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Relationships between natural enemy diversity and biological control

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Natural enemy diversity generally strengthens biological control, but individual studies have found everything from positive to negative effects. We discuss the factors that promote these different outcomes. We argue that a trait-based approach is helpful to improve our understanding of the relationship between enemy diversity and biological control, and suggest that enemy diversity is likely to be particularly important as an insurance against effects of climate change. Future research should increase the scale and ecological realism of enemy diversity studies, and consider both the strength and stability of biological control. Such research is likely to reveal even stronger evidence that conserving enemy biodiversity will improve biological pest control.

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Introduction

Increasing enemy species richness generally strengthens biological control [1,2,3•]. However, all possible outcomes have been observed and weakened biological control with increasing enemy richness occurred in nearly 30% of studies in the meta-analysis by Letourneau et al. [1]. Understanding when and why enemy biodiversity enhances prey suppression is critical for how we manage pests, and has challenged ecologists for decades [4,5,6,7,8,9].

In diverse enemy communities, the strength of prey suppression is determined by the net effect of multiple mechanisms [10]. Enemy diversity strengthens prey suppression via *resource partitioning*, where enemy species consume different sub-populations or life stages of the target prey, *facilitation*, where one enemy species enhances prey capture by a second enemy species, and *positive selection effects*, where greater enemy diversity increases chances that a particularly effective enemy species is present. Enemy diversity weakens prey suppression via *intraguild predation*, where enemy species consume one another in addition to the focal prey, *behavioural interference*, where one enemy species reduces prey capture by a second enemy species, and *negative selection effects*, where greater enemy diversity increases the likelihood that a particularly strong intraguild/interfering enemy is present. Recent studies have made progress in conclusively demonstrating the operation of these mechanisms by employing clever experimental designs, statistical procedures, and molecular methods [11,12,13•,14••].

In this review, we discuss recent progress in our ability to predict enemy diversity effects on shared prey. We focus our attention on the ecological factors that moderate enemy diversity effects, distinguishing between those that are intrinsic to the natural enemy community (i.e., the traits of the enemy community) and those that are extrinsic to the natural enemy community (traits of the prey and environmental conditions) (Table 1, Figure 1). We examine the possibility that diverse enemy assemblages are valuable because they maintain stable biological control in the face of environmental change (Figure 1), a hypothesis that has received surprisingly little attention. Finally, we conclude by suggesting profitable avenues for future research.

Intrinsic ecological factors that moderate the effect of natural enemy diversity

There is accumulating evidence that an understanding of the composition of natural enemy traits (Table 1) can improve our ability to predict how diverse enemy communities affect biological control. In a meta-analysis, Griffin et al. [2] found that the effect of enemy species diversity on prey suppression was more positive when the taxonomic distinctness of the enemy community was high (i.e., the enemies were distantly related). Since distantly related enemies are likely to possess different traits, higher enemy trait diversity may have led to improved prey suppression. Using a compilation of traits known to influence ecosystem functions delivered by animals (incl.

Table 1

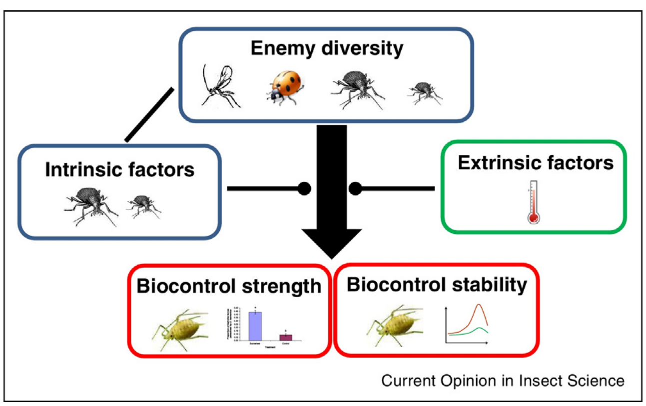
Factors moderating effects of enemy diversity on biological control, with examples of papers.

Instrinsic factors (enemy traits)	Extrinsic factors (prey traits and environmental variables)
Body size [22•,58]	Prey life cycle [36,37]
Foraging mode [9,35]	Prey diversity [63,64]
Microhabitat use [9,29]	Prey density [24,65]
Diet breadth [10,11]	Prey patchiness [38]
Phenology [33,61]	Plant composition/Habitat complexity [66,67]
Diel activity [61]	Host plant taxon [30]
Relative abundance [62]	Temperature [28,39•]
	Spatial and temporal scale [2]

biocontrol), Gagic et al. [15••] compared the relationship between a range of indices of functional diversity, species richness and abundance and estimates of ecosystem functioning. They found that functional trait diversity was consistently a better predictor of ecosystem functioning than measures of species diversity and abundance. However, in some cases the availability of an individual trait was the strongest predictor of the function. Thus the abundance of individual traits in enemy communities may in some cases be the best predictor of biological control.

One trait that has received considerable attention is body size. Metabolic theory predicts that many processes, including predation, should be strongly affected by body size [16]. Body size has been found to predict prey consumption rates and population growth rates well in both aquatic and terrestrial food webs [17,18,19], but see [20]. Importantly, body mass is an easy trait to measure, and it is directly comparable across a wide range of taxa, which makes it attractive to work with. Schneider et al. [21] predicted trophic interaction strengths in a generalist predator–decomposer community by combining an allometric trophic network model and microcosm experiments. The model sets limits on abundance, diet breadth and feeding strength based on body mass of the enemies and prey. It accurately predicted the trophic interactions between all species in the microcosm experiments [21]. It also appears that body size can be a strong predictor of prey suppression in the field. When comparing the ability of different diversity measures to predict aphid suppression, Rusch et al. [22•] found that the community-weighted mean body size of enemies was the strongest predictor of aphid suppression, with communities with smaller enemy species providing stronger control. To explain this result, the authors presented evidence that high densities of large ground beetles disrupted aphid biocontrol by smaller spiders. This is in line with results from a meta-analysis, which concluded that adding a top predator to the community decreases prey consumption because of increased intraguild predation [23]. Interestingly, the results of both Rusch et al. [22•] and Schneider et al. [21] suggests that ground-predator communities with a high diversity in enemy body sizes are prone to negative enemy-enemy interactions that can disrupt biological control. Likewise, interspecific variation in body size promotes intraguild predation among foliar predator species, such as coccinellid larvae [24]. In general, as the size difference between predator species increases, the food-web motif is expected to shift from competition, to intraguild predation, to a food chain with the larger predator species eating only the intraguild predator [25]. Thus, in the case of body size, increasing trait diversity may often weaken rather than strengthen biological control.

Figure 1



The effect of increasing enemy species diversity on the strength and stability of biological control depends on the traits in the enemy community (intrinsic factors), and on prey traits and environmental conditions (extrinsic factors). For example, when greater species diversity increases variation in enemy body sizes, negative enemy-enemy interactions like intraguild predation can weaken the strength of biological control [22•]. However, intraguild predation only occurs when enemy species forage in the same microhabitat, a phenomenon that can depend on temperature [39•]. Such context-dependency complicates the relationship between enemy diversity and biological control. When enemy species vary in their response to extrinsic factors like temperature, theory predicts that diverse enemy communities will provide more reliable biological control.

Behavioural traits of enemies are more difficult to measure, but also have important implications for prey suppression (Table 1). Complementary microhabitat use by enemy species reduces the opportunity for negative interactions and can strengthen prey suppression. Foliar and ground enemies [26,27], enemies occupying different strata in the plant canopy [28,29], and enemies feeding on the edge and centre of leaves [30,31] can have additive and possibly synergistic effects on prey suppression (but see McCoy et al. [32] for a discussion of methodological challenges involved in accurately identifying synergism). Enemy species with complementary phenologies also provide temporally continuous prey suppression without negative enemy-enemy interactions [33]. Enemy species typically display differences in activity levels. A recent study showed that, even within a species, a mixture of