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

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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.

**References**


