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Perspective

If and when successful classical biological control fails

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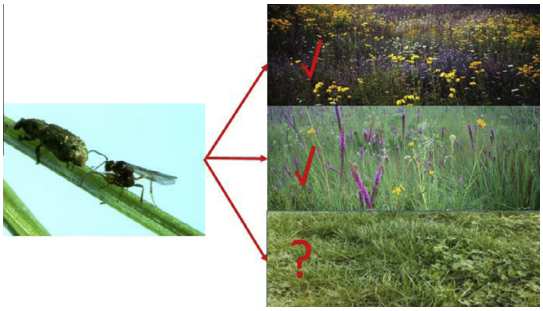
HIGHLIGHTS

- The reason for persistence of successful classical biological control is discussed.
- Possible mechanisms for classical biological control failure are considered.
- NZ control failure because of host sexual versus control agent asexual reproduction.
- Unique species-depauperate nature of NZ pastoral ecosystems is described.
- Simple ecosystem exaggerates effect of parasitoid/host reproductive differences.

GRAPHICAL ABSTRACT



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ABSTRACT

Classical biological control of insects has a long history of success, with high benefit–cost ratios. However, most attempts to introduce a biological control agent have been unsuccessful, largely because the agent does not establish in the new environment. This perspectives paper discusses the possibility that even successful biological control may eventually fail, although records show that this is far from a common event. A documented example of eventual biological control failure is discussed and the prospect for future failures analyzed. Part of this analysis is based on an introduced weevil pest in New Zealand and its successful parasitoid biological control agent. The potential fragility of this host–parasitoid relationship is considered, as well as why it may indeed be starting to show signs of instability; this is particularly from the point of view of New Zealand's often species-poor agricultural ecosystems.

1. Introduction

Classical biological control of pest animals, weeds and diseases involves the release of specialist natural enemies of foreign origin in a target species' ecosystem with the objective of permanently reducing its numbers and impact. Such a control system can be elegant, self-sustaining, non-polluting and inexpensive – *when it works* (Gurr and Wratten, 2000). To this might be added: 'and as long as it continues to work'. If previously-successful biological control starts to fail, the consequences could be enormous, given the high benefit-cost ratios of many past successes (Page and Lacey 2006; de Clerqet et al., 2011). A wide range of factors point to the

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accelerating need for biological control. Indeed, this requirement continues to grow as world trade and speed of transport systems accelerate and the need to suppress invasive exotic pest species is greater than ever (e.g. Goldson 2011). However, there are numerous challenges including increasing pesticide resistance in many insect species, more rigorous environmental scrutiny of existing compounds leading to their removal from use, very high pesticide registration costs resulting in fewer successful new molecules coming to market and heightened consumer awareness of residues and environmental impacts (Gurr, Wratten and Snyder 2012). Also economic and practical considerations mean that there is demand for self-sustaining solutions to pest problems, such as classical biological control, that do not require frequent and expensive management interventions (e.g. de Schutter, 2010; Wratten et al., 2013).

Declining opportunities for conventional solutions is coinciding with human population growth and with this, the demand for what has been referred to as 'sustainable intensification' (e.g. Pretty 1997; Godfray et al., 2012). Biological control can contribute to this requirement, but since 1880, so-called classical biological control of insect pests has remained at a success rate of around 10% (Gurr and Wratten, 2000). If the successful 10% also start to fail, then the consequences would be profound.

In spite of this low rate, successful classical biological control may to date have appeared to be a 'magic bullet' because it can deliver long-term outcomes. However, there is some evidence that resistance could arise. For example, Henter and Via (1995a) found significant variation in susceptibility to a parasitic wasp *Aphidius ervi* in Haliday *Acyrthosiphon pisum* (Harris) clones collected from a single population. The wasps oviposited in aphids from both resistant and susceptible lines, but the eggs failed to develop in the resistant hosts indicating that this aphid population had the potential to evolve resistance. However, field-collected material taken in early and late summer, covering several generations, revealed no response to selection by the wasps. The authors speculated that amongst other things, this could have been caused by fitness costs associated with resistance or interference caused by other control systems. Similarly, Kraaijeveld and Godfray (1997) working on *Asobara tabida* (Nees) parasitism of *Drosophila melanogaster* Meigen found that the extent to which the latter was selected to invest in defenses against pathogens and parasites depended on the advantages that ensue should infection/parasitism occur, but also on the costs of maintaining defenses in the absence of such potential selection pressures. Also there is the suggestion of evolution of resistance whereby the host *Hypera postica* (Gyllenhaul) has apparently exhibited an increase in the encapsulation rate of the parasitoid *Bathyplectes curculionis* (Thomson) (Berberet et al., 2003). More broadly, Hufbauer and Roderick (2005) have analyzed in some detail, the implications of microevolution in biological control.

In spite of such indications, there are indeed remarkably few, maybe only one, published examples of successful classical biological control clearly failing through the onset of resistance in the prey/host. Indeed, often where successful classical biological control has not persisted, this has turned out to be in conjunction with changed management practices such as altered pesticidal regimes, or changed genetic composition of the control agents through releases of additional strains etc. The former appears to be the case with the biological control of the walnut aphid (*Chromaphis juglandicola* Kaltenbach) by *Trioxys pallidus Haliday (Aphididae)* in California (N. Mills, UC Berkeley; pers. comm.). This process may now be occurring in New Zealand with the accelerating use of broad-spectrum pesticides against the recently-colonized tomato–potato psyllid (*Bactericera cockerelli* Sulc.) on solanaceous crops. It appears that the only definitive example of the evolution of prey/host resistance is from Canada. Here, the larch sawfly, *Pristiphora erichsonii* Hartig (Hymenoptera: Tenthredinidae), was controlled for 27 years by the ichneumonid wasp, *Mesoleius tenthredinus* Morley before failing through widespread host encapsulation of the parasitoid's eggs (Ives and Muldrew 1984; Dahlsten and Mills 1999). A Bavarian strain of *M. tenthredinis* was later found that could overcome the immune response of *P. erichsonii*, and crosses between the Bavarian and Canadian strains also inherited this ability (Turnock et al., 1976). Related to this, Turnock and Muldrew (1971) suggested that the likelihood that resistance of this type will develop can be reduced by providing more than one effective control agent, and recent experimental results have supported this (Kraaijeveld et al., 2012).

Overall, such complexity and infrequency of the occurrence of biological control resistance is in marked contrast to the extent, rapidity and unequivocal nature of the appearance of resistance to pesticides and transgenic pest-resistant crops (e.g. Tabashnik et al., 2013). There has been some discussion as to why classical control should be so robust (e.g. Holt and Hochberg 1997). Based on the work of such contributors as Henter and Via (1995a) and Kraaijeveld and Godfray (1997), there are indications of a series of factors that are thought to contribute to biological control stability. A probable important factor is that biocontrol control agents can co-evolve with a pest and thereby counteract resistance developing in the latter (Henter and Via, 1995a,b). Should a pest develop resistance in this way, it may incur metabolic or other costs (e.g. a reduction in fecundity) as a consequence (Kraaijeveld and Godfray, 1997). There could also be mechanisms that stabilize susceptibility through the provision of either spatial (e.g. Hanski, 1981) or temporal refugia (e.g. Godfray, Hassell and Holt, 1994). Low disturbance regimes can also preserve biological control effectiveness (e.g. Jonsson et al., 2012). Related to this, diverse agro-ecosystems may stabilize biological control, as they often comprise a wide range of natural-enemy guilds that contribute to pest suppression (Tylianakis and Romo, 2010).

Evidence now suggests that at least some of these drivers of biological control stability could well break down. A case study in this context is New Zealand's pastoral ecosystem. This currently supports high biological control efficacy of several introduced weevil pests (e.g. Barlow and Goldson, 1993; Barker and Addison 2006; Gerard et al., 2011). However, as discussed below, there may now be some reason to look again at the durability of such success, despite the history of biological control persistence – see earlier. This concern is based on the relatively low alpha diversity of invertebrates in New Zealand's intensive pastoral ecosystem compared with native grassland systems. The former are effectively incomplete 'transplants' of the biodiversity found in the northern hemisphere origin of New Zealand's pasture plants (ryegrass and white clover) with relatively few New Zealand native herbivorous arthropod species persisting in that environment. Thus, while New Zealand's farmland may superficially appear to be similar to large pastoral 'monocultures' elsewhere e.g. forb-rich European meadows, the latter include far more native and endemic biodiversity, suggesting greater ecological stability and a larger community of biological control agents. This contrasts with New Zealand pasture which probably has weaker food-web assemblages (*sensu* Bersier et al., 2002) than in many other regions. These circumstances suggest that in the case of parasitoid-based systems at least, should classical biological control programs begin to weaken through the acquisition of, for example, immune-based pest resistance, then the 'background biological control' may not be powerful enough to ameliorate the potential consequences.

Exotic pest populations in New Zealand's grasslands often build up to very high and damaging densities (e.g. Barker et al., 1989; Goldson et al., 1998; Gerard et al., 2009), probably because of the homogeneity of the pasture ecosystem and absence of species-rich guilds, discussed above (Goldson et al., 1997). Release from natural enemies in a new range is well known from the invasion literature