

2.4 Rapid Biocontrol Evolution in New Zealand's Species-sparse Pasturelands

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This contribution discusses the implications of evidence for the loss of efficacy of the parasitoid *Microctonus hyperodae* Loan (Hymenoptera: Braconidae) against the exotic weevil pasture pest, the Argentine stem weevil (ASW) *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae) in New Zealand. This decline has occurred to the extent that increased weevil damage levels are now being reported (Popay *et al.*, 2011). Of particular significance is the parthenogenetic reproduction of the parasitoid versus the sexual reproduction of ASW. While the weevil can adapt via genetic recombination associated with sexual reproduction, the same does not apply to the clonal parasitoid. This may have led to what is sometimes called an 'unequal evolutionary arms race' (e.g., Goldson *et al.*, 2015). To explore this further, the genotypes of both the parasitoid and the weevil are being investigated using the method known as genotyping-by-sequencing (J. Jacobs, unpublished data).

In addition to this apparent reproductive asymmetry, it has been postulated that New Zealand's pastoral ecosystems have also contributed to the acquisition of resistance (Goldson *et al.*, 2014; Tomasetto *et al.*, 2017). In spite of the superficial appearance of similarity, New Zealand's pastoral ecosystems are very different from their Palaeartic-equivalent grazed grasslands. The 'improved' sown pastures in New Zealand, covering about 40% of the land area, originally comprised indigenous forest and native grasses which have been cleared over the last 150 years. The sown pastures now comprises incomplete assemblages of deliberately and accidentally introduced species. More specifically, many of New Zealand's pastures are dominated by perennial ryegrass, *Lolium perenne* L. (Poaceae) and white clover, *Trifolium repens* L. (Fabaceae). This combination has been and remains, the most cost-effective and sustainable means of providing forage for the country's livestock industries. Thus New Zealand pastures are in effect, a partial and very incomplete transplant from elsewhere and as such, cannot be considered to be 'evolved' ecosystems such as are found in the Palaeartic. Pasture ecosystems, e.g., in the UK, effectively occupy gaps in a predominantly sylvan landscape. Taken as a whole, British landscapes comprise a continuum of invertebrate species across both the grassland

and forest ecosystems in stark contrast to New Zealand's abrupt boundary between its indigenous and exotic habitats between which there is little interchange of species (Brockerhoff *et al.*, 2012).

Exotic pest populations in New Zealand's grasslands often build up to very high and damaging densities, despite these species being of minor significance in their native ranges. For example, ASW can scarcely be detected in its natural range, whereas in New Zealand they can reach densities of up to 700 m⁻² (Barker and Addison, 1993). Part of the reason for this is likely to be the absence of natural enemy guilds in New Zealand's grasslands (e.g., Goldson *et al.*, 1997); this is an example of the 'enemy release hypothesis' (e.g., Hong and Stiling, 2006). The extraordinary lack of co-evolved diversity in the New Zealand is highlighted by the fact that there are 117 *Listronotus* spp. in temperate South America (Donato *et al.*, 2003) compared to New Zealand's one.

UK (2017) lists the numbers of significant natural enemy species found in UK crop and grasslands allowing a comparison to be made with similar estimates for New Zealand's grasslands. For many taxa the numbers of species of natural enemies are far lower in New Zealand suggesting less natural enemy diversity. For example, in the UK there are 274 species of Syrphidae (Diptera), compared with about 45 species in New Zealand. Tellingly, only ten of these New Zealand species are estimated to occur in pastures. Related to this, Thomas *et al.* (1992) and others, have shown that in the UK, natural enemies tend to overwinter in the boundaries of fields and then migrate into the pasture/croplands in spring, consistent with the idea of British woodland and grassland being an ecological continuum. In New Zealand, however, while there is considerable indigenous natural enemy diversity in the native ecosystems, much of it does not move into the country's agro-ecosystems. McLachlan and Wratten (2003), have shown this clearly with predatory spiders.

The success of classical biological control in New Zealand pastures dealing with invasive weevil species has been extraordinarily high. Barlow and Goldson (1993), Basse *et al.* (2015) and Barker (2013) have shown high levels of control of *Sitona discoideus* Gyllenhal in lucerne *Medicago sativa* L., *S. obsoletus* (Gmelin) (Coleoptera: Curculionidae) in clover and ASW in pasture. This has all been via species and ecotypes of *Microctonus*. Such success in all three biocontrol programmes is unexpected since historically, the chance of a successful biological control initiative has been estimated to be about 10% (Gurr and Wratten, 2000). Thus, in New Zealand the chance of this result was 1:1000. Such success again, can be attributed to the lack of ecosystem complexity and consequently parasitoid natural enemies (e.g., hyperparasites). The very thing that allowed the pest species to thrive also allowed the parasitoid species to thrive, resulting in the recorded very high levels of parasitism.

Thus, there has been strong selection by *M. hyperodae* on the ASW, in the absence of other interfering or competing species. This effect has probably been heightened by the uniformity of New Zealand pastures, that preclude the provision of either spatial (e.g., Hanski, 1981) or temporal refugia (e.g., Godfray *et al.*, 1994) for the weevil host. In summary, the unequal evolutionary arms race has been accentuated by the pastoral ecosystem itself. New Zealand's farmlands are typical of an island ecology affected by invasive species. It is therefore perhaps significant that the only other recorded example of similar rapid evolution in response to parasitism has been in Hawaii, where a cricket became resistant to a parasitic fly (Pascoal, 2014).

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