finding, and sex ratio. Hence, hypotheses and predictions regarding establishment success can be tested experimentally.

In contrast, on the genetic side, the focus has been on how bottlenecks and founding events influence genetic and evolutionary processes. Models of genetic processes in small populations (Nei et al. 1975; Allendorf 1986; Estoup and Guillemaud 2010) and of speciation (e.g., Mayr 1942; Carson 1968) have analyzed the consequences of introductions for subsequent evolutionary trajectories. Predictions from these models also can be tested experimentally, but with a focus on genetic consequences (effects on heterozygosity, allelic diversity, inbreeding) and subsequent performance and adaptability of populations rather than on establishment success.

This divide between disciplines is fairly natural, as each discipline has focused on the areas intuition would suggest are important in the separate domains. However, there is much to be gained from ecologists focused on demography and evolutionary biologists focused on genetic processes incorporating each other's perspectives and insights, particularly as we realize more and more the importance of eco-evolutionary dynamics (Fussmann et al. 2007; Ellner et al. 2011; Morris 2011; Schoener 2011; Turcotte et al. 2011).

Two nascent research avenues might lead to a further unification of research on genetic and demographic processes acting in small, introduced populations. The first is the concept of the genetic Allee effect, which links demographic population size, effective population size (genetic variability), fitness, population growth, and persistence. This concept might not appear as a theoretical revolution from the perspective of population dynamics or of population genetics, with both fields potentially posing the question: Why add a new semantic layer to already well-defined phenomena? However, considering genetic Allee effects may provide a way to formalize the links between demographic and genetic processes that co-occur in small populations and to open a dialog between population genetics and population dynamics. As such, we think that it may provide a useful perspective.

The second novel avenue for research is brought by the emergent concept of evolutionary rescue, which is being developed precisely to analyze how evolution and demography interplay in populations experiencing a novel environment. For this, models have 'coupled population dynamics and evolution by natural selection to identify conditions for which evolution succeed – or fails – to rescue a closed population from extinction following abrupt environmental change' (Gomulkiewicz and Holt 1995). One type of environmental change under scrutiny is the foundation of a new population into a novel environment, the persistence of which is envisaged as a race between demographic and evolutionary process (Gomulkiewicz and Holt 1995). Such models make explicit assumptions about initial population size, threshold population size (below which the population is at high extinction risk) population growth, and fitness changes across time as a result of the initial change in environment, mutation rates, and subsequent selection. Evolutionary rescue models do capture the

essential eco-evolutionary processes that might occur in biological control introductions. Their theoretical predictions are now being tested with simple organisms such as yeasts in laboratory environments (e.g. Bell and Gonzalez 2009, 2011). Nonetheless, evolutionary rescue models could also serve as an invaluable theoretical frame to analyze combined effects of evolutionary genetics and demography on the persistence of introduced natural enemies.

Escaping from closed populations – escaping from extinction?

Classically, the establishment of introduced populations has been considered as a local, spatially isolated process. Indeed, the definition of establishment requires that the introduced population sustain itself through local reproduction and recruitment without additional reinforcements (Lockwood et al. 2005), and even if migration has sometimes been assumed (Drake and Lodge 2006), all published models on population introduction consider isolated populations (Hopper and Roush 1993; Grevstad 1999b; Shea and Possingham 2000). However, in nature, populations are introduced within an ecological landscape, where spatial processes at an intermediate scale (i.e. within the range of individual dispersal distance, yet beyond the local population) may play a determining role in both establishment success and long-term persistence.

Indeed, the connectivity of local populations has several major consequences for establishment. First, local extinctions or quasi-extinctions can be compensated by the recolonization by propagules from other local populations (rescue effect; Brown and Kodric-Brown 1977), which enhances persistence at the metapopulation scale. In addition, if local populations are heterogeneous in quality or size, the largest or most productive populations can reinforce smaller populations, so that they may, for instance, pass over an Allee threshold (source-sink dynamics; Pulliam 1988). Finally, frequent gene flow between local populations should reduce the negative effects of drift and inbreeding, while the risk of constraining local adaptations might remain minimal within this intermediate spatial scale (see section on genetic processes). Interesting predictions about the influence of the size and number of introduction events and the connectivity between introduction sites could be derived from a well-developed theoretical framework of the optimization of the design of nature reserves from conservation biology (single large or several small, the SLOSS problem; Ovaskainen 2002; McCarthy et al. 2005).

The integration of genetic rescue, via gene flow, in the framework of metapopulation systems appears as a particularly exciting avenue for research. Metapopulation models can describe introductions of biological control agents well if we consider source, laboratory-reared, and released populations as three major components of a large and heterogeneous metapopulation system. Adapting metapopulation models could be made (i) by implementing contrasted regimes of gene flow between populations, (ii) by modeling contrasted selection pressures and population sizes depending on the type of population, and (iii) above all, by focusing on the persistence of the released populations instead of the overall success of the metapopulation. Such models would probably be suitable to investigate the most favorable situations in terms of gene flow (number of sampled and introduced individuals, frequency of introductions) between the three components of the metapopulation. A priority should be made of investigating such predictions through experimental approaches, to inspire innovative strategies for classical biological introductions.

A small but growing body of experimental data

Generally, our review reveals disequilibrium between theory and data, with remarkably few empirical results available to test theoretical predictions rigorously. A clear trend toward the development of well-designed manipulative field experiments is nonetheless extremely promising. The work of Grevstad (1999a) pioneered the use of biological control as a method for studying the biology of introduced species. She demonstrated how biological control introductions could be manipulated and replicated, allowing hypothesis testing based on robust inference statistics. Other studies have since been published, using insect herbivores or parasitoids as model organisms (Memmott et al. 2005; Fauvergue et al. 2007; Fauvergue and Hopper 2009). Such experiments are nevertheless risky. For instance, a recent attempt was made to test the effect of intra-specific hybridization on establishment success, using introductions of the parasitoid *Psyttalia lounsburyi* in France for the biological control of the Olive fruit fly (Malausa et al. 2010a,b; Cheyppe-Buchmann et al. 2011). Sixty releases were made across the whole South East of the country, and intensive sampling was carried out during four successive years. However, the parasitoid failed to establish in the end, and thus, the hypothesis could not be tested. Faced with the methodological challenge of organizing large-scale field experiment, the use of mesocosms may appear as an elegant alternative (Begon et al. 1996; Sait et al. 2000; Bjornstad et al. 2001; Hochberg and Weis 2001).

Despite the fact that stochasticity, demography, and genetics are highly interacting in small populations, attempts to address their effects in combination are almost inexistent. Interestingly, empirical studies that have focused on one type of process eventually suggested the occurrence of others (e.g. Fauvergue and Hopper 2009 for the interaction of Allee effects and genetics; E. Vercken, F. Vincent, L.

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Mailleret, N. Ris, E. Tabone and X. Fauvergue, unpublished data, for the interaction of demographic stochasticity and genetics). This suggests that experimental work investigating the processes at play in small introduced populations should not be restricted to a single type of process and should systematically control or monitor at least a few indices revealing the occurrence of other types. A perfect type of experiment would take the advantage of factorial designs to manipulate demographic and genetic conditions independently and in interaction (e.g. demographic populations size × genetic variability). Such kind of experiment would unravel the relative importance of the different processes for the dynamics on introduced populations. Our review also calls for the analyses of mean fitness mean and genetic variance in fitness, in addition to population growth and establishment/extinction (Fig. 2), as the only possible way to discriminate among the different processes occurring in small populations.

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