



Does experimental evolution produce better biological control agents? A critical review of the evidence

Manolis Lirakis^{1,2*}  & Sara Magalhães³ 

¹Institut für Populationsgenetik, Veterinärmedizinische Universität Wien, Wien 1210, Austria, ²Vienna Graduate School of Population Genetics, Veterinärmedizinische Universität Wien, Wien 1210, Austria, and ³Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, Lisboa, Portugal

Accepted: 26 March 2019

Key words: adaptation, artificial selection, biocontrol agent, improvement, natural enemy, pest management, review, selection

Abstract

Biological control of crop pests is considered a good alternative or complement to the use of pesticides. However, legislation restricts the importation of natural enemies of pests. A potential way to circumvent this limitation is by using experimental evolution and/or artificial selection to improve native biological control agents. Here, we review studies that have used these methodologies and evaluate their success. Experimental evolution or artificial selection has been used on a wide range of traits, with most focusing on improving the performance of natural enemies in ecologically relevant environments, such as in the presence of pesticides or at different temperatures. Although most studies were poorly replicated, the selected traits generally improved following the selection process. However, correlated responses (often in the form of trade-offs) with other traits of interest were common. We suggest that the selection procedure can be improved by increasing replication and performing experimental evolution under more semi-natural environments, to ensure that the most useful traits are being selected.

The use of experimental evolution in biological control

Food production is continuously threatened by native and invasive pest species. Controlling crop pests can be done via the use of pesticides, but these entail environmental and public health issues and they are often ineffective due to the rapid evolution of pesticide resistance. Biological control of pests is the main alternative to chemical control, as the evolution of resistance in pest insects against biocontrol agents appears to be very rare (Ehler et al., 2004). However, the use of natural enemies also poses legal and ethical challenges of its own. Indeed, as such practice can pose a threat to local biodiversity (De Clercq et al., 2011; Simberloff, 2012; Hajek et al., 2016), the importation of new species/populations has been highly restricted (Nagoya Protocol on Access and Benefit Sharing, Convention on Biological Diversity – <https://www.cbd.int/abs>) (Cock et al., 2010; van Lenteren

et al., 2011). Moreover, biological control agents should be selected such that unintentional effects on species other than the crop pest they target are limited. Although this is valid for both native and non-native biocontrol agents, the latter represent an added risk as they are by definition alien to the agroecosystem in which they are inserted. Given the possible increase in crop losses to insect pests due to global warming (Deutsch et al., 2018) and the restrictions and added dangers of natural enemies importation, optimizing existing and native biocontrol agents by selecting from their intraspecific variation in ‘biocontrol’ traits can be an alternative (although the ethical issue of disrupting ecosystems needs to be accounted for).

Experimental evolution is a generic term that groups any methodology that follows the real-time evolution of populations (Garland & Rose, 2009; Kawecki et al., 2012). It ranges from studies of ‘artificial selection’, in which the experimenter selects individuals with particular traits and let them breed to form the next generation (selective breeding), to studies of ‘quasi-natural experimental evolution’ (hereafter ‘experimental evolution’ for the sake of

*Correspondence: Manolis Lirakis, Veterinärmedizinische Universität Wien, Institut für Populationsgenetik, Wien 1210, Austria.
E-mail: emm.lirakis@gmail.com

simplicity), in which populations are exposed to particular environments during several generations and adaptation is tested by comparing trait values in those populations and in populations maintained in control environments (Kawecki et al., 2012; Magalhães & Matos, 2012).

Improvement in natural enemies through experimental evolution is not a new idea (Mally, 1916; DeBach, 1958; Sailer, 1961) and has frequently been reviewed (Table S1). Indeed, it seems more feasible to apply this methodology to biocontrol agents, which are generally short-lived and small-bodied arthropods, than to livestock and crops (Kruitwagen et al., 2018). Still, whereas the improvement in crops has been largely dependent upon selective breeding, this is not the case for the production of natural enemies. Why is that? One reason may be that selective breeding in agriculture has been done for thousands of years and thus is currently a fine-tuned methodology, whereas improvement of natural enemies for biological control is a recent strategy, still under development. Another reason could be that this method is time- and space-consuming, requiring a substantial amount of biological and ecological knowledge, compared to classical importation (Hoy, 1986, 1988a). Nevertheless, recent years have witnessed a renewed interest in improving biocontrol agents via experimental evolution or artificial selection, judging from recent reviews (Arora & Shera, 2014; Venkatesan & Jalali, 2015; Routray et al., 2016; Lommen et al., 2017; Kruitwagen et al., 2018). However, none of these reviews focuses specifically on experimental evolution and/or artificial selection.

To fill this gap, we performed an exhaustive search of studies that used experimental evolution to improve natural enemies of crop pests, focusing on arthropods and nematodes. We searched in the Web of Science, Google Scholar, and Google for combinations of the keywords 'biocontrol' or 'biological control' or 'natural enemy' and 'experimental evolution' or 'artificial selection' or 'genetic improvement'. Subsequently, we checked the reference list of those publications as well as the articles that cite them. We only kept the articles that specifically carry out artificial selection or experimental evolution; hence, we excluded studies solely examining genetic variation and/or heritability of traits for biocontrol agents. A list of the studies we reviewed can be found in Table S2.

In this review, we systematically address the achievements and pitfalls of the use of experimental evolution to improve biological control agents. First, we refer to the methodological underpinnings of experimental evolution and how they are (not) met in studies on biocontrol agents. Subsequently, we review the various traits that were subjected to selection and comment on the outcomes of those experiments. Finally, we summarize our findings

and discuss how experimental evolution of natural enemies could be improved. We do not focus on the genetics and genomics of biocontrol traits, as this has been the object of recent reviews (Routray et al., 2016; Lommen et al., 2017; Kruitwagen et al., 2018).

Methodological issues in experimental evolution

Experimental evolution is a powerful, yet demanding methodology, designed to detect evolutionary changes in real time. Therefore, one should ensure that it is correctly implemented. In particular, special care in the experimental design should be taken to: (1) maximize the chance of obtaining a response in the trait of interest, and (2) ensure that the trait change observed is genetically determined. Both these issues are important from a biological control perspective. Hence, we here first address the methodological requirements of experimental evolution, and refer to whether these are met in biological control studies.

High standing genetic variation in the initial population

In multicellular organisms, experimental evolution generally relies on the selection from the standing genetic variation. Hence, to maximize the chances of observing a response, selection needs to be performed using a genetically variable population. This can be achieved by collecting a high number of individuals to initiate the population (e.g., White et al., 1970) or by mixing populations (e.g., from various geographic locations and/or with different evolutionary histories; e.g., Roush & Hoy, 1981a). Mixing populations can further break undesirable linkage disequilibria between loci coding different traits, thus facilitating the selection process. However, genotypes belonging to all populations need to be effectively represented in the final pool. This can be done by performing one-on-one crosses between individuals of different populations, and/or by keeping track of the relative proportion of genotypes of each population. In all cases, the population should be maintained at high numbers. Unfortunately, many studies do not provide any information on the number of individuals that formed the base population (Table S2).

Additionally, the replicate selection lines should be started with a high-enough number of individuals, to avoid a large bottleneck at the onset of the experimental evolution. This number depends on the genetic variability of the base population and on the feasibility of having large populations (Fry, 2003; Kawecki et al., 2012). Population size will affect the timing at which a response is expected. Indeed, in polygenic traits, the lower the population size, the longer the process of evolutionary change. Although

many studies started the experimental evolution populations with a few hundred to a few thousand individuals, others used a small number of individuals or do not mention this information (Table S2).

Replicates and controls

Experimental evolution follows the process of adaptation at the population level. Therefore, its replication level is the population, not the individual. It is thus key to follow

Table 1 Studies that applied replication during experimental evolution (or artificial selection) and/or where control and selected populations were maintained in a common environment

Study	Replication	Common environment	Trait	Natural enemy
Wilkes (1942)	√	–	Thermal adaptation	<i>Dahlbominus fuscipennis</i> (Hymenoptera: Eulophidae)
White et al. (1970)	–	√	Thermal adaptation	<i>Aphytis lingnanensis</i> (Hymenoptera: Aphelinidae)
Ashley et al. (1974)	–	√	Thermal adaptation	<i>Trichogramma pretiosum</i> (Hymenoptera: Trichogrammatidae)
Parker & Orzack (1985)	√	–	Proportion of females	<i>Nasonia vitripennis</i> (Hymenoptera: Pteromalidae)
Field & Hoy (1985)	–	√	Diapause	<i>Galendromus occidentalis</i> (Acari: Phytoseiidae)
Field & Hoy (1986)	–	√	Diapause, insecticide resistance	<i>Galendromus occidentalis</i> (Acari: Phytoseiidae)
Gilkesson & Hill (1986)	√	–	Diapause	<i>Aphidoletes aphidimyza</i> (Diptera: Cecidomyiidae)
Gaugler et al. (1989)	√	–	Foraging behaviour	<i>Steinernema feltiae</i> (Nematoda: Steinernematidae)
Gaugler & Campbell (1991)	√	–	Foraging behaviour	<i>Steinernema feltiae</i> (Nematoda: Steinernematidae)
Tomalak (1994)	√	–	Foraging behaviour	<i>Steinernema feltiae</i> (Nematoda: Steinernematidae)
Kostiainen & Hoy (1994)	–	√	Insecticide resistance	<i>Euseius finlandicus</i> (Acari: Phytoseiidae)
Thistlewood et al. (1995)	√	–	Insecticide resistance	<i>Neoseiulus fallacis</i> (Acari: Phytoseiidae)
Grewal et al. (1996)	√	–	Thermal adaptation	<i>Steinernema feltiae</i> (Nematoda: Steinernematidae)
Shapiro et al. (1996)	√	–	Thermal adaptation	<i>Heterorhabditis bacteriophora</i> (Nematoda: Heterorhabditidae)
Margolies et al. (1997)	√	–	Plant adaptation	<i>Phytoseiulus persimilis</i> (Acari: Phytoseiidae)
Kraaijeveld et al. (2001)	√	√	Tolerance to pest	<i>Asobara tabida</i> (Hymenoptera: Braconidae)
Carrière & Boivin (2001)	√	–	Thermal adaptation	<i>Trichogramma pretiosum</i> (Hymenoptera: Trichogrammatidae)
Wang et al. (2004)	√	–	Thermal adaptation	<i>Trichogramma ostrinae</i> (Hymenoptera: Trichogrammatidae)
Henry et al. (2008)	√	–	Tolerance to pest	<i>Aphidius ervi</i> (Hymenoptera: Braconidae)
Nachappa et al. (2010)	√	–	Foraging behaviour	<i>Phytoseiulus persimilis</i> (Acari: Phytoseiidae)
Salame et al. (2010)	√	–	Foraging behaviour, desiccation tolerance	<i>Steinernema feltiae</i> (Nematoda: Steinernematidae)
Dion et al. (2011)	√	–	Tolerance to pest	<i>Aphidius ervi</i> (Hymenoptera: Braconidae)
Anbesse et al. (2013b)	–	√	Desiccation tolerance	<i>Heterorhabditis bacteriophora</i> (Nematoda: Heterorhabditidae)
Rouchet & Vorburger (2014)	√	√	Tolerance to pest	<i>Lysiphlebus fabarum</i> (Hymenoptera: Braconidae)

the evolution process in several populations exposed to the same selection regime, in order to rule out effects of drift or of a biased set up. Also, trait changes in the selection regimes should be compared to those occurring in populations exposed to a control environment, which are not expected to evolve. Unfortunately, most studies have not created replicate populations within each selection regime. Replication of experimental evolution appears mostly in entomopathogenic nematodes studies and in some studies on *Trichogramma* and *Aphidius* wasps (Table 1 and Table S2).

Controlling for environmental effects

After experimental evolution, changes in trait values are measured, by comparing them in individuals coming from the selective or from the control environment. However, these environments are likely to affect trait values without modifying the genetic composition of populations, via phenotypic plasticity or environmental maternal effects. These effects cannot be dissociated from the genetic changes we wish to detect. Consequently, it is important to place all populations in a common environment for one or two generations before examining traits of interest, to eliminate non-genetic effects. This was specifically mentioned only in a handful of studies (Table 1 and Table S2), raising the question whether other studies did follow this procedure. Hence, possibly, many of the responses documented are actually simply due to phenotypic plasticity.

Traits tested

We herewith provide a brief overview of the traits that were selected in biocontrol agents, the changes observed, their potential correlated responses, and field evaluations of the selected populations. These traits can be broadly categorized into life-history traits, traits related to responses of the natural enemy towards the pest, and traits that reflect the performance of biocontrol agents in specific environments. A list of all natural enemies used in these studies and their taxonomic groups can be found in Table S3.

Life-history traits

Developmental time. Because pre-adult stages generally feed less on the crop pest than adult stages, fast development of the natural enemy is likely to improve biological control. Only two studies specifically selected for this trait. Weseloh (1986) found no significant change in the developmental time of the parasitic wasp *Cotesia melanoscela* (Ratzeburg). In contrast, Siddiqui et al. (2015) selected for slow and fast

development in the ladybird predatory beetle *Propylea dissecta* (Mulsant), and found that fast developers showed higher predation rates than slow developers and controls.

Sex ratio. A higher proportion of females in a population is expected to result in higher population growth. Three studies have performed artificial selection on the sex ratio of parasitic wasps, all of which showed a significant response (Wilkes, 1947; Simmonds, 1947; Parker & Orzack, 1985). Still, none of these studies evaluated whether selected strains had improved ability to control crop pests.

Fecundity. Similar to the increased production of females, higher fecundity is expected to lead to higher rates of population growth of the natural enemy. Curiously, we found a single study performing artificial selection on this trait, in the parasitoid wasp *Trichogramma brassicae* Bezdenko. The study reported increased fecundity in the selected strain but this strain did not have an advantage over non-selected strains in the greenhouse and the change in the phenotype was partially lost after selection was relaxed (Pintureau, 1991).

Diapause. Diapause is a phenotype that suspends development, allowing organisms to overwinter and withstand stressful environments. However, this phenotype could compromise biological control if crop pest populations continue to grow while natural enemies become dormant. Selection for non-diapause was achieved in the mites *Galendromus occidentalis* (Nesbitt) (Hoy, 1984), *Neoseiulus cucumeris* (Oudemans), and *Neoseiulus barkeri* Hughes (van Houten et al., 1995), and in the midge *Aphidoletes aphidimyza* (Rondani) (Gilkeson & Hill, 1986). Selection did not lead to trade-offs with other traits in all these species (Field & Hoy, 1984, 1985, 1986; Gilkeson & Hill, 1986; van Houten et al., 1995). In fact, the non-diapausing strain of *A. aphidimyza* exhibited faster development (Gilkeson & Hill, 1986). Also, the character remained stable until at least 18 month following the end of selection in the selected *Neoseiulus* species (van Houten et al., 1995), again suggesting no costs. However, the selected *G. occidentalis* strain failed to control the two-spotted spider mite in field trials, probably due to interbreeding with diapausing mites present in the field and, thus, the loss of the non-diapausing character (Field & Hoy, 1984, 1986). In contrast, selected *N. cucumeris* mites established successfully in a small-scale greenhouse experiment and were reproductively active under diapause-inducing conditions (van Houten et al., 1995).

Dispersal. Adult biocontrol agents that do not fly may remain in the crop of interest for longer periods and thus control pests more efficiently. Few studies thus attempted at producing biocontrol agents with low dispersal via selective breeding, all of them using the lady beetle *Harmonia axyridis* (Pallas) (Ferran et al., 1998; Seko et al., 2008; Nakayama et al., 2010). However, although the beetles from selected populations stayed on the plants for longer periods than controls, their progeny suffered from low egg-to-adult viability and fecundity (Ferran et al., 1998; Seko et al., 2008, 2014; Seko & Miura, 2009, 2013; Nakayama et al., 2010, 2013; Adachi-Hagimori et al., 2011, 2019). Therefore, the efficiency of these flightless strains in biological control of aphids was questioned in these studies (although see Lommen et al., 2019).

Natural enemy responses towards the pest

Foraging behaviour. Predators that are better able to find prey, that consume more prey, or that have increased conversion efficiency of prey into predator eggs are expected to be better biological control agents. Curiously, we found few studies that performed artificial selection on these traits, with mixed results. In parasitoids, attempts to improve the pest finding ability of *T. brassicae* were not successful (Pintureau, 1991). In entomopathogenic nematodes, a few studies performed artificial selection on the host-finding ability of *Steinernema feltiae* (Filipjev) towards several hosts (Gaugler et al., 1989; Gaugler & Campbell, 1991; Tomalak, 1994; Salame et al., 2010). These studies led to a successful improvement in the host-finding behaviour, but this ability was slightly lost after selection was ceased (Gaugler et al., 1989) or selection entailed a cost in longevity in some instances (Gaugler et al., 1990; Gaugler & Campbell, 1991). Cross-effectiveness of a selected strain against an alternative pest was also observed (Grewal et al., 1993).

The single study that selected for foraging traits in predatory mites used *Phytoseiulus persimilis* Athias-Henriot (Nachappa et al., 2010). All traits (prey finding, prey consumption, and conversion efficiency) substantially changed during selection, except for the line selected for lower prey-finding ability. Additionally, the selected phenotypes remained stable after selection ceased, suggesting an absence of costs. Although the selection process entailed several correlated responses in other life-history traits, all selected strains performed better than control strains when tested on entire plants, both in terms of predation rates and of population growth (Nachappa et al., 2011).

Tolerance to pest. The efficacy of biocontrol agents often hinges upon their degree of acceptance of hosts/prey, and how they can tolerate their responses (e.g., the

immune response of the host). Most experimental evolution studies concerning this trait used parasitoid wasps (Allen, 1954; Weseloh, 1986; Kraaijeveld et al., 2001; Henry et al., 2008). Such increased tolerance was sometimes accompanied by a shift in host preference. For example, parasitoid wasps [*Asobara tabida* (Nees)] that evolved increased tolerance to *Drosophila melanogaster* Meigen (Kraaijeveld et al., 2001) also accepted the encapsulating *D. melanogaster* for oviposition more often than control, unselected lines (Rolff & Kraaijeveld, 2001). Selection for acceptance of aphids as prey was also applied in the spider *Tenuiphantes tenuis* (Blackwall) (Beck & Toft, 2000).

Selection for increased tolerance of hosts/prey was often accompanied with correlated responses, sometimes in the form of trade-offs. Indeed, adaptation of the parasitoid *Aphidius ervi* Haliday to pea aphids [*Acyrtosiphon pisum* (Harris)] or foxglove aphids [*Aulacothum solani* (Kaltenbach)] in the laboratory entailed a trade-off in the ability of the parasitoid to parasitize and produce offspring on the alternative host, both in the laboratory and in a greenhouse (Henry et al., 2008, 2010). Similarly, adaptation of the spider *T. tenuis* was accompanied by trade-offs with fecundity and developmental time (Beck & Toft, 2000).

Two additional studies tested whether parasitoid wasps evolved in response to the resistance that the symbiotic bacterium, *Hamiltonella defensa* Moran et al., confers to its host (in this case the pest). In both studies, parasitic wasps evolved increased survival in their aphid host when the latter carried protective symbionts (Dion et al., 2011; Rouchet & Vorburger, 2014). In one case, this adaptation was shown to be specific to the particular symbiont that wasps were exposed to, as it did not result in cross-adaptation to other isolates (Rouchet & Vorburger, 2014). However, the latter study did not detect any trade-offs with other traits, whereas Dion et al. (2011) found that selected wasps were smaller than control ones.

Performance of biocontrol agents in specific environments

Insecticide resistance. The vast majority of studies we found selected for insecticide resistance in various biological control agents (Figure 1, Table 1). This is not surprising, as the insecticides used to control pests are a great threat to natural enemies. The insecticides used include organophosphates (e.g., guthion, dimethoate, chlorpyrifos, and malathion), organochlorines (e.g., DDT and endosulfan), pyrethroids (e.g., permethrin and fenvalerate), carbamates (e.g., carbaryl and methomyl), and neonicotinoids (e.g., imidacloprid, nitenpyram, and thiamethoxam). In almost all studies, resistance against the applied insecticide increased, from as low as 1.8-fold (Kostiainen & Hoy, 1994) to ca. 40-fold (Roush & Hoy,

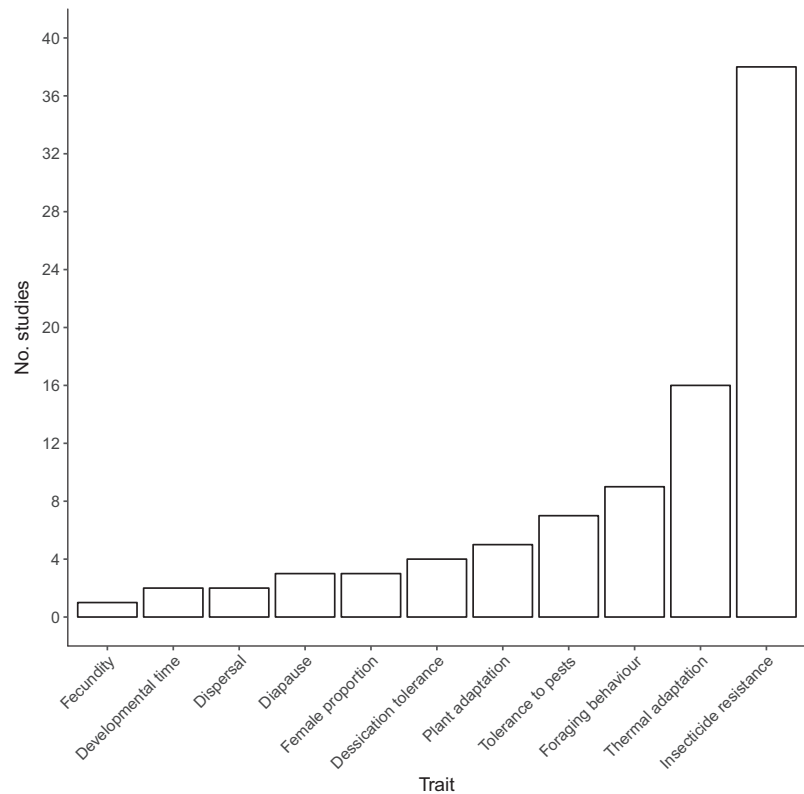


Figure 1 Number of studies dealing with a particular trait subject to experimental evolution or artificial selection in biological control agents. Only the studies that describe the selection process were taken into account.

1981a; Grafton-Cardwell & Hoy, 1986), 65-fold (Zhu et al., 1996), 71-fold (Balanza et al., 2019) and even several hundred-fold (Croft & Meyer, 1973). Some studies, however, failed to obtain a response to insecticides in natural enemies (Adams & Cross, 1967; Croft & Meyer, 1973; Schulten et al., 1976; Hoy & Knop, 1979; Markwick, 1986; Hamamura, 1987; Havron et al., 1991; Javier et al., 1991). In others, insecticide resistance did not increase because the source population was already resistant (Roush et al., 1980; Strickler & Croft, 1982; Baker, 1995).

The persistence of pesticide resistance once selection was relaxed varied across studies. Indeed, whereas in some cases resistance persisted in the absence of the insecticide (Croft & Meyer, 1973; Roush & Hoy, 1980; Hoy, 1990; Kostianin & Hoy, 1994; Glazer et al., 1997; Sayyed et al., 2010; Mansoor et al., 2017), in others it declined (Robertson, 1957; Meyer, 1975; Croft & Hoving, 1975; Spollen & Hoy, 1992; Zhu et al., 1996; Jalali et al., 2006b), possibly because the acquired resistance was a plastic response or due to costs of resistance in an insecticide-free environment.

Many studies further demonstrated cross-resistance among insecticides, including between different chemical groups of insecticides (Croft & Meyer, 1973; Schulten et al., 1976; Hoy et al., 1980; Roush & Hoy, 1980; Hoy &

Knop, 1981; Croft et al., 1982; Strickler & Croft, 1982; Field & Hoy, 1986; Markwick, 1986; Hoy, 1988b; Hoy & Cave, 1989; Kostianin & Hoy, 1994; Glazer et al., 1997; Devi et al., 2007). In contrast, no cross-resistance was observed after selection for insecticide resistance in *Chrysoperla carnea* (Stephens) (Grafton-Cardwell & Hoy, 1986; Mansoor et al., 2017; Mansoor & Shad, 2019), whereas Schulten et al. (1976), Mansoor et al. (2017), and Mansoor & Shad (2019) observed increased susceptibility to pirimicarb and lindane after selection for parathion resistance in *P. persimilis*, and increased susceptibility to spinosad in *C. carnea* selected for nitenpyram and buprofezin resistance.

Other studies tested the existence of correlated responses between the acquired insecticide resistance and other traits, with variable results. For example, selection for carbaryl resistance in *G. occidentalis* led to a higher proportion of females in the population (Roush & Hoy, 1980, 1981b) and selection for abamectin resistance led to increased fecundity on clean leaves (Hoy & Ouyang, 1989).

Field tests were further performed in several of these studies to evaluate the performance of the selected strains/populations, mostly for predatory mites. In general, the tests showed that the improved biocontrol agent

established well (Croft & Hoying, 1975; Meyer, 1975; Roush et al., 1980; Hoy et al., 1980, 1983, 1985, 1989, 1990; Roush & Hoy, 1981b; Strickler & Croft, 1982; Hoy, 1982, 1988b, 1990; Field & Hoy, 1984; Hoy & Cave, 1991; Navajas et al., 2001). A few studies further demonstrated that pest control was improved when insecticides were applied (Roush & Hoy, 1980, 1981b; Hoy, 1982; Hoy et al., 1983; Jalali et al., 2002, 2006b,c; Ballal et al., 2009; Venkatesan et al., 2016).

Thermal adaptation. Natural enemies should tolerate a wide range of temperatures in the field to control pests at all seasons. Thermal adaptation in the laboratory could improve this tolerance. In early attempts, artificial selection was applied to parasitic wasps to either low (Wilkes, 1942) or both low and high (White et al., 1970) temperatures. In both cases, a rapid response was observed, with no relevant costs. In White et al. (1970) in specific, cold-adapted flies were also tolerant to high temperatures, adult longevity increased in all selection regimes, and the proportion of females tended to decrease at very low temperatures.

More recent studies, however, found that *Trichogramma pretiosum* Riley parasitic wasps selected for increased tolerance to low temperatures had a cost at high temperatures (Carrière & Boivin, 2001). In addition, selection at the high temperature resulted in a decrease in fecundity at that temperature. Similar trade-offs between opposite temperature regimes were also observed in the entomopathogenic nematodes *S. feltiae* (Grewal et al., 1996) and *Heterorhabditis bacteriophora* Poinar (Shapiro et al., 1996; Segal & Glazer, 2000; Ehlers et al., 2005; Mukuka et al., 2010; Anbesse et al., 2013a). Costs were also found in *Trichogramma chilonis* Ishii adapting to high temperatures (Srivastava & Singh, 2015). Although fitness components like fecundity and egg-to-adult viability improved, adult survival decreased during the experiment. Other studies also found rapid trait evolution at various temperatures, with either no costs (Jalali et al., 2006a) or positively correlated responses (Jalali et al., 2002; Ashok Kumar et al., 2008).

In contrast, a few studies failed to obtain responses to artificial selection at different temperatures in biocontrol agents. For example, Ashley et al. (1974) attempted to select for temperature tolerance in *Trichogramma* parasitic wasps, without success. The same (lack of) response was obtained in other studies with parasitic wasps (Jalali et al., 2002; Wang et al., 2004) and nematodes (Dunphy & Webster, 1986). Limited information concerning the genetic variation present in the populations used in these studies hampers drawing solid conclusions on the potential causes of unsuccessful selection.

Desiccation tolerance. Desiccation may also hamper the effectiveness of biocontrol agents. Attempts to improve desiccation tolerance were performed in the entomopathogenic nematodes *H. bacteriophora* and *S. feltiae* (Strauch et al., 2004; Mukuka et al., 2010; Salame et al., 2010; Anbesse et al., 2013b). All studies were successful at improving desiccation tolerance. In one study, improving desiccation tolerance also led to improved heat tolerance (Salame et al., 2010).

Plant adaptation. Finally, it is important to improve the performance of a natural enemy on a particular plant. As natural enemies often rely on herbivore-induced plant volatiles to find their prey (Turlings & Erb, 2018), one trait of importance is how they respond to those volatiles. For example, *P. persimilis* predatory mites were successfully selected for increased attraction to plant volatiles. However, selected mites remained for shorter periods on patches with prey, when compared to unselected mites (Margolies et al., 1997). Also, selection for increased olfactory response in the parasitic wasp *Cotesia glomerata* (L.) led to improved flight orientation and landing success (Wang et al., 2003). Entomopathogenic nematodes (*H. bacteriophora*) also increased their response to root volatiles following artificial selection (Hiltpold et al., 2010). Although this response entailed a minor trade-off with the nematode's infectivity, the selected strain performed well in field tests.

On the plant, natural enemies may perform poorly due to the chemical and physical environment that the plant provides. This may be improved by selection experiments. Indeed, Drukker et al. (1997) observed that a *P. persimilis* population maintained on tomato plants exhibited improved fitness traits compared to a control population. Also, Jalali et al. (2002) improved the efficacy of *T. chilonis* against *Helicoverpa armigera* (Hübner) on tomato plants.

Discussion

In this review, we provide an overview of studies examining the use of experimental evolution in biological control. Despite being mostly poorly replicated, most attempts led to changes in the value of the trait of interest. In addition, many studies tested for the occurrence of correlated responses to selection, with results ranging from positive correlations to trade-offs. Although these studies cover a broad range of traits, most focused on improving insecticide resistance in biocontrol agents. Such studies are still dominant today (Figure 2) with the aim to develop resistant agents that can safely be integrated in pest management systems.

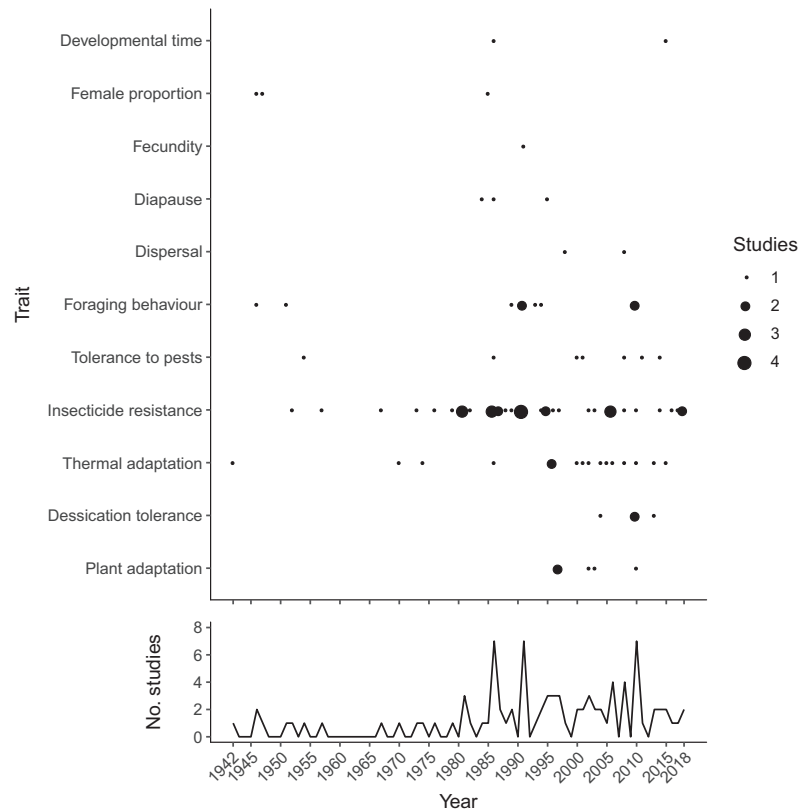


Figure 2 Number of studies dealing with a particular trait subject to experimental evolution or artificial selection in biological control agents across time, per trait (upper panel) and for all studies combined (lower panel). Only the studies that describe the selection process were taken into account.

Curiously, we found that the most obvious traits to select upon (predation/parasitism rate and fecundity) were actually seldom studied. This paucity of studies may be due to the general expectation that the traits most related to fitness have the least genetic variance (Houle, 1992; Falconer & Mackay, 1996). However, the few studies that studied such traits generally obtained responses to selection and sometimes without trade-offs. Therefore, it may be that selecting such traits will actually represent an important future research avenue.

Although most studies identified a response to selection, most did not replicate the experimental evolution process, that is, they used one selection line per regime. This raises the question whether the observed response can be attributed to selection or it is just a product of chance. This represents an important caveat if the results obtained are to be used to further understand the interaction between the natural enemy and its crop pest. For example, identifying the genes responsible for the change observed is meaningless, as the allelic change has not been driven by natural selection. Much in the same way, most studies do not place organisms in a common environment when examining the outcome of experimental evolution. Therefore, the observed response may result from environmental effects (phenotypic plasticity, maternal effects, etc.), rather than

from a genetic change in the population following natural selection. These methodological pitfalls might have contributed to the limited use of biological control agents improved via experimental evolution, as such improvements may actually be transient and context-dependent, rather than genetically fixed.

Furthermore, although most studies succeeded in selecting phenotypes of interest, such studies have declined during the last years (except for insecticide resistance, Figure 2). As discussed in the beginning of this review, experimental evolution has been described as a time- and space-consuming process requiring a substantial amount of biological and ecological knowledge. Still, most studies reported a positive response to selection and many studies did not detect any cost. Such positive results raise hope for a renewed interest in this methodology for the generation of better biocontrol agents.

The success of the experimental approach can only be validated if improved strains perform well in the field. Unfortunately, only few studies tested this, mostly those selecting for insecticide resistance, reduced dispersal, and non-diapause. Promisingly, most of them showed a good establishment and performance of the improved strain. Reasons for this limited number of tests in the field could be due to the absence of permits. Alternatively, it may be

difficult to monitor these strains, if they stem from a natural enemy already occurring in the field, except if genetic markers have been developed. Finally, another possibility is that, as stated above, the 'improved strains' did not actually improve, as the methodological caveats present in most studies hamper a solid conclusion on the genetic basis, and thus stability, of such improvement.

In some field studies, the improved population did not perform well possibly because trade-offs preclude its establishment or its ability to control the pest. Additionally, some studies suggest that the selected population lost the acquired trait through interbreeding with the local population (Meyer, 1975; Hoy et al., 1980, 1983; Roush et al., 1980; Hoy & Knop, 1981; Roush & Hoy, 1981a,b; Field & Hoy, 1984, 1986; Hoy, 1985, 1987). Therefore, possible reproductive incompatibilities between selected/wild populations (e.g., Hoy & Knop, 1981; Hoy, 1985) should be carefully examined before releasing the selected strain.

During experimental evolution of the natural enemy for whichever trait of interest, the adaptation/co-evolution of the pest and the natural enemy-pest system dynamics under selection should be studied too. In the studies we reviewed, this has received little attention (Morse & Croft, 1981; Field & Hoy, 1986; Liu et al., 2003; Nachappa et al., 2011). Selecting for traits related to the pest per se (e.g., improved foraging or parasitic efficiency, or preference) definitely requires the simultaneous study of the evolution of counter-defenses of the pest. For example, *Drosophila* flies that are hosts of parasitoids also rapidly evolve resistance to these natural enemies via increased encapsulation (Kraaijeveld & Godfrey, 1997; Kraaijeveld et al., 1998). Therefore, the net effect of the improved parasitoid strain remains to be evaluated. However, it must be noted that pest resistance to natural enemies, unlike pest resistance to specific environments, can still be countered by adaptation of natural enemies to such resistance. An integration of the response of the pest and biocontrol agents will allow a more thorough analysis of the potential success of improving natural enemies via experimental evolution.

To conclude, the studies presented in this review suggest that experimental evolution is a promising methodology to select better biological control agents, potentially improving this control strategy. We suggest that the interest of the community in this method should not fade away, but rather get stronger. This is particularly relevant today, in the modern era of genomics, as this method could further be enhanced by genomic approaches, for example, genomic selection (Routray et al., 2016; Lommen et al., 2017; Kruitwagen et al., 2018). The implementation of experimental evolution, maybe under more semi-natural

environments where the natural enemy and the pest co-evolve, may substantially benefit biological control in the future. If the methodological issues of experimental evolution discussed in this review are taken into account, it can provide biological control with an unprecedented boost in its successful application.

Acknowledgements

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie Grant agreement No 641456.

References

- Adachi-Hagimori T, Shibao M, Tanaka H, Seko T & Miura K (2011) Control of *Myzus persicae* and *Lipaphis erysimi* (Hemiptera: Aphididae) by adults and larvae of a flightless strain of *Harmonia axyridis* (Coleoptera: Coccinellidae) on non-heading *Brassica cultivars* in the greenhouse. *BioControl* 56: 207–213.
- Adachi-Hagimori T, Shibao M, Seko T & Miura K (2019) Release of the flightless strain of *Harmonia axyridis* (Coleoptera: Coccinellidae) against two aphid species on Komatsuna (*Brassica rapa* var. *perviridis*) in open fields. *Journal of Economic Entomology* 112: 115–118.
- Adams CH & Cross WH (1967) Insecticide resistance in *Bracon mellitor* a parasite of the boll weevil. *Journal of Economic Entomology* 60: 1016–1020.
- Allen HW (1954) Propagation of *Horogenes molestae*, an Asiatic parasite of the oriental fruit moth, on the potato tuberworm. *Journal of Economic Entomology* 47: 278–281.
- Anbesse S, Sumaya NH, Dörfler AV, Strauch O & Ehlers RU (2013a) Stabilisation of heat tolerance traits in *Heterorhabditis bacteriophora* through selective breeding and creation of inbred lines in liquid culture. *BioControl* 58: 85–93.
- Anbesse S, Sumaya NH, Dörfler AV, Strauch O & Ehlers RU (2013b) Selective breeding for desiccation tolerance in liquid culture provides genetically stable inbred lines of the entomopathogenic nematode *Heterorhabditis bacteriophora*. *Applied Microbiology and Biotechnology* 97: 731–739.
- Arora R & Shera PS (2014) Genetic improvement of biocontrol agents for sustainable pest management. *Basic and Applied Aspects of Biopesticides* (ed. by K Sahayaraj), pp. 255–285. Springer, New Delhi, India.
- Ashley TR, Gonzalez D & Leigh TF (1974) Selection and hybridization of *Trichogramma*. *Environmental Entomology* 3: 43–48.
- Ashok Kumar G, Jalali SK, Venkatesan T, Nagesh M & Lalitha Y (2008) Genetic improvement of egg parasitoid *Trichogramma chilonis* Ishii for combined tolerance to multiple insecticides and high temperature. *Journal of Biological Control* 22: 347–356.

- Baker JE (1995) Stability of malathion resistance in two hymenopterous parasitoids. *Journal of Economic Entomology* 88: 232–236.
- Balanza V, Mendoza JE & Bielza P (2019) Variation in susceptibility and selection for resistance to imidacloprid and thiamethoxam in Mediterranean populations of *Orius laevigatus*. *Entomologia Experimentalis et Applicata* 167: this issue.
- Ballal CR, Srinivasan R & Jalali SK (2009) Evaluation of an endosulfan tolerant strain of *Trichogramma chilonis* on cotton. *BioControl* 54: 723–732.
- Beck JB & Toft S (2000) Artificial selection for aphid tolerance in the polyphagous predator *Lepthyphantes tenuis*. *Journal of Applied Ecology* 37: 547–556.
- Carrière Y & Boivin G (2001) Constraints on the evolution of thermal sensitivity of foraging in *Trichogramma*: genetic trade-offs and plasticity in maternal selection. *American Naturalist* 157: 570–581.
- De Clercq P, Mason PG & Babendreier D (2011) Benefits and risks of exotic biological control agents. *BioControl* 56: 681–698.
- Cock MJW, van Lenteren JC, Brodeur J, Barratt BIP, Bigler F et al. (2010) Do new access and benefit sharing procedures under the convention on biological diversity threaten the future of biological control? *BioControl* 55: 199–218.
- Croft BA & Hoying SA (1975) Carbaryl resistance in native and released populations of *Amblyseius fallacis*. *Environmental Entomology* 4: 895–898.
- Croft BA & Meyer RH (1973) Carbamate and organophosphorus resistance patterns in populations of *Amblyseius fallacis*. *Environmental Entomology* 2: 691–696.
- Croft BA, Wagner SW & Scott JG (1982) Multiple- and cross-resistances to insecticides in pyrethroid-resistant strains of the predatory mite, *Amblyseius fallacis*. *Environmental Entomology* 11: 161–164.
- DeBach P (1958) Selective breeding to improve adaptations of parasitic insects. *Proceedings of the 10th International Congress of Entomology (Montreal, 1956)* 4: 759–767.
- Deutsch CA, Tewksbury JJ, Tigchelaar M, Battisti DS, Merrill SC et al. (2018) Increase in crop losses to insect pests in a warming climate. *Science* 361: 916–919.
- Devi PS, Jalali SK & Venkatesan T (2007) Evidence of cross-tolerance in newer insecticides tolerant strain of *Trichogramma chilonis* Ishii to other insecticides. *Indian Journal of Entomology* 69: 101–104.
- Dion E, Zélé F, Simon JC & Outreman Y (2011) Rapid evolution of parasitoids when faced with the symbiont-mediated resistance of their hosts. *Journal of Evolutionary Biology* 24: 741–750.
- Drukker B, Janssen A, Ravensberg W & Sabelis MW (1997) Improved control capacity of the mite predator *Phytoseiulus persimilis* (Acari: Phytoseiidae) on tomato. *Experimental and Applied Acarology* 21: 507–518.
- Dunphy GB & Webster JM (1986) Temperature effects on the growth and virulence of *Steinernema feltiae* strains and *Heterorhabditis heliothidis*. *Journal of Nematology* 18: 270–272.
- Ehler L, Sforza R & Mateille T (2004) *Evolution and Biological Control*. CABI Publishing, Wallingford, UK.
- Ehlers RU, Oestergaard J, Hollmer S, Wingen M & Strauch O (2005) Genetic selection for heat tolerance and low temperature activity of the entomopathogenic nematode-bacterium complex *Heterorhabditis bacteriophora-Photorhabdus luminescens*. *BioControl* 50: 699–716.
- Falconer SD & Mackay FCT (1996) *Introduction to Quantitative Genetics*, 4th edn. Harlow, England: Pearson, Prentice Hall.
- Ferran A, Giuge L, Tournaire R, Gambier J & Fournier D (1998) An artificial non-flying mutation to improve the efficiency of the ladybird *Harmonia axyridis* in biological control of aphids. *BioControl* 43: 53–64.
- Field RP & Hoy MA (1984) Biological control of spider mites on greenhouse roses. *California Agriculture* 38: 29–32.
- Field RP & Hoy MA (1985) Diapause behavior of genetically-improved strains of the spider mite predator *Metaseiulus occidentalis* (Acarina: Phytoseiidae). *Entomologia Experimentalis et Applicata* 38: 113–120.
- Field RP & Hoy MA (1986) Evaluation of genetically improved strains of *Metaseiulus occidentalis* (Nesbitt) (Acarina: Phytoseiidae) for integrated control of spider mites on roses in greenhouses. *Hilgardia* 54: 1–32.
- Fry JD (2003) Detecting ecological trade-offs using selection experiments. *Ecology* 84: 1672–1678.
- Garland TJ & Rose MR (2009) *Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments*. University of California Press, Berkeley, CA, USA.
- Gaugler R & Campbell JF (1991) Selection for enhanced host-finding of scarab larvae (Coleoptera: Scarabaeidae) in an entomopathogenic nematode. *Environmental Entomology* 20: 700–706.
- Gaugler R, Campbell JF & McGuire TR (1989) Selection for host-finding in *Steinernema feltiae*. *Journal of Invertebrate Pathology* 54: 363–372.
- Gaugler R, Campbell JF & McGuire TR (1990) Fitness of a genetically improved entomopathogenic nematode. *Journal of Invertebrate Pathology* 56: 106–116.
- Gilkeson LA & Hill SB (1986) Genetic selection for and evaluation of nondiapause lines of predatory midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). *Canadian Entomologist* 118: 869–879.
- Glazer I, Salame L & Segal D (1997) Genetic enhancement of nematicide resistance in entomopathogenic nematodes. *Bio-control Science and Technology* 7: 499–512.
- Grafton-Cardwell EE & Hoy MA (1986) Genetic Improvement of common green lacewing, *Chrysoperla carnea* (Neuroptera: Chrysopidae): selection for carbaryl resistance. *Environmental Entomology* 15: 1130–1136.
- Grewal PS, Tomalak M, Keil CBO & Gaugler R (1993) Evaluation of a genetically selected strain of *Steinernema feltiae* against the mushroom sciarid *Lycoriella mali*. *Annals of Applied Biology* 123: 695–702.
- Grewal PS, Gaugler R & Wang Y (1996) Enhanced cold tolerance of the entomopathogenic nematode *Steinernema feltiae*

- through genetic selection. *Annals of Applied Biology* 129: 335–341.
- Hajek AE, Hurley BP, Kenis M, Garnas JR, Bush SJ, et al. (2016) Exotic biological control agents: a solution or contribution to arthropod invasions? *Biological Invasions* 18: 953–969.
- Hamamura T (1987) Biological control of the Kanzawa spider mite, *Tetranychus kanzawai* Kishida, in tea [*Camellia sinensis*] fields by the predacious mite, *Amblyseius longispinosus* (Evans), which is resistant to chemicals (Acarina; Tetranychidae, Phytoseiidae). *Japan Agricultural Research Quarterly* 21: 109–116.
- Havron A, Rosen D, Prag H & Rössler Y (1991) Selection for pesticide resistance in *Aphytis* I. *A. holoxanthus*, a parasite of the Florida red scale. *Entomologia Experimentalis et Applicata* 61: 221–228.
- Henry LM, Roitberg BD & Gillespie DR (2008) Host-range evolution in *Aphidius* parasitoids: fidelity, virulence and fitness trade-offs on an ancestral host. *Evolution* 62: 689–699.
- Henry LM, May N, Acheampong S, Gillespie DR & Roitberg BD (2010) Host-adapted parasitoids in biological control: does source matter? *Ecological Applications* 20: 242–250.
- Hiltbold I, Baroni M, Toepfer S, Kuhlmann U & Turlings TCJ (2010) Selection of entomopathogenic nematodes for enhanced responsiveness to a volatile root signal helps to control a major root pest. *Journal of Experimental Biology* 213: 2417–2423.
- Houle D (1992) Comparing evolvability and variability of quantitative traits. *Genetics* 130: 195–204.
- van Houten YM, van Stratum P, Bruin J & Veerman A (1995) Selection for non-diapause in *Amblyseius cucumeris* and *Amblyseius barkeri* and exploration of the effectiveness of selected strains for thrips control. *Entomologia Experimentalis et Applicata* 77: 289–295.
- van Lenteren JC, Cock MJW, Brodeur J, Barratt BIP, Bigler F et al. (2011) Will the convention on biological diversity put an end to biological control? *Revista Brasileira de Entomologia* 55: 1–5.
- Hoy MA (1982) Aerial dispersal and field efficacy of a genetically improved strain of the spider mite predator *Metaseiulus occidentalis*. *Entomologia Experimentalis et Applicata* 32: 205–212.
- Hoy MA (1984) Genetic improvement of a biological control agent: multiple pesticide resistance and nondiapause in *Metaseiulus occidentalis* (Nesbitt) (Phytoseiidae). *Acarology* 6, Vol. II (ed. by DA Griffiths & CE Bowman), pp. 673–679. Ellis Horwood, Chichester, UK.
- Hoy MA (1985) Recent advances in genetics and genetic improvement of the Phytoseiidae. *Annual Review of Entomology* 30: 345–370.
- Hoy MA (1986) Use of genetic improvement in biological control. *Agriculture, Ecosystems and Environment* 15: 109–119.
- Hoy MA (1987) Developing insecticide resistance in insect and mite predators and opportunities for gene transfer. In H. M. LeBaron, R. O. Mumma, R. C. Honeycutt, J. H. Duesing, J. F. Phillips & M. J. Haas (Eds.), *ACS Symposium Series Vol. 334, Biotechnology in Agricultural Chemistry Chapter 10*, pp 125–138.
- Hoy MA (1988a) Biological control of arthropod pests: traditional and emerging technologies. *American Journal of Alternative Agriculture* 3: 63–68.
- Hoy MA (1988b) Selecting for pesticide resistance in *Trioxys pallidus*. *Walnut Research Reports* 1988: 80–103.
- Hoy MA (1990) Selecting for pesticide resistance in *Trioxys pallidus*. *Walnut Research Reports* 1990: 117–122.
- Hoy MA & Cave FE (1989) Toxicity of pesticides used on walnuts to a wild and azinphosmethyl-resistant strain of *Trioxys pallidus* (Hymenoptera: Aphidiidae). *Journal of Economic Entomology* 82: 1585–1592.
- Hoy MA & Cave FE (1991) Selecting for pesticide resistance in *Trioxys pallidus*. *Walnut Research Reports* 1991: 141–148.
- Hoy MA & Knop NF (1979) Studies on pesticide resistance in the phytoseiid *Metaseiulus occidentalis* in California. *Recent Advances in Acarology, Vol. I* (ed. by J Rodriguez), pp. 89–94. Academic Press, New York, NY, USA.
- Hoy MA & Knop NF (1981) Selection for and genetic analysis of permethrin resistance in *Metaseiulus occidentalis*: genetic improvement of a biological control agent. *Entomologia Experimentalis et Applicata* 30: 10–18.
- Hoy MA & Ouyang Y-L (1989) Selection of the western predatory mite, *Metaseiulus occidentalis* (Acari: Phytoseiidae), for resistance to abamectin. *Journal of Economic Entomology* 82: 35–40.
- Hoy MA, Knop NF & Joos JL (1980) Pyrethroid resistance persists in spider mite predator. *California Agriculture* 34: 11–12.
- Hoy MA, Westigard PH & Hoyt SC (1983) Release and evaluation of a laboratory-selected, pyrethroid-resistant strain of the predaceous mite *Metaseiulus occidentalis* (Acari: Phytoseiidae) in southern Oregon pear orchards and a Washington apple orchard. *Journal of Economic Entomology* 76: 383–388.
- Hoy MA, Groot JJR & van de Baan HE (1985) Influence of aerial dispersal on persistence and spread of pesticide-resistant *Metaseiulus occidentalis* in California almond orchards. *Entomologia Experimentalis et Applicata* 37: 17–31.
- Hoy MA, Cave FE, Beede RH, Grant J, Krueger WH et al. (1989) Guthion-resistant walnut aphid parasite release dispersal and recovery in orchards. *California Agriculture* 43: 21–23.
- Hoy MA, Cave FE, Beede RH, Grant J, Krueger WH et al. (1990) Release, dispersal, and recovery of a laboratory-selected strain of the walnut aphid parasite *Trioxys pallidus* (Hymenoptera: Aphidiidae) resistant to azinphosmethyl. *Journal of Economic Entomology* 83: 89–96.
- Jalali SK, Venkatesan T, Singh SP, Sadhana P & Murthy KS (2002) Evaluation of improved and selected species/strains of egg parasitoids. Report Number 5.1.1 (Trichogrammaimprovedandselectedstrains-1.pdf).
- Jalali SK, Murthy KS, Venkatesan T, Lalitha Y & Devi PS. (2006a) Adaptive performance of *Trichogramma chilonis* Ishii at low temperature. *Annals of Plant Protection Sciences* 14: 5–7.
- Jalali SK, Singh SP, Venkatesan T, Murthy KS & Lalitha Y (2006b) Development of endosulfan tolerant strain of an egg parasitoid *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae). *Indian Journal of Experimental Biology* 44: 584–590.

- Jalali SK, Venkatesan T, Murthy KS, Rabindra RJ, Lalitha Y et al. (2006c) Field efficacy of multiple insecticides tolerant strain of *Trichogramma chilonis* against American bollworm, *Helicoverpa armigera* on cotton. *Indian Journal of Plant Protection* 34: 173–180.
- Javier PA, Havron A, Morallo-Rejesus B & Rosen D (1991) Selection for pesticide resistance in *Aphytis* III. Male selection. *Entomologia Experimentalis et Applicata* 61: 237–245.
- Kawecki TJ, Lenski RE, Ebert D, Hollis B, Olivieri I & Whitlock MC (2012) Experimental evolution. *Trends in Ecology and Evolution* 27: 547–560.
- Kostiainen T & Hoy MA (1994) Genetic improvement of *Amblyseius finlandicus* (Acari: Phytoseiidae): laboratory selection for resistance to azinphosmethyl and dimethoate. *Experimental and Applied Acarology* 18: 469–484.
- Kraaijeveld AR & Godfray HCJ (1997) Trade-off between parasitoid resistance and larval competitive ability in *Drosophila melanogaster*. *Nature* 389: 278–280.
- Kraaijeveld AR, van Alphen JJM & Godfray HCJ (1998) The coevolution of host resistance and parasitoid virulence. *Parasitology* 116: 29–45.
- Kraaijeveld AR, Hutcheson KA, Limentani EC & Godfray HCJ (2001) Costs of counterdefenses to host resistance in a parasitoid of *Drosophila*. *Evolution* 55: 1815–1821.
- Kruitwagen A, Beukeboom LW & Wertheim B (2018) Optimization of native biocontrol agents, with parasitoids of the invasive pest *Drosophila suzukii* as an example. *Evolutionary Applications* 11: 1473–1497.
- Liu SS, Li YX & Tang ZH (2003) Host resistance to an insecticide favors selection of resistance in the parasitoid, *Cotesia plutellae* (Hymenoptera: Braconidae). *Biological Control* 28: 137–143.
- Lommen STE, de Jong PW & Pannebakker BA (2017) It is time to bridge the gap between exploring and exploiting: prospects for utilizing intraspecific genetic variation to optimize arthropods for augmentative pest control – a review. *Entomologia Experimentalis et Applicata* 162: 108–123.
- Lommen STE, Koops KG, Cornelder BA, de Jong PW & Brakefield PM (2019) Genetics and selective breeding of variation in wing truncation in a flightless aphid control agent. *Entomologia Experimentalis et Applicata* 167: this issue.
- Magalhães S & Matos M (2012) Strengths and weaknesses of experimental evolution. *Trends in Ecology and Evolution* 27: 649–650.
- Mally CW (1916) On the selection and breeding of desirable strains of beneficial insects. *South African Journal of Science* 13: 191–195.
- Mansoor MM & Shad SA (2019) Resistance of green lacewing, *Chrysoperla carnea* (Stephens), to buprofezin: cross resistance patterns, preliminary mechanism and realized heritability. *Biological Control* 129: 123–127.
- Mansoor MM, Raza ABM, Abbas N, Aqueel MA & Afzal M (2017) Resistance of green lacewing, *Chrysoperla carnea* Stephens to nitenpyram: cross-resistance patterns, mechanism, stability, and realized heritability. *Pesticide Biochemistry and Physiology* 135: 59–63.
- Margolies DC, Sabelis MW & Boyer JE (1997) Response of a phytoseiid predator to herbivore-induced plant volatiles: selection on attraction and effect on prey exploitation. *Journal of Insect Behavior* 10: 695–709.
- Markwick NP (1986) Detecting variability and selecting for pesticide resistance in two species of phytoseiid mites. *Entomophaga* 31: 225–236.
- Meyer RH (1975) Release of carbaryl-resistant predatory mites in apple orchards. *Environmental Entomology* 4: 49–51.
- Morse JG & Croft BA (1981) Developed resistance to azinphosmethyl in a predator-prey mite system in greenhouse experiments. *Entomophaga* 26: 191–201.
- Mukuka J, Strauch O, Hoppe C & Ehlers RU (2010) Improvement of heat and desiccation tolerance in *Heterorhabditis bacteriophora* through cross-breeding of tolerant strains and successive genetic selection. *BioControl* 55: 511–521.
- Nachappa P, Margolies DC, Nechols JR & Morgan TJ (2010) Response of a complex foraging phenotype to artificial selection on its component traits. *Evolutionary Ecology* 24: 631–655.
- Nachappa P, Margolies DC, Nechols JR & Campbell JF (2011) Variation in predator foraging behaviour changes predator-prey spatio-temporal dynamics. *Functional Ecology* 25: 1309–1317.
- Nakayama S, Seko T, Takatsuki J-I, Miura K & Miyatake T (2010) Walking activity of flightless *Harmonia axyridis* (Coleoptera: Coccinellidae) as a biological control agent. *Journal of Economic Entomology* 103: 1564–1568.
- Nakayama S, Takatsuki J, Seko T, Ando S, Miura K & Miyatake T (2013) Aphid consumption and residence time of larvae of flightless lady beetles, *Harmonia axyridis* (Coleoptera: Coccinellidae), on aphid-infested plants. *Applied Entomology and Zoology* 48: 223–227.
- Navajas M, Thistlewood H, Lagnel J, Marshall D, Tsagkarakou A & Pasteur N (2001) Field releases of the predatory mite *Neoseiulus fallacis* (Acari: Phytoseiidae) in Canada, monitored by pyrethroid resistance and allozyme markers. *Biological Control* 20: 191–198.
- Parker EDJ & Orzack SH (1985) Genetic variation for the sex ratio in a parasitic wasp, *Nasonia vitripennis*. *Genetics* 110: 93–105.
- Pintureau B (1991) Sélection de deux caractères chez une espèce de Trichogrammes, efficacité parasitaire des souches obtenues (Hym Trichogrammatidae). *Agronomie* 11: 593–602.
- Robertson JG (1957) Changes in resistance to DDT in *Macrocen-trus ancylivorus* Rohw. (Hymenoptera: Braconidae). *Canadian Journal of Zoology* 35: 629–633.
- Rolf J & Kraaijeveld AR (2001) Host preference and survival in selected lines of a *Drosophila* parasitoid, *Asobara tabida*. *Journal of Evolutionary Biology* 14: 742–745.
- Rouchet R & Vorburger C (2014) Experimental evolution of parasitoid infectivity on symbiont-protected hosts leads to the emergence of genotype specificity. *Evolution* 68: 1607–1616.
- Roush RT & Hoy MA (1980) Selection improves Sevin resistance in spider mite predator. *California Agriculture* 34: 11–14.

- Roush RT & Hoy MA (1981a) Genetic improvement of *Metaseiulus occidentalis*: selection with methomyl, dimethoate, and carbaryl and genetic analysis of carbaryl resistance. *Journal of Economic Entomology* 74: 138–141.
- Roush RT & Hoy MA (1981b) Laboratory, glasshouse, and field studies of artificially selected carbaryl resistance in *Metaseiulus occidentalis*. *Journal of Economic Entomology* 74: 142–147.
- Roush RT, Peacock WL, Flaherty DL & Hoy MA (1980) Dimethoate-resistant spider mite predator survives field tests. *Hilgardia* 34: 12–13.
- Routray S, Dey D, Baral S, Das AP & Mahantheshwara B (2016) Genetic improvement of natural enemies: a review. *Agricultural Reviews* 37: 325–332.
- Sailer RI (1961) Possibilities for genetic improvement of beneficial insects. *Germ Plasm Resources* (ed. by RE Hodgson), pp. 295–303. American Association for the Advancement of Science, Washington, DC, USA.
- Salame L, Glazer I, Chubinishvili MT & Chkhubianishvili T (2010) Genetic improvement of the desiccation tolerance and host-seeking ability of the entomopathogenic nematode *Steinernema feltiae*. *Phytoparasitica* 38: 359–368.
- Sayed AH, Pathan AK & Faheem U (2010) Cross-resistance, genetics and stability of resistance to deltamethrin in a population of *Chrysoperla carnea* from Multan, Pakistan. *Pesticide Biochemistry and Physiology* 98: 325–332.
- Schulten GGM, van de Klashorst G & Russell VM (1976) Resistance of *Phytoseiulus persimilis* A. H. (Acari: Phytoseiidae) to some insecticides. *Zeitschrift für Angewandte Entomologie* 80: 337–341.
- Segal D & Glazer I (2000) Genetics for improving biological control agents: the case of entomopathogenic nematodes. *Crop Protection* 19: 685–689.
- Seko T & Miura K (2009) Effects of artificial selection for reduced flight ability on survival rate and fecundity of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *Applied Entomology and Zoology* 44: 587–594.
- Seko T & Miura K (2013) Genetic improvement of invertebrate natural enemies-breeding and quality control of a flightless lady beetle. *Japanese Journal of Applied Entomology and Zoology* 57: 219–234.
- Seko T, Yamashita K & Miura K (2008) Residence period of a flightless strain of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in open fields. *Biological Control* 47: 194–198.
- Seko T, Sumi A, Nakano A, Kameshiro M, Kaneda T & Miura K (2014) Suppression of aphids by augmentative release of larvae of flightless *Harmonia axyridis*. *Journal of Applied Entomology* 138: 326–337.
- Shapiro DI, Glazer I & Segal D (1996) Trait stability and fitness of the heat tolerant entomopathogenic nematode *Heterorhabditis bacteriophora* IS5 strain. *Biological Control* 6: 238–244.
- Siddiqui A, Omkar Paul SC & Mishra G (2015) Predatory responses of selected lines of developmental variants of ladybird, *Propylea dissecta* (Coleoptera: Coccinellidae) in relation to increasing prey and predator densities. *Biocontrol Science and Technology* 25: 992–1010.
- Simberloff D (2012) Risks of biological control for conservation purposes. *BioControl* 57: 263–276.
- Simmonds FJ (1947) Improvement of the sex-ratio of a parasite by selection. *Canadian Entomologist* 79: 41–44.
- Spollen KM & Hoy MA (1992) Genetic improvement of an arthropod natural enemy: relative fitness of a carbaryl-resistant strain of the California red scale parasite *Aphytis melinus* DeBach. *Biological Control* 2: 87–94.
- Srivastava M & Singh AK (2015) Development of superior strain of *Trichogramma chilonis* Ishii for temperature tolerance. *Journal of Biological Control* 29: 68–74.
- Strauch O, Oestergaard J, Hollmer S & Ehlers RU (2004) Genetic improvement of the desiccation tolerance of the entomopathogenic nematode *Heterorhabditis bacteriophora* through selective breeding. *Biological Control* 31: 218–226.
- Strickler K & Croft BA (1982) Selection for permethrin resistance in the predatory mite *Amblyseius fallacis*. *Entomologia Experimentalis et Applicata* 31: 339–345.
- Thistlewood HMA, Pree DJ & Crawford LA (1995) Selection and genetic analysis of permethrin resistance in *Amblyseius fallacis* (Garman) (Acari: Phytoseiidae) from Ontario apple orchards. *Experimental And Applied Acarology* 19: 707–721.
- Tomalak M (1994) Selective breeding of *Steinernema feltiae* (Filipjev) (Nematoda: Steinernematidae) for improved efficacy in control of a mushroom fly, *Lycoriella solani* Winnertz (Diptera: Sciaridae). *Biocontrol Science and Technology* 4: 187–198.
- Turlings TCJ & Erb M (2018) Tritrophic interactions mediated by herbivore-induced plant volatiles: mechanisms, ecological relevance, and application potential. *Annual Review of Entomology* 63: 433–452.
- Venkatesan T & Jalali SK (2015) Development, characterization and field assessment of multiple insecticides and high temperature tolerant strain of an egg parasitoid, *Trichogramma chilonis* Ishii against crop pests. *New Horizons in Insect Science: Towards Sustainable Pest Management* (ed. by AK Chakravarthy), pp. 327–345. Springer, New Delhi, India.
- Venkatesan T, Jalali SK, Sivakumar G, Verghese A, Geetha GT & Pattar S (2016) Pesticide Tolerant Strain of Aphid Lion *Chrysoperla zastrowi sillemi*, An Important Predator of Sucking Pests. ICAR-National Bureau of Agricultural Insect Resources, Bangalore, India.
- Wang Q, Gu H & Dorn S (2003) Selection on olfactory response to semiochemicals from a plant-host complex in a parasitic wasp. *Heredity* 91: 430–435.
- Wang B, Ferro DN, Wu J & Wang S (2004) Temperature-dependent development and oviposition behavior of *Trichogramma ostrinia* (Hymenoptera: Trichogrammatidae), a potential biological control agent for the European corn borer (Lepidoptera: Crambidae). *Environmental Entomology* 33: 787–793.
- Weseloh RM (1986) Artificial selection for host suitability and development length of the gypsy moth (Lepidoptera: Lymantriidae) parasite, *Cotesia melanoscela* (Hymenoptera: Braconidae). *Journal of Economic Entomology* 79: 1212–1216.

- White EB, DeBach P & Garber MJ (1970) Artificial selection for genetic adaptation to temperature extremes in *Aphytis lingnanensis* Compere (Hymenoptera: Aphelinidae). *Hilgardia* 40: 161–192.
- Wilkes A (1942) The influence of selection on the preferendum of a chalcid (*Microplectron fuscipennis* Zett.) and its significance in the biological control of an insect pest. *Proceedings of the Royal Society of London B* 130: 400–415.
- Wilkes A (1947) The effects of selective breeding on the laboratory propagation of insect parasites. *Proceedings of the Royal Society of London B* 134: 227–245.
- Zhu K, Ke L & Xin J (1996) Selection and genetic analysis of fenvalerate resistance in *Amblyseius pseudolongispinosus* (Acari: Phytoseiidae). *Systematic and Applied Acarology* 1: 5–10.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Reviews of the improvement in natural enemies through experimental evolution or artificial selection.

Table S2. Studies that applied experimental evolution or artificial selection to improve natural enemies. Groups of studies in alternative light–dark gray shades are duplicate studies or involve the same evolved/selected strains. In column ‘Trait selected’, red indicates duplicate studies. In column ‘Initial population + size//Base population size//Generation size’, red indicates that evolved/selected strains from previous studies were used. In column ‘Selection response’, red indicates failed attempts to select for a trait. In column ‘Replicates’, green indicates replicated experimental evolution. In column ‘Common environment’, blue indicates that all test populations were maintained in a common environment.

Table S3. Natural enemies that were improved through experimental evolution or artificial selection.