

Response to Thomas *et al.*: biocontrol and indirect effects

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In a recent *TREE* article [1], we identified three categories of unintended indirect effects that can arise from host-specific biological control agents: (i) ecological replacement; (ii) compensatory responses; and (iii) food-web interactions. Although our review focused on the biocontrol of plant pests, we suggested these concepts also apply to the biocontrol of invertebrate pests. Thomas *et al.* [2] argue that our treatment of ecological replacement was unjustified and that indirect effects owing to compensatory responses and food-web subsidies do not apply to biocontrol of invertebrate pests.

Thomas *et al.* state that indirect effects owing to ecological replacement are not unique to biocontrol, so biocontrol should not be singled out in this matter. This reasoning implies that biocontrol practitioners need not concern themselves with such unintended effects simply because they also arise from other control methods. We disagree. We believe all control methods should be the object of concern and scientific evaluation. Moreover, the problems that arise from indirect effects owing to ecological replacement represent a shortfall in biocontrol practice. By contrast, the problems that arise from indirect effects owing to compensatory responses and food-web subsidies represent shortfalls in biocontrol theory. This distinction has not previously been made [3–5], but it is important for advancing our understanding of pest control. Thomas *et al.*'s assertion that problems with ecological replacement highlight the need for proper evaluation of pests before control merely echoes our key point regarding ecological replacement [1].

Thomas *et al.* contend that insect pests are unlikely to exhibit compensatory responses. They argue that non-specific immune responses to biocontrol attack would not be likely to increase pest vigor sufficiently to impact nontarget species. They might be correct, but we suggest that the primary mechanism for compensatory response in invertebrate pests might be behavioral. Research indicates that invertebrate predators can indirectly affect herbivore prey through interaction modifications arising from behavioral shifts where herbivores switch hosts [6]. Thus, a biocontrol attack on a polyphagous invertebrate pest could result in a shift by the pest from primary to secondary hosts. Such a response could result in unintended herbivory on other plants and unintended competition with invertebrate herbivores. Host shifts by biocontrol insects causing indirect effects on native

herbivores are known [7]. It seems reasonable that a biocontrol insect could cause a host shift by an herbivore pest that indirectly affects other insects and plants.

With regard to food-web subsidies, Thomas *et al.* argue that if the interaction between a natural enemy and insect pest is very weak, the biocontrol will remain rare and fail to subsidize food webs. This argument misses the point. The strength of the interaction is relative, and the overall direction of the interaction is the key. If the top-down effect is strong enough to suppress the pest below the ecological threshold (see Figures 1,2 from [1]), there will be no food-web subsidy, because the biocontrol will decline with the pest (if it is host specific). However, if the biocontrol fails to reduce the pest sufficiently, there is potential for a food-web subsidy to result from strong bottom-up effects. For example, ladybird beetles (Coccinellidae) are commonly used for invertebrate pest control. These natural enemies not only become quite abundant, but many also aggregate seasonally, thereby increasing their potential to generate food-web subsidies. In Californian agricultural systems, the convergent ladybird *Hippodamia convergens* is an important biocontrol agent of aphid pests that migrates to natural habitats to form dense winter aggregations [8] where it potentially offers food-web subsidies with unknown consequences. The potential for food-web subsidies from biocontrol of invertebrate pests exists and should be explored.

Finally, Thomas *et al.* suggest our advocacy for strong biocontrol agents is misleading because guilds of weak biocontrol agents might serve to complement control efforts. We emphasize that the importance of interaction strength also applies to biocontrol guilds. A biocontrol guild should have a strong negative effect that suppresses the target pest. If an individually weak biocontrol agent contributes to forming a strong biocontrol guild through additive or synergistic effects, then its use is justified, because the measure of interaction strength applies to the guild. If the guild does not substantially suppress its target then the potential for harmful indirect effects is even greater. This is why we emphasized the need for additional research on natural enemy complexes. Strong, host-specific biocontrols or biocontrol guilds remain the best protection against nontarget effects.

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Letters

Human expansion: the roles of castaways and cultural practices

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The recent review in *TREE* by Hurles *et al.* [1] emphasizes the importance of linguistic and genetic studies in tracing human expansion into the Pacific and, of course, nobody could argue against that. Yet, there are two other aspects that should not be overlooked.

The first aspect deals with examples of temporary settlements from other parts of the world. These were established by early seafarers and fishermen (often repeatedly and over many years), who did not usually take womenfolk with them on their collecting trips. Women stayed at home, whilst the men went hunting or fishing and usually returned with their quarry or catch. Sometimes, however, the men would get lost or be blown off course. Thus, the Falkland Islands probably had the occasional group of Yaghan castaways, stranded and surviving on the islands, but with no way to either reproduce (because of the absence of women) or to return home [2]. Martin [3] introduces the term 'ephemeral discovery' to describe North American colonization before 12 000 years ago by men who crossed the Bering Strait without bringing women with them. To establish an increasing population under these circumstances was, of course, impossible, but the population did leave traces and had some ecological impact. 'Ephemeral colonists' could have unintentionally introduced alien species of plants and animals, they could have decimated local populations of especially sought-after food or medicinal species, and they would have created shelters and tools for themselves from locally available resources. Thus, their presence,

even without leading to permanent settlements, would have had some consequence.

The second aspect is that cultural practices, for instance the preparation of bark cloth [4], or dietary habits and restrictions [5,6], can provide very useful clues as to the origins and migratory routes of a people. Dietary practices in particular are very resistant to change and it has been suggested that entomophagy, (i.e. the consumption of insect species) spread with the expansion of humans from southern Asia into the Pacific [7]. Such studies should be integrated with linguistic and genetic analyses to provide a clearer picture of the expansion of humans throughout the world.

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