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EDITORIAL

Evolution and biological control

Opinions about the value of biological control are often extreme. Colloquially, biological control most often refers to *classical biological control*, in which one species is introduced from another region to control pests such as arthropod herbivores in agricultural systems, or weeds in managed and natural systems.[1] As such, biological control has the potential to be a low-cost, chemical free, means to control pests. Numerous biological control programs have been unqualified successes (Bellows 2001), such as the control of cacti in Australia with the moth *Cactoblastis cactorum* (Raghu and Walton 2007), of cottony-cushion scale (*Icerya purchasi*) in California with the vedalia lady beetle, *Rodolia cardinalis* (Caltagirone and Doutt 1989), and of glassy-winged sharpshooters in French Polynesia with the egg parasitoid *Gonatocerus ashmeadi* (Grandgirard et al. 2009). Yet, classical biological control, as with any introduction of a species into a new area, necessarily involves the unknown and therefore carries some inherent risk (Simberloff and Stiling 1996) – what will these organisms actually *do* in a novel ecosystem?

The most unpredictable element in biological control is the extent to which the realized niche is modified in the new environment. This effect has been responsible for some disastrous outcomes of classical biological control, many of which occurred during an era when vertebrates were being introduced around the world by Europeans for a variety of reasons (e.g., introducing the birds of Shakespeare to America, Mirsky 2008), including for biological control (Howarth 1991). The introductions as biological control agents of cane toad to Australia (Crossland et al. 2008) and mongoose to Hawaii (Hays and Conant 2007) are notorious. Introductions of generalist invertebrate agents also have had dire consequences, such as the introduction of predatory snails to French Polynesia (Murray et al. 1988; Coote 2007). In retrospect, some of the unintended consequences of biological control could have been avoided with more ecological knowledge (McEvoy and Coombs 2000) or more societal appreciation for native species (which has developed with time, Henneman and Memmott 2001), but with other introductions, it would have been impossible to know ahead of time what the risks would be (e.g., gall fly agents of knapweeds providing supplementary food to mice that harbor hantavirus, Pearson and Callaway 2006). Many of the unknown outcomes of biological control are purely ecological – what is the risk that a wasp, introduced to parasitize an agricultural pest, will also be able to feed on a native insect? Other unknowns involve evolution – will a herbivore adapt over time to be able to feed on a new non-target host or hybridize with a closely related species?

[1]Biological control can also include the use of indigenous predators, parasites, pathogens, or herbivores to control pests, through augmentation or other facilitation of the consumer/resource interaction.

This volume explores the evolutionary aspects of biological control. Although often overlooked, evolutionary considerations are critical to all stages of classical biological control, from agent selection, to quarantine, release, establishment, and ultimately success in pest control (Ehler et al. 2004). Many questions are unresolved. For example, should agents be chosen that have a long history with the host or are 'new associations' more likely to succeed (Hokkanen and Pimentel 1989)? Can one improve effectiveness through artificial selection (Hopper et al. 1993)? Will postcolonization adaptation of the agent increase the likelihood of success, and/or are hosts equally likely to evolve resistance over time (Roderick 1992; Holt and Hochberg 1997; Hufbauer 2001)? Are generalist consumers more likely to survive in novel environments or are specialists more effective (Murdoch et al. 1985; Waage 1990; Brodeur 2012)? More recently, concern for the environment, as well as theory examining the reasons for success of generalist predators, prompted a shift to the release of specialized consumers typically preceded by extensive testing aimed at delimiting the host range of candidate biological control agents. While this approach has clearly made biological control more predictive ecologically, research focused on host range currently lacks measures of genetic variation in host use and responses of those hosts, and thus evolutionary uncertainties remain.

Research themes

The papers in this volume address fundamental questions concerning the role of evolution in biological control. The ultimate goal, as in any science, is for the research to have predictive power. These papers take a giant step in that direction.

Does evolution occur in the process of biological control and what types of traits are involved?

Previous work shows that there are opportunities for rapid evolutionary change associated with biological introductions, yet most biological control programs are not designed to measure evolution or take into account its effects (Hufbauer and Roderick 2005). Papers in this volume examine the four drivers of microevolutionary change: selection, gene flow, genetic drift, and mutation. Topics include the role and possibilities for selection in both field (Bean et al. 2012; McEvoy et al. 2012) and laboratory (Benvenuto et al. 2012; Brodeur 2012; Tayeh et al. 2012) settings, the importance of genetic diversity and its origins (Cory and Franklin 2012), including hybridization (Benvenuto et al. 2012; Szücs et al. 2012), and the consequences of small population sizes and population structure (de Boer et al. 2012; Fauvergue et al. 2012). Traits studied in these papers are varied and include components of fitness, aspects of efficacy of control, characters associated with consumer/resource interactions, as well as behavioral and life history traits associated with environmental factors and climate.

Does genetic variation limit the ability of introduced organisms to be successful in new environments?

The numbers of individuals introduced for biological control are typically small resulting in reduced genetic diversity of the initial founding population (Roderick and Navajas 2003). Does this matter? Fauvergue et al. (2012) explore the theory and empirical results associated with small populations. They examine the demographic and genetic processes at play in small populations and how these processes affect individual fitness, population growth rate, and establishment probability. One result is that, in addition to population size, population structure and the extent of connectivity between populations are likely to contribute significantly to establishment probability. de Boer et al. (2012) illustrate how bottlenecks associated with biological control can be particularly detrimental in parasitoid Hymenoptera that exhibit complementary sex determination. In another study, Szücs et al. (2012) show that hybridization can increase fitness in a herbivorous beetle, *Longitarsus jacobaeae*, used for biological control of the ragwort, *Jacobaea vulgaris*, suggesting that genetic variation may be limited in this system.

Can the success of biological control be improved through selection?

Classical biological control typically involves a process of prerelease testing or rebuilding of population sizes, providing the opportunity for improving performance through selection (Hopper et al. 1993). Benvenuto et al. (2012) manipulated strains of the parasitoid wasp, *Trichogramma chilonis,* in an effort to improve performance. The resulting hybrid strains exhibited a range of outcomes, from inbreeding depression to heterosis, emphasizing that genetic improvement of biocontrol agents will be challenging. Other work presented in this volume illustrates that changes associated with prerelease domestication can have important consequences in the field, including increased specificity leading paradoxically to reduced efficacy (Brodeur 2012) and increased susceptibility to pathogens (Tayeh et al. 2012).

Are introductions as a result of classical biological control useful models for biological invasions and vice versa?

As noted by Fauvergue et al. (2012) and McEvoy et al. (2012), classical biological control and introductions associated with biological invasions share many characteristics, prompting the question as to whether each can serve as a model for the other. In particular, classical biological control can be considered a manipulated introduction and as such provides many opportunities to examine the factors associated with success in novel environments. While the analogy between the two disciplines is not perfect, a comparison between the two processes can be used to generate testable hypotheses.

Future directions

Papers in this volume point to three themes for future work that together will be critical in understanding the role of evolution in biological control and adding predictive power to an emerging field.

Species interactions and global change

Human activity, through changes in land use, population, and other factors, is causing a cascade of global effects, including shifts in climate (Barnosky et al. 2012). Extensive work to date has modeled climate tolerances of organisms, including those used for biological control agents, providing predictions for geographical shifts of organisms as temperature and precipitation change (Migeon et al. 2009; Mills and Kean 2010). However, a critical next step for biological control will be to understand how also the *interactions* of organisms change under these new environmental conditions. What will be the potential roles for evolutionary adaptation vs. ecological plasticity in these modified habitats? For example, if a weed now controlled by a herbivore changes its distribution as a result of warming, will the insect herbivores be able to move into the same habitats and/or will adaptation to new climate conditions be necessary? And, will the hosts be more or less likely to evolve resistance (Waage and Greathead 1988; Holt and Hochberg 1997)? Work presented here shows that adaptation to new climates by biological control agents is possible and can be associated with changes to either warmer (Bean et al. 2012) or cooler (McEvoy et al. 2012) environments. Additionally, climate change presents new possibilities for invasive species, as more tropical species become established in temperate zones. For example, introductions of tropical species of spider mites into Europe have increased 50% in the last 30 years (Navajas et al. 2010). Accordingly, the practice of biological control will need to adopt new strategies for choosing agents and their release.

Higher order interactions

Interactions between agent and pest are central to biological control but represent only a small part of typical food webs (Cory and Myers 2000). Researchers are now coming to grips with the importance of other interactions that affect the success of biological control; here, we note three of these. (i) The impacts of microorganisms and symbionts are now well recognized in ecological and evolutionary processes. These organisms are important both as control agents (Brodeur 2012; Cory and Franklin 2012), but also as symbionts influencing biocontrol interactions (Tayeh et al. 2012). Clearly, microorganisms and their evolution will become more important in biological control as researchers become more aware of their role and diversity in ecological communities (Cory and Franklin 2012). Still lacking is a general understanding of how the evolution of microorganisms and macroorganisms differs in biological control settings, and what these potential differences might mean for long-term stability and control. (ii) Another important area will be to understand interactions among species at the same trophic level, particularly cryptic species that were introduced inadvertently or populations of the same species introduced from different regions (Navajas et al. 1998; Boubou et al. 2012). Such sets of introductions will encompass more genetic and phenotypic variation, with potential for greater ecological and evolutionary consequences. Work presented by both Szücs et al. (2012) and Benvenuto et al. (2012) supports this hypothesis. (iii) Previous work has identified nontarget and other indirect ecological effects of biological control (Cory and Myers 2000; McEvoy and Coombs 2000; Louda et al. 2003; Pearson and Callaway 2006), but evolutionary responses of nontarget and other organisms in the food web are also likely, with consequences for community structure and effective pest control. For example, Phillips and Shine (2006) have documented behavioral and physiological adaptations in the Australian black snake that enable it to feed on the otherwise lethally toxic cane toad.

Environmental benefits and risks

Clearly important for the future of biological control will be to understand and assess the environmental risks associated with introductions of organisms into novel environments, risks that are also being considered in other realms, such as the movement toward 'Pleistocene rewilding' of North America (Donlan et al. 2006) and serious consideration of assisted migration for species whose habitat is threatened by land use or climate change (Loss et al. 2011). Assessing environmental risks associated with biological invasions (Leung et al. 2002; Perrings et al. 2002) and with releasing exotic biological control agents (Lenteren et al. 2006) is now becoming more common, but risk assessment associated with evolutionary change will be more difficult (Roderick and Navajas 2003). Papers in this volume illustrate that evolution in biological control systems is possible under relatively short time periods in both the field (McEvoy et al. 2012; Szücs et al. 2012) and more managed settings (Benvenuto et al. 2012; Brodeur 2012; Tayeh et al. 2012). At the same time, a better understanding of how evolution may benefit biological control is also needed – for example, how quickly can consumers adapt to the new environment of the pest or adapt to new pest genotypes? These are questions from the early days of biological control that we are only now addressing a century later.

New tools and approaches

There has been much progress in understanding the importance of evolution in biological control, and the discipline is on the edge of moving to a predictive science, from one still largely consisting of a set of case studies. Each of the areas noted earlier requires a multi-disciplinary strategy that will necessarily require expertise in natural history and experimental design, but also in social science and environmental management. New tools and approaches will be critical, including next-generation molecular biology, computational modeling, climate change biology, bioinformatics, and collection science. For the field of biological control generally, we argue that a recognition that evolution happens should hone the underlying fundamental research involved rather than hamstring the practice. We hope that the extreme opinions of biological control become more balanced; it is neither a panacea nor Pandora's box (Howarth 1983), but one of many tools available to manage pests.

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