

# Biological control and indirect effects

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In a recent article in *TREE* [1], Pearson and Callaway consider how indirect effects can lead to even host-specific biological control agents impacting on nontarget species. Although the authors raise some interesting points, we feel that the indirect effects that they explore might not be as generally applicable to biological control as they contend.

The first indirect effect considered is 'ecological replacement', which describes the potential for nontarget impacts through reduction of a pest or weed that has become integrated into a native community. From the examples given (e.g. the case of rabbits manipulating habitat suitability for the large blue butterfly), it is clear that an exotic weed or pest might itself have a positive functional role in the ecosystem. Under these conditions, reduction of this species could have a significant impact on one or more nontarget species, irrespective of natural enemy specificity. However, such negative effects would result from reducing the pest by any means, whether chemical, biological, mechanical, or through land-use and/or habitat change. As such, singling out biocontrol does not seem entirely justified. Moreover, this indirect effect runs counter to the authors' main conclusion that 'strong' natural enemies should be safer. What it does highlight is the need for proper ecological and socioeconomic evaluation of pests before control to determine probable costs and benefits [2].

The second indirect mechanism discussed is the potential for 'compensatory response' by a weed or pest following attack by a biocontrol agent, which might increase negative interactions between the target and nontarget species. Here, in spite of the suggestion that the general concepts in the paper apply to biocontrol of both invertebrate pests and plants, it is unclear how compensatory responses could occur with invertebrate biocontrol. For example, nonspecific immune responses following attack by a nonlethal pathogen or parasitoid can affect performance of concomitant pathogens and parasitoids [3], but it seems unlikely that this could increase the vigour of a pest to such an extent that competition with, for example, indigenous herbivores, was increased.

The issue of differences in mode of action between biocontrol agents of plants and biocontrol agents of invertebrates also has bearing on the third indirect mechanism identified, that of 'food-web interactions'.

Pearson and Callaway provide an interesting example of food-web interactions between knapweed, gall flies and deer mice to illustrate how insect natural enemies of plants might themselves become superabundant and act as supplementary food to subsidize populations of other species. They identify this to be a particular risk when the natural enemy is weak and so is not self-limited by reductions in target host density. However, if the interaction between a specific natural enemy and insect pest is very weak (i.e. the agent kills very few target hosts), the enemy will tend to remain rare with little chance of generating food-web effects [4].

Whilst we support the premise that host specificity should not be the single criterion for agent selection, arguing additionally for use of 'strong' agents is somewhat misleading. As the authors indicate, the key to effective control when using multiple agents is to construct complementary assemblages and avoid redundancy. In this context, even a weak natural enemy might be functionally significant [5]. However, a strong, highly specific natural enemy might still have substantial nontarget impacts via transient natural enemy spill over or enrichment, en route to equilibrium [4,6]. With this kind of complexity, we believe that the most salient message from the article is that to quantify or predict impact of biocontrol on target or nontarget species, we need more research on the population and community dynamics of multi-species predator-prey assemblages.

## References

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