1.6 Inadvertent Reconstruction of Exotic Food Webs: Biological Control Harms and Benefits

J.M. Kaser[1], A.L. Nielsen[1], P.K. Abram[2] and G.E. Heimpel[3]

[1]Department of Entomology, Rutgers University, Bridgeton, New Jersey, USA, joe.kaser@rutgers.edu, [2]Agriculture and Agri-food Canada, Agassiz Research and Development Centre, Agassiz, British Columbia, CANADA, [3]Department of Entomology, University of Minnesota, Saint Paul, Minnesota, USA

The movement of exotic and invasive species around the planet continues to accelerate (Hulme, 2009), resulting in a global trend toward homogenization of biodiversity (Capinha *et al.*, 2015). In the process, invasive species are frequently re-connected with accidentally introduced natural enemies from their native ranges (e.g., Colazza *et al.*, 1996; Ramani *et al.*, 2002; Heimpel *et al.*, 2010; Talamas *et al.*, 2015; Medal *et al.*, 2015). These natural enemies are often polyphagous and have the potential to suppress the invasive resource population as well as interact with native species through a variety of direct and indirect pathways. Using a combination of mathematical modeling and experimental work in the lab and field, we examined the case of the introduced aphid parasitoid *Aphelinus certus* Yasnosh (Hymenoptera: Aphelinidae) which attacks the invasive soybean aphid in North America. We contrast these findings with other natural enemy-invasive species interactions in the context of biological control risk-benefit assessment.

***Aphelinus certus* and the soybean aphid in North America:** The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), was first reported in North America in 2000, and it quickly spread throughout much of the USA and Canada (Ragsdale *et al.*, 2011). The soybean aphid has become the most important insect pest in North America cultivated soybeans, whereas in its native range in Asia it is only an occasional pest (Heimpel *et al.*, 2004; Liu *et al.*, 2004). The 'enemy release hypothesis' is a plausible explanation for this difference in pest status, and an importation biological control program has been pursued. Interestingly, a parasitoid species that was investigated in quarantine, but that was not released due to concerns over risk to non-target native aphids, was eventually introduced inadvertently. This parasitoid, *Aphelinus certus*, was first reported in 2005 in the eastern U.S, and it has since spread so that it now co-occurs with the soybean aphid throughout most of the species' North American range. The introduction pathway for *A. certus* is unknown.

We expanded on host range testing efforts initiated by Keith Hopper (at the U.S. Department of Agriculture) (Hopper *et al.*, 2017), and evaluated 18 aphid species as potential hosts for *A. certus* in the laboratory. We confirmed that *A. certus* can develop in several native aphid species, and documented parasitism of some non-target species, by *A.*

certus in the field. We conclude that the decision not to release *A. certus* was well-founded. However, using a field exclusion cage experiment, we demonstrate that population growth of the soybean aphid is significantly reduced when in the presence of *A. certus* at ambient field densities. *Aphelinus certus* has become the overwhelmingly dominant parasitoid attacking the soybean aphid in areas where we conducted surveys (Minnesota, USA). Moreover, during a three-year field study, we observed that *A. certus* populations tracked very closely to soybean aphids over a wide range of densities ($R^2 = 0.90$ for a simple linear regression of ln-transformed densities). Thus, biological control of soybean aphid by *A. certus* is likely already resulting in less insecticide use by growers that utilize action thresholds.

Modeling biological control risks and benefits: We employed a general mathematical modeling approach to further evaluate conditions that may influence risks to non-target species versus benefits to biological control of pests (Kaser and Heimpel, 2015). Model simulations demonstrate that a range of outcomes are possible and that natural enemy-mediated indirect effects may vary dramatically depending on which factors delimit host range (i.e., preference versus performance). Apparent competition can result in a biological control benefit, even at low levels of non-target impact. However, if a parasitoid experiences egg limitation, high oviposition rates on resistant non-target hosts can dramatically decrease biological control efficacy while still causing significant harm to non-target populations (Kaser and Heimpel, 2015).

Recently, we expanded upon this modeling effort to evaluate possible natural enemy-mediated indirect impacts of non-reproductive mortality (i.e. cases where the host dies but the parasitoid does not successfully reproduce). We pursued this investigation in part because parasitoid-induced host egg abortion – a phenomenon that occurs when both the host egg and the developing parasitoid die – appears to be common for native scelionid egg parasitoids attacking the invasive brown marmorated stink bug, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae) (Abram *et al.*, 2014, 2016). We found that host egg abortion can have important biological control benefits if the parasitoid population can be maintained on other suitable hosts species in the community. We also note that *H. halys* represents another case where a parasitoid, *Trissolcus japonicus* (Ashmead) (Hymenoptera: Scelionidae) being evaluated for importation biological control was introduced inadvertently (Talamas *et al.*, 2015).

Conclusions: The case study involving the soybean aphid and *A. certus* clearly demonstrates the tradeoffs involved in biological risk-benefit assessment. *A. certus* presents a risk to native North American aphids, but if it contributes to a large reduction in soybean aphid populations, there may be ecological benefits as well. For example, populations of the invasive harlequin lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), are strongly linked to the soybean aphid in North America (Bahlai *et al.*, 2015), and reductions in *H. axyridis* populations would likely benefit native aphids as well as native coccinellids. There have recently been a handful of cases in which an exotic pest has reconnected with a parasitoid coincidentally being studied for importation biological control (Heimpel *et al.*, 2010; Talamas *et al.*, 2015; Medal *et al.*, 2015). These cases present opportunities to increase our understanding of invasion biology and improve our chances of successful importation biological control. Natural enemy-mediated indirect effects are common in nature, and they may be particularly important in understanding the potential impact of polyphagous natural enemies that successfully develop on abundant invasive species.

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