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# Effects of global environmental changes on parasitoid–host food webs and biological control

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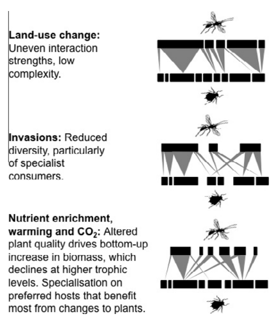
## HIGHLIGHTS

- Food-web approaches quantify changes to community-wide interactions.
- For biocontrol, webs quantify attack rates, non-target impacts, use of alternative hosts, etc.
- An increasing number of studies are finding effects of environmental changes on parsitoid–host networks.
- Changes to biomass at different trophic levels, web complexity and interaction evenness have all been shown.

## GRAPHICAL ABSTRACT

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## ABSTRACT

Global environmental changes threaten biodiversity and the interactions between species, and food-web approaches are being used increasingly to measure their community-wide impacts. Here we review how parasitoid–host food webs affect biological control, and how their structure responds to environmental change. We find that land-use intensification tends to produce webs with low complexity and uneven interaction strengths. Dispersal, spatial arrangement of habitats, the species pool and community differences across habitats have all been found to determine how webs respond to landscape structure, though clear effects of landscape complexity on web structure remain elusive. The invasibility of web structures and response of food webs to invasion have been the subject of theoretical and empirical work respectively, and nutrient enrichment has been widely studied in the food-web literature, potentially driving dynamic instability and altering biomass ratios of different trophic levels. Combined with food-web changes observed under climate change, these responses of food webs could signal changes to biological control, though there have been surprisingly few studies linking food-web structure to pest control, and these have produced mixed results. However, there is strong potential for food-web approaches to add value to biological control research, as parasitoid–host webs have been used to predict indirect effects among hosts that share enemies, to study non-target effects of biological control agents and to quantify the use of alternative prey resources by enemies. Future work is needed to link food-web interactions with evolutionary responses to the environment and predator–prey interactions, while incorporating recent advances in predator biodiversity research. This holistic understanding of agroecosystem responses and functioning, made possible by food-web approaches, may hold the key to better management of biological control in changing environments.



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## 1. Introduction

The world is undergoing unprecedented rates of environmental change, which drive local and global extinctions, range shifts, and the assembly of novel communities and ecosystems (Hobbs et al., 2006; Sala et al., 2000; Walther, 2010). In addition, more subtle changes can occur to the interactions between species (Tylianakis et al., 2008a) including the herbivore–plant, predator–prey and parasitoid–host interactions that underpin biological control in productive ecosystems. In some cases, the response of these interactions to a particular global change driver can be predictable. For example, nitrogen deposition tends to generate bottom-up increases in the strength or frequency of herbivore–plant, predator–prey and parasitoid–host interactions (e.g., Moon and Stiling, 2000; Throop and Lerdau, 2004; Tylianakis et al., 2008a). In contrast, responses of these trophic interactions to other global change drivers (such as climate, land-use change, invasions, and $CO_2$ enrichment) can be highly variable, with increases, decreases and no change in the strength (e.g. mortality rate) or frequency of interactions observed across studies, species and regions (Tylianakis et al., 2008a).

Given these inherent difficulties in deriving generalities of how pairwise interactions between species will respond to environmental changes, it may seem even more difficult to derive predictions about the responses of entire communities. However, a growing number of empirical studies quantify how networks of interacting species (e.g., food webs) respond to environmental changes (Bascompte, 2009; de Ruiter et al., 2005a; Petchey et al., 1999; Tylianakis et al., 2010). By averaging out the idiosyncratic responses of individual species and pairwise interactions, a network approach can provide a more holistic overview of community changes. Moreover, networks provide additional information on the architecture of interactions, which can affect ecosystem functioning (Petchey et al., 1999; Poisot et al., 2013; Thompson et al., 2012) and emergent properties such as stability or robustness to the loss of species (Bascompte et al., 2006; Bastolla et al., 2009; de Ruiter et al., 2005b; Dunne et al., 2002; Ings et al., 2009; Ives and Cardinale, 2004; McCann, 2000; Montoya et al., 2006; Thebault and Fontaine, 2010).

Many empirical food-web studies involve parasitoids and their hosts, because of the relative ease of measuring their trophic interactions compared with those of mobile generalist predators that consume multiple prey individuals during their lifetime. This research is gaining significant momentum in the ecological literature, yet its application to biological control remains rare, despite the obvious potential relationship between parasitoid–host food webs and the suppression of pest insects.

Therefore, the aim of this review is to highlight the utility of a network approach for understanding the responses of parasitoid–host systems and biological control to global environmental changes. To make the case for their applied relevance, we begin by summarizing the few examples to date where network approaches have been used to study biological control systems, and highlight aspects that could potentially inform pest management. We then summarize the increasing number of studies that have documented changes to parasitoid–host food webs in response to environmental changes, and aspects of theory that may explain these changes and their relationship with biological control. At the same time, we emphasize those areas in which empirical data are lacking. Finally, we draw attention to recent progress in network studies that may prove particularly useful in understanding biological control systems, and highlight some of the major research directions needed to improve understanding of biological control within parasitoid–host networks in a changing environment.

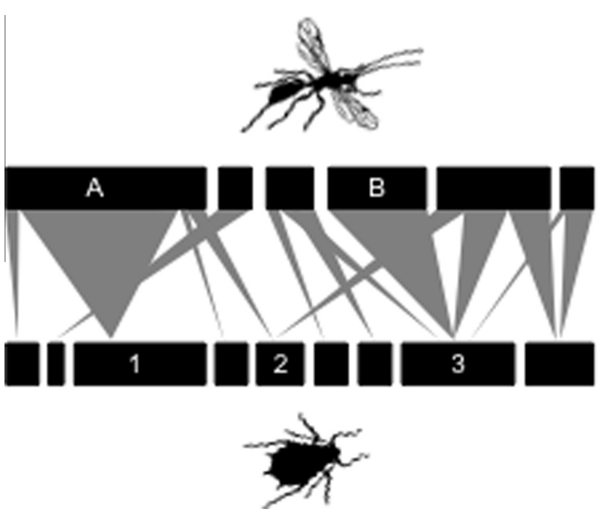


**Fig. 1.** Schematic of a quantitative parasitoid–host food web, showing several aspects relevant for biological control. The bars on the top and bottom row represent different parasitoid and host species respectively. The width of the bars represents their relative abundance. A grey link between a parasitoid and host species indicates a trophic interaction, and the width of the link at the top represents its relative frequency within the web. This web has a relatively uneven structure typical of agricultural systems, with a strong (i.e. very frequent) link between parasitoid A and host 1, and the remaining links are comparatively weaker (e.g., between parasitoid A and host 2). Because hosts 1 and 2 share a parasitoid (A), they have the potential to engage in apparent competition, whereby increased abundance of one host could drive increased population size of parasitoid A, and consequently elevated attack rates on the other host. Host 3 is the most highly connected, making it likely to receive higher and more constant attack rates (due to predator diversity effects). However, by virtue of its connectedness, host 3 is also more likely to engage in apparent competition with other host species. Compared with parasitoid A, parasitoid B is less likely to have non-target impacts because of its narrow host range. For this reason, parasitoid B will also be less likely to benefit from habitat management to provide alternative host resources, and its population dynamics may be less stable because they depend entirely on the availability of a single host.

## 2. Why does food-web structure matter for biological control?

Superficially, biological control appears to involve simple plant-pest-enemy chains, however, the reticulate food-web connections between multiple herbivores and a suite of predators may determine the success of any particular control program. Several studies of parasitoid–host food webs have involved species in agroecosystems, possibly due to their tractability and low diversity compared with natural systems. Yet despite this, direct tests of how food-web structure affects biological control remain surprisingly rare, and those that have been carried out have yielded contrasting results. One key example was a manipulative experiment involving food webs containing 193 species of parasitoids and 370 herbivore hosts from a variety of families in southwest English farms (Macfadyen et al., 2009). The authors found that differences in the structure of food webs did not affect parasitism rates across a variety of host species or the robustness of the food web as a whole to simulated species loss. The authors then introduced a novel herbivore (a gracillarid leafminer *Phyllonorycter leucographella*) to experimentally simulate a new pest incursion, and found that higher species richness of parasitoids and differences in food-web structure did not affect control of the new 'pest' (Macfadyen et al., 2009).

Similarly, (Gagic et al., 2011) found significant variability in the structural complexity (number of parasitism links per species) of food webs involving cereal aphids and their primary and hyperparasitoids (i.e. secondary parasitoids of primary parasitoids), even though in their case there was little variation in species richness at each trophic level. However, in contrast to the results of MacFadyen et al. (2009), the structure of the food webs was found