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

Jason M. Tylianakis\textsuperscript{a,b} & Amrei Binzer\textsuperscript{c,d}

\textsuperscript{a} Corresponding author: School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand. jason.tylianakis@canterbury.ac.nz Ph: +64 3 364 2735
\textsuperscript{b} Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, United Kingdom.
\textsuperscript{c} J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Berliner Str. 28, 37073 Göttingen, Germany.
\textsuperscript{d} Max Planck Institute for Evolutionary Biology, August-Thienemann-Straße 2, 24306 Plön, Germany.
abinzer@uni-goettingen.de

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.

Keywords
Network, apparent competition, bottom-up, climate, top-down, trophic cascade

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 CO2 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.

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 to affect parasitism rates, with more connected webs (more links per species, see Fig. 1) being associated with lower parasitism rates on aphids but higher rates of hyperparasitism (Gagic et al., 2011).
This was because the increased connectedness of the aphid-parasitoid web was driven by more hosts being used by each parasitoid species (i.e. higher parasitoid generality), rather than more parasitoid species attacking each host (“vulnerability” in food web terminology), which occurred in the hyperparasitoid web and can correlate positively with attack rates (Tylianakis et al., 2007; see also Fig.1). Overall, rates of both primary and hyper-parasitism increased in landscapes with a lower proportion of arable land (Gagic et al., 2011).

These few conflicting studies imply potential, but equivocal, relevance of food webs for biological control, and additional work across a range of contexts is needed. Yet, both empirical and theoretical ecology suggest a number of ways in which network approaches have the potential to inform pest management. For example, ecological theory suggests that predators and parasitoids are best able to suppress their prey when they can maintain high densities by exploiting other prey or food resources (Polis and Strong, 1996; Tylianakis et al., 2004) (e.g., parasitoid A, but not B, in Fig. 1). This uncouples predator dynamics from those of any single prey species, and allows the predators to maintain high densities even when densities of any individual prey species decline (Polis and Strong, 1996). For this reason, generalist predators are often highly effective biological control agents (Schmitz & Barton, this issue), though they also typically have severe non-target impacts and often disrupt control by other enemies (Snyder and Ives, 2001; Symondson et al., 2002). Therefore, when selecting control agents to minimize non-target impacts, or when attempting to enhance agents by providing alternative prey resources in a conservation biological control program (Landis et al., 2000), it would be very beneficial to know their potential prey range, the frequency with which they feed on each prey species, and the potential for different alternative prey to enhance predator densities. This information can readily be extracted from quantitative food webs, and studies on apparent competition (competition via a shared natural enemy; Holt, 1977) in parasitoid-host webs have produced some interesting findings.

In one example, Carvalheiro et al. (2008) found that a tephritid seed predator (Mesoclanis polana) introduced to Australia for biological control of the invasive
plant Bitou (*Chrysanthemoides monilifera*) not only provided ineffective control, but it also harboured native parasitoid species that also attacked native seed-feeders. Its abundance was therefore correlated negatively with the diversity and abundance of native species due to apparent competition. The authors quantified food webs involving 60 primarily native plant species, 73 seed-herbivore species (9 of which came from Bitou), and 42 parasitoid species (8 of which likely came from the tephritid control agent). This allowed them to determine which species shared natural enemies with the control agent, and could therefore suffer increased parasitism when enemy densities grew on the abundant food resource provided by the control agent and its invasive host plant.

Similarly, Henneman and Memmott (2001) reared Hawaiian Lepidoptera larvae from a remote native forest to generate quantitative food webs (like Fig. 1). They found that 83% of parasitoids reared from native moths were historically-introduced classical biological control agents, 14% were accidental immigrants, and only 3% were native species. This suggests the potential for widespread non-target impacts of control agents on native species, and the food-web approach used here could be used to quantify which native species would be most heavily affected, and how they might respond to elevated parasitoid abundances following pest outbreaks (see Fig. 1).

In a related example, Alhmedi et al. (2011) found that aphids in crop and non-crop habitats may share large numbers of natural enemies, and that stinging nettles in particular may provide important alternative prey for natural enemies. However, Rand et al. (2012) used a food-web approach to show that at least the primary parasitoids of nettle and cereal aphids do not overlap, reducing the potential for apparent competition and enhancement of cereal aphid parasitoids using alternative hosts on nettle. These examples demonstrate that parasitoid or host overlap in food webs can be a useful tool for identifying potential indirect effects, but Morris et al.,(2004), however, went a step further and tested experimentally the utility of food webs for predicting apparent competition. They used quantitative parasitoid-leafminer food webs to predict which leafminers would share natural enemies and
thus have the potential to engage in apparent competition. They then removed
some of these species, and found that parasitism rates declined on the species with
which the removed leafminers shared enemies, and this even led to one species
increasing in density (Morris et al., 2004).

In addition to predicting non-target effects, food webs constructed from global
databases can be used to choose agents that are less likely to have their
effectiveness reduced by apparent competition with native species (Paynter et al.,
2010). Indirect effects may even cascade throughout the food web, through a
mixture of top-down, bottom-up and horizontal effects across trophic levels. For
example, a recent study by Sanders et al. (2013) involved removal of a parasitoid
species from experimental bean-aphid-parasitoid food webs, and found
extraordinary indirect pathways of extinction. Removal of the parasitoid released its
host aphids from top-down pressure, and thereby improved their competitive ability
against other aphid species. These other aphids became rarer as a result of
interspecific competition, causing increased extinction rates in their parasitoids that
were not removed (Sanders et al., 2013). These results emphasize the utility of a
food-web approach for understanding the consequences of species extinctions and
additions, including the effects of control agents on non-target species, though
indirect effects predicted from food-web connections may not necessarily function
as expected, and some experimental verification may be needed (Tack et al., 2011).

In addition to these indirect effects, parasitoid-host food webs have been used to
understand the bottom-up effects of host plants on higher trophic levels. For
example, Jones et al. (2011) demonstrated that genetic diversity of grasses was
positively associated with primary- and particularly hyperparasitoid species diversity,
even though herbivore diversity remained unaffected. This suggests that there was
some direct effect of plant genetic diversity on higher trophic levels, or an unknown
effect of plant genotypes on herbivores that affects higher trophic levels. Such
effects were also observed in a study that compared aphid, parasitoid and
hyperparasitoid food webs on feral and cultivated brassicas (Bukovinszky et al.,
2008). Differences in physical and physiological plant traits led to larger aphid
individuals and populations on feral *Brassica*, which caused a pathway of changes up to higher trophic levels. The number of primary parasitoid species and parasitized aphids was higher on feral plants, though aggregative responses of parasitoids were insufficient to compensate for the higher host densities, so per capita rates of parasitism were in fact lower. However, bottom-up effects were strongest at the next trophic level, with nearly a twofold difference in hyperparasitoid densities and elevated species and link diversity in hyperparasitoid food webs on feral plants (Bukovinszky et al., 2008). Such food-web impacts at higher trophic levels bear clear relevance for plant breeding and genetic modification, though it remains unclear whether genetically-modified plants have greater differences in their parasitoid-host food webs than occurs normally across genetic lines (von Burg et al., 2011).

As these indirect effects across food webs become better understood, there may be avenues in the future for manipulating food-web structure to improve the resilience or levels of control. Food-web ecologists have paid considerable attention to the factors that determine the mean length of food chains (Post, 2002), which in a biological control setting determines the negative effects of the fourth trophic level on control agents. Increases in the connectivity of food webs increase the number of predator or parasitoid species attacking each prey or host species (Fig. 1), and this diversity has been shown on multiple occasions to improve control of prey (Cardinale et al., 2003; Snyder et al., 2006; Tylianakis et al., 2007). However, the opposite pattern of less-connected webs having higher attack rates has also been found (Gagic et al., 2011; Montoya et al., 2003), and the benefits of multiple predators attacking each prey species may depend on characteristics of the crop or pest community (Tylianakis and Romo, 2010). They might, for example, be greatest when prey have complex life cycles (Ramirez and Snyder, 2009; Wilby and Thomas, 2002) or are patchily distributed in space or time (Tylianakis et al., 2008b). Nevertheless, recent theoretical advances in the application of predator diversity research to food webs (i.e. using interaction structure as a measure of trophic complementarity; Poisot et al., 2013) may provide an important way forward in managing natural enemy diversity in a way that maximizes attack rates and minimizes unintended indirect effects. In any case, the above examples provide clear evidence that food-
web approaches have a significant, often unexplored, potential application to biological control. Given this potential importance, it will be necessary to understand how food-web structure will change in the future, and recent work with parasitoid-host food webs has begun to provide some answers.

3 Global environmental change and parasitoid-host food webs

A growing number of studies are finding effects of global environmental changes on the structure of parasitoid-host food webs. In many cases, these changes are not a mere consequence of changing species richness, meaning that web analyses provide additional information on impacts beyond that which could be assessed with traditional biodiversity metrics (Tylianakis et al., 2010). For example, the impacts of land-use change on biodiversity can be highly variable, and often unrelated to changes in food-web structure. Below we outline the few studies to date that have quantified changes to parasitoid-host food webs under the major drivers (Sala et al., 2000) of global environmental change. Concomitantly, we highlight advances in theoretical work that can help to explain the empirical web results.

3.1 Land-use change

Probably the greatest body of literature on global change and parasitoid-host food webs has examined their responses to aspects of land-use change. The early work in this area examined the effects of land-use intensification by comparing different crop types. For example, Tylianakis et al. (2007) compared 48 food webs involving cavity-nesting bees and wasps and their parasitoids across a land-use intensity gradient in Ecuador. The authors found that food webs in the most intensive systems (rice and pasture) had highly uneven interaction strengths, dominated by one or two interactions, and that these changes to the patterns of interactions were not driven simply by changes in species diversity. This structure characteristic of intensive habitats, containing few strong and many weak interactions (e.g., Fig. 1), is known from theoretical work to promote stability in food webs (McCann et al., 1998), and if it is a general feature of agricultural food webs, it could be beneficial for providing consistency in biological control. In support of this hypothesis, later work on the same food webs revealed that the most intensively-managed systems showed the
least variability in their structure across months and from site to site, in keeping with
the prediction of high spatial and temporal stability (Laliberté and Tylianakis, 2010).
This low interaction turnover in highly-modified systems was likely the result of open
habitats providing few physical or structural impediments to host finding by
parasitoids, which allowed them to consistently locate and attack their preferred
host species (Laliberté and Tylianakis, 2010).

Those differences in web structure were greatest when comparing shaded vs. open
habitats, but even more subtle differences in land use can generate differences in
parasitoid-host food-web structure. For example, MacFadyen et al. (Macfadyen et
al., 2009) found differences in the overall structure of food webs in organic,
compared with conventional, mixed farms, alongside higher diversity of plants,
herbivores and parasitoids. Similarly, Albrecht et al. (Albrecht et al., 2007) found that
the diversity and abundance of hosts (cavity-nesting bees and wasps) and their
parasitoids, along with the diversity, complexity and evenness of their trophic
interactions, were higher in restored than in intensively-managed meadows, and
these changes were related to higher plant diversity.

These results demonstrate that differences in land management, even of a particular
habitat type, can generate differences in the structure of parasitoid-host food webs,
with more-natural systems tending to have food webs with higher complexity and
evenness of interactions. Yet, such differences between habitats raise a number of
interesting questions. First, in biological control systems the movement of species
across habitat types is important (Dreyer and Gratton, this issue), for example when
field margins, urban greenspaces, diverse crops or natural habitats are used to
increase the abundances or efficacy of natural enemies (Bianchi et al., 2006; Landis
et al., 2000)(Burkman and Gardiner, this issue)(Chisholm et al., this issue), or when
attempting to reduce non-target effects of natural enemies that ‘spill over’ from
crop systems into natural habitats (Rand et al., 2006). Yet, the extent to which either
of those processes occurs depends on the propensity of enemies to move across the
boundary between habitats, and on the extent to which they use resources (e.g.,
hosts/prey) in each habitat. To quantify both of these processes, MacFadyen and
Muller (2013) measured the movement of parasitoids across habitats (canola, wheat, pasture, fallow, and perennial native vegetation), and the host use of each species in each habitat. They found that natural vegetation harbored diverse parasitoid assemblages, but there were few examples of parasitoid species attacking hosts in both native and crop vegetation. This was not simply due to parasitoids remaining in a single habitat, as the authors recorded considerable movement into canola fields from both cereals and native habitats (Macfadyen and Muller, 2013).

The interplay of dispersal, the available species pool, and differences in community composition across habitats is therefore likely to be an important determinant of food-web structure in habitat patches, and research to disentangle the relative importance of different mechanisms is needed. Furthermore, because species differ in their habitat requirements, patches within mosaic agricultural landscapes may contain varied subsets of the regional species pool, which will determine which species are available to interact with others (Tscharntke et al., 2007). Furthermore, both patch and landscape characteristics can determine parasitoid nutritional and life-history state, and thereby affect foraging behavior and attack rates (Roitberg and Gillespie, this issue). In a study of two plants, an herbivore, its two parasitoids and their hyperparasitoids in a fragmented habitat in Finland, Van Nouhuys and Hanski (2002) showed that not all species are present in all patches across the landscape. Consequently, the interactions among species depended strongly on the presence/absence of other potential interacting partners, and the length of the food chain in each patch depended on metapopulation dynamics. The spatial arrangement of different habitats, their proximity to one another, and the distance between patches of a single habitat can thus be expected to significantly affect parasitoid-host interactions.

Not surprisingly, therefore, various studies have examined how landscape structure and habitat fragmentation affect the structure of parasitoid-host food webs, as well as other types of species interaction network (Hagen et al., 2012). Seminal work on simple tritrophic systems showed that landscape complexity (in particular the amount of non-crop habitat) can alter parasitoid-host interactions and reduce crop
damage (Thies and Tscharntke, 1999). However, extrapolation of these findings to
diverse food webs has not been straightforward. For example, Kaartinen and Roslin
(2011) found that leafminer-parasitoid food webs on isolated oaks contained fewer
species and a different composition to connected oaks, but the food-web structure
(several measures of complexity and interaction evenness) did not change. In
contrast, a study of wheat aphids and their parasitoids and hyperparasitoids in
Germany found that parasitoid diversity was not related to landscape complexity
(amount of non-crop area) for either primary or secondary parasitoids (Rand et al.,
2012). These authors also found overall rates of primary parasitism to be generally
low, but hyperparasitism increased significantly with increasing landscape
complexity, largely due to the response of one hyperparasitoid species. Similarly,
Gagic et al. (Gagic et al., 2011) found little variation in the richness of aphids or
parasitoids along a landscape complexity gradient; however, they found significant
changes in feeding interactions. Surprisingly, food webs were less complex in
structurally-complex landscapes (those with less arable land), though this was largely
driven by specialization on a single aphid host that dominated in complex
landscapes. Nevertheless, primary- and hyperparasitism were higher in complex
landscapes, such that primary parasitoids were better able to achieve successful
biological control of aphid hosts.

This positive relationship between landscape complexity and parasitism rates is also
predicted by theory, with a spatially-explicit grid-based simulation model of rape
pollen beetle and its specialist parasitoids showing that parasitism rate is negatively
influenced by fragmentation and isolation (Visser et al., 2009), congruent with the
empirical results of Thies and Tscharntke (1999). This simulation result occurred
regardless of the amount of semi-natural habitat in which the host and parasitoids
occurred. However, population dynamics of the parasitoids in virtual landscapes
revealed that the effect of habitat fragmentation on parasitoid persistence
depended on total habitat availability in the landscape. When habitat was abundant
at the landscape scale, parasitoid persistence decreased with increasing
fragmentation (Visser et al., 2009), and it would be interesting to extend this model
to include multiple parasitoid and host species. Patterns of parasitoid extinction with
habitat loss have been observed empirically in food webs. For example, Fenoglio et al. (2012) found that loss of Argentinean forest habitat from the landscape initiated a bottom-up cascade of extinctions from plants to leaf miners to parasitoids, with reductions in parasitoid richness ultimately driving decreases in parasitism rates. Previous work by the authors (Cagnolo et al., 2009) also suggested that food-web parameters, such as trophic level and trophic generality, determined their sensitivity to habitat fragmentation.

However, the effect of habitat loss on biological control may also depend on the connectivity of the remaining habitat (Mitchell et al., 2013). At low habitat availability, the model of Visser et al. (2009) found parasitoid persistence to be highest at intermediate levels of fragmentation, even though parasitism rate was negatively influenced by fragmentation and isolation irrespective of total habitat availability. From a management perspective, their results suggest that maximizing habitat connectivity when habitat is abundant will maximize both parasitism rates and parasitoid dynamic persistence. However, in landscapes with little habitat, it may not be possible to maximize both parasitism and parasitoid persistence (Visser et al., 2009). This importance of connectivity emphasizes that the patterning, as well as the total amount, of habitat within the landscape can be important.

3.2 Invasion

Although we are not aware of any specific parasitoid-host examples, the theoretical work relating predator-prey food-web structure to invasion has focused more on the aspects of structure that promote invasibility (rather than response of structure to invasion), though this still has considerable relevance for biological control. For example, dynamic simulations of food webs across a range of connectedness revealed that invaders are more likely to succeed if they are generalists, herbivores or omnivores, or consumers with a narrow feeding niche that are relatively invulnerable to predation (Romanuk et al., 2009). This suggests that pest species such as leaf rollers or miners may establish more easily, and that generalist predators that feed at multiple trophic levels may be the most successful control
agents. Food webs tended to be more easily invaded if they had low connectedness, high mean biomass and higher species richness (Romanuk et al., 2009), congruent with results for herbivore invasion in a Lotka-Volterra assembly model on food webs of increasing connectedness (Baiser et al., 2010). However, in the latter study, top predators invaded highly-connected webs more successfully due to an increase in intermediate prey species. These studies suggest that complex food webs may resist pest invasion, but also promote the fourth trophic level (e.g., hyperparasitoids), a finding congruent with the empirical results of Gagic et al. (2011) discussed above. Also, it is important to recognize that classical biological control is, in itself, an invasion process. Therefore, the above characteristics that make food webs more easily invaded are likely to promote establishment of control agents.

In contrast to these theoretical studies, empirical work has focused more on the impact of invasions on food-web structure than vice versa. For example, Timms et al., (2012) measured the impact of gypsy moth (Lymantria dispar) invasion on parasitoid-host food webs in Canadian forest. They found no significant impact on web structure, and little sharing of parasitoids with native species, indicating a low potential for apparent competition with native caterpillars. However, the impacts of invaders on other species in food webs may depend on the connectedness of those species (Fig. 1). For instance, an invasive plant has been shown to have cascading negative effects on native herbivore and parasitoid abundance and parasitoid richness, but these effects were confined to trophic specialists, not generalists (Carvalheiro et al., 2010). This decline in specialist consumers disrupted top-down control, and released generalist herbivores from apparent competition with specialists. If weeds or crops were regarded as ‘invasive’ plants (relative to the natural food web), these results suggest that their direct and indirect interactions with native species in the landscape web could potentially facilitate the decline of specialist natural enemies and the population growth of generalist pests. Heleno et al. (Heleno et al., 2009) also found a decrease in insect richness with plant invasion, though they did not distinguish the effect of diet breadth or find any significant changes in food-web structure. However, they did test for effects of plant invasion on insect biomass, and found that it declined due to large insects on native plants.
being replaced by smaller insects on alien plants, with no concomitant change in insect abundance. Therefore, even though pests may increase in abundance, a decline in biomass may partly mitigate any increases in their overall levels of herbivory.

3.3 Nutrient enrichment

Although nutrient enrichment (particularly nitrogen deposition) is considered to be a major driver of global environmental change (Sala et al., 2000), its relevance to biological control is lessened by the commonly high (often deliberately elevated) fertility of agricultural systems. Nevertheless, the literature on nutrient enrichment and food webs bears relevance for understanding biological control in low vs. high fertility regions and crops, and for understanding differences between natural vs. agricultural food webs.

Empirical work has found subtle plant-mediated effects of nutrient enrichment on parasitoid-host food web structure. A Brazilian study of Asteraceae, seed-head herbivores and their parasitoids along a soil fertility gradient found changes in abundance and richness at each trophic level (Fonseca et al., 2005). However, after controlling for changes in richness, there was no change in network connectedness or top-down control along the gradient, and effects of soil nutrients were partly obscured by their covariation with tree density and the preference of Asteraceae for high-light environments. However, a more recent study controlled for such effects by adding nitrogen experimentally to plots of seminatural grassland, in factorial combinations with warming treatments (de Sassi and Tylianakis, 2012). The added nutrients caused a bottom-up increase in biomass, which declined in intensity at higher trophic levels. Specifically, plant biomass showed the greatest increase, and lepidopteran herbivores showed a tendency to increase in biomass with elevated nitrogen, though this effect was entirely plant-mediated. In contrast, parasitoid biomass and rates of parasitism were unaffected by nitrogen addition, indicating that the parasitoid aggregative and/or population responses were insufficient to compensate for the increase in host biomass (de Sassi and Tylianakis, 2012). These food-web effects are congruent with known responses of agricultural systems to...
fertilization, whereby crop biomass increases and bottom-up subsidies to natural enemies are often not sufficiently rapid to control herbivore outbreaks. Despite increases in total caterpillar abundance in this grassland experiment, the relative abundance of different parasitoid and host species was unchanged (de Sassi et al., 2012). However, increased body size of caterpillars, particularly two very abundant species, in the fertilized plots led parasitoids to consistently focus their attack on these larger hosts. This shows that nutrient enrichment may drive trait-mediated changes in food-web interactions and that total parasitism rates may not convey changes to the frequency of individual parasitoid-host interactions within the web (de Sassi et al., 2012). Due to changes in the sex ratios of parasitoid eggs allocated to hosts of different sizes (e.g. preferential oviposition with female eggs in larger hosts; Henri et al., 2012), host species that show the greatest increases in body size could become greater sources of female parasitoids, thereby amplifying apparent competition with hosts that share these parasitoids.

Theoretical exploration of host-parasitoid systems under nutrient enrichment are lacking, though the importance of enrichment for food webs in general has a long history of research. Seminal work on two-species predator–prey systems found that enrichment generates oscillations and finally drives species into extinction - the so-called ‘paradox of enrichment’ (Rosenzweig, 1971). This finding has subsequently been broadened by Rip and McCann (2011), who demonstrated that any process that increases the flow of energy relative to consumer loss rates causes biomass to shift in favor of higher trophic levels, and thus destabilizes systems. However, this destabilization has been shown to occur in size-structured food webs with type II (logarithmic), but not type III (sigmoidal), functional responses to prey density (Rall et al., 2008), indicating that trait-mediated shifts in predator numerical responses to prey density (such as those observed empirically by de Sassi et al. (2012)) may be crucial for determining system stability under nutrient enrichment. The extent to which nutrient enrichment destabilizes parasitoid-host food webs, where predators are usually smaller than their prey (in contrast to the model of Rall et al. (2008)), remains to be determined. However, the theoretical and empirical work summarized above suggests that instability, host population growth and failure of control by
parasitoids may accompany nutrient enrichment, thereby weakening biological control in heavily-fertilized crops.

3.4 CO₂ and Climate change

Despite considerable work on pairwise predator-prey or parasitoid-host interactions under elevated CO₂ (reviewed in Tylianakis et al., 2008a), there has been no work to our knowledge on parasitoid-host food webs. However, the fertilization effect of CO₂ on plant growth may drive bottom-up changes to food webs similar to those of nutrient enrichment discussed above. Indeed, a recent study of a tritrophic food chain on alfalfa found that plant and herbivore (Spodoptera exigua) biomass increased under elevated CO₂, whereas the beneficial indirect effects of parasitoids (Cotesia marginiventris) on alfalfa biomass declined (Dyer et al., 2013), congruent with the effects of nitrogen enrichment on biomass at different trophic levels in parasitoid-host food webs (de Sassi and Tylianakis, 2012).

In addition to their effects on plant growth, greenhouse gases such as CO₂ drive changes to climate (IPCC, 2007), and the effects of climate on parasitoid-host food webs have received more attention than the direct effects of CO₂. Interestingly, a number of these studies have also examined the interactive effects of climate and other drivers such as nutrient enrichment or elevated CO₂, and non-additive effects among the different drivers appear to be common. For example, Binzer et al. (2012) examined a three-species food chain using a bioenergetic model that incorporates temperature and body-mass dependencies of biological process rates. They found that increasing fertility at a constant temperature increased the carrying capacity and the efficiency with which consumers use their resources (evidenced by the half-saturation density declining with increased carrying capacity). However, with increasing fertility, consumer biomass began to fluctuate, with this destabilization being driven by both bottom-up and top-down pressures, and eventually driving the predator and prey to extinction (leaving only the primary producer). However, this ‘paradox of enrichment’ was reversed by increasing temperature, which reduced the carrying capacity and stabilized the system up to a certain point. But beyond this, increased temperature increased the metabolic demands of consumers beyond their
consumptive capabilities (Binzer et al., 2012). This temperature threshold changed with nutrient enrichment, such that the two drivers had interactive effects. Both the stabilizing and destabilizing effects of warming became more pronounced with increasing body size, and the authors explored models without body size, and with consumers ten times or 100 times the size of their resource.

In parasitoid-host systems, where the predator is generally the same size or smaller than the prey and the prey is much smaller than its plant resource, the results of Binzer et al. (2012) might suggest that nutrient enrichment would be less likely to drive extinctions, but that higher temperatures may negatively affect biological control. Future work is needed to extend these multiple global change driver models to parasitoid-host systems and more complex food webs. However, recent empirical work may provide some insights. For example, de Sassi and Tylianakis (2012) found that warming had no significant effect on plant biomass (in contrast to the effects they observed of nitrogen enrichment), but herbivore biomass approximately doubled (consistent with the increase in carrying capacity modelled by Binzer et al. (2012)), and the effects of nitrogen and temperature on herbivore biomass were sub-additive. As with nitrogen (see 3.3 Nutrient enrichment above), temperature had no significant effect on parasitoid biomass, such that the ratio of parasitoid to host biomass declined with increasing temperature, indicating a failure of top-down regulation (de Sassi and Tylianakis, 2012). In the same experiment, elevated temperature and nitrogen had separate negative effects on pairwise parasitoid-host interaction frequencies, but their effects were sub-additive, congruent with the increase in host density (de Sassi et al., 2012) and the prediction that higher temperatures should prevent nutrient-driven extinctions and nutrient enrichment should prevent temperature-driven extinctions (Binzer et al., 2012). Furthermore, elevated temperature produced the same exaggerated preference of parasitoids for larger and more abundant hosts as did nitrogen, indicating that any change in the quality of certain host species (either as a result of direct temperature-induced changes in growth or of indirect, plant-mediated effects of nutrient addition) may cause them to receive a disproportionate share of parasitoid attacks (de Sassi and Tylianakis, 2012).
Similarly congruence among the effects of two global change drivers was observed for simple food chains under elevated CO$_2$ and temperature. Either driver on its own drove increased host pupal mass, and caused a reduction in parasitism and decreased plant (alfalfa) biomass due to disruption of the trophic cascade (Dyer et al., 2013, discussed above). However, increased temperature accelerated larval development and this effect was dampened by elevated CO$_2$. Furthermore, elevated temperature drove increases in saponins (plant metabolites) that enhanced herbivore survival, whereas elevated CO$_2$ did not, highlighting again that different pathways from different drivers can lead to similar changes in herbivores and their parasitism rates (Dyer et al., 2013).

Thus, changes in host abundance and quality may be important mechanisms for climate effects on parasitoid-host food webs, but a number of other mechanisms are also possible. For example, climate-driven changes to the phenology of hosts and/or their parasitoids may lead to a loss of synchrony (Parmesan, 2006; Visser and Both, 2005), and these mismatches have been shown theoretically to affect food-web interactions (Logan and Wolesensky, 2007). Furthermore, much of the parasitoid-host food web research to date has focused on increases in temperature, though extreme weather events such as drought and heat waves may also affect parasitoid-host interactions (Gillespie et al., 2012), or even alter the effect of temperature. For example, Romo and Tylianakis (2013) used a series of experiments to test how two components of climate change (drought and warming) affected interactions between aphid parasitoids and their host (the cabbage aphid *Brevicoryne brassicae*) on kale plants. They found that parasitoids tended to control their hosts better under conditions of simulated drought or warmer temperatures, but these effects were reversed when both climate components were combined. Likewise, separate warming and drought treatments reduced parasitoid longevity, elevated temperature increased parasitoid emergence success, and drought increased offspring production, but combined warming and drought produced the lowest parasitoid emergence of all treatments (Romo and Tylianakis, 2013). These non-
additive effects are rarely examined, but potentially important, determinants of how specific biological control interactions will respond to future conditions. Therefore, even though interaction effects among drivers were common, the effects of temperature or CO\textsubscript{2} alone on pairwise interactions are highly variable (Tylianakis et al., 2008a), as the above recent studies by Romo and Tylianakis (2013) and Dyer et al., (2013) highlight in the case of temperature. Extrapolating these pairwise changes across complex interaction networks will be even more difficult, making future research on food-web responses to these drivers critical.

4 Conclusions and avenues for future research
The above research on parasitoid-host food webs suggests a number of important ways in which they can inform biological control in a changing environment. Food webs also provide a framework for the quantification of biomass accumulation at different trophic levels, which provides more ability to generalize responses of plants under environmental change to crop yields than do studies of single chains or pairwise species interactions. Despite this, a key requirement for such work to remain relevant to biological control is that trophic cascades and increased plant yields can be detected and quantified. Unfortunately, observational and even some experimental studies have the limitation that bottom-up effects can be difficult to separate from top-down cascades. For example, above we described how nutrient enrichment, climate warming, elevated CO\textsubscript{2}, and even plant genotype have been shown to generate bottom-up changes to parasitoid-host food webs, which inhibits attribution of any plant biomass changes to trophic cascades (i.e. biological control) unless consumer-free control treatments are included in the experimental design. Although not yet applied to parasitoid-host systems in changing environments, a significant amount of work has examined the factors that determine food chain length (i.e. the number of trophic levels) in food webs (Post, 2002). In particular, there has been historical debate over whether high primary productivity (as is observed under elevated nitrogen or CO\textsubscript{2}) can generate longer food chains (Briand and Cohen, 1987; Kaunzinger and Morin, 1998), which in a biological control context
could enhance hyperparasitoids or other predators at the fourth trophic level. If productivity is important in this regard, the mechanisms that generate this enhancement would necessarily be bottom-up, yet higher densities at the fourth trophic level magnify top-down pressures on control agents and potentially release pests from control.

Therefore, future work must wherever possible identify and quantify the pathways through which changes to food webs occur. For example, in their food-chain study, Dyer et al. (2013) tested how changes in plant metabolites mediated the effects of temperature and elevated CO$_2$, which provided a deeper mechanistic understanding of their observed patterns. Likewise, changes to species composition or diversity can affect the structure of food webs (e.g., food web connectedness tends to decline as the number of species increases), so these characteristics should be measured to include as covariates in regression analyses or mediating variables in path analyses testing for changes in food-web structure (e.g., Laliberté and Tylianakis, 2010; Thebault and Fontaine, 2010).

Theoretical work has clearly improved our understanding of the causes and consequences of food-web structure. Dynamic food-web models can be a useful tool to understand how food webs will be affected by global change, because they combine descriptions of static web structure with dynamic population models (e.g., based on Yodzis and Innes (1992)). This allows, amongst other things, disentangling of bottom-up and top-down effects in communities. Moreover, they can be used to develop hypotheses that can be tested experimentally. However, whilst in the recent past considerable progress has been made in modeling the effects of global environmental change on predator-prey food webs (e.g. Brose et al., 2012, and other papers from the same special issue), dynamic models of parasitoid-host interactions are still largely missing. Developing an overarching modeling framework that incorporates both kinds of feeding interactions in complex species communities is paramount to understanding global change in complex ecosystems. However, before this can be done, a considerable amount of basic information is needed to realistically parameterize the theoretical models. There is, for example, a lack of
systematic information of parasitoid metabolic rates, how they alter their host’s metabolism, and how this is influenced by global change drivers. It will also be important to determine how drivers of environmental change alter parasitoid searching efficiency, particularly in the context of biological control. This will necessitate the synthesizing of existing information on parasitoid functional responses and further experimental determination of environmental change effects on parasitoid searching behavior. Once developed, such models could predict the effects of global environmental change on parasitoid-host food webs, and facilitate planning for effective future biological control.

Despite several studies being carried out in agroecosystems, there remains a disconnect between food-web research and applied goals. Previous work suggests that more connected webs, or those with high diversity of predators attacking each prey species (e.g. host species 3 in Fig. 1), should have higher attack rates (Cardinale et al., 2003; Poisot et al., 2013; Snyder et al., 2006; Tylianakis et al., 2007) or resilience to change (Petchey et al., 1999; Yachi and Loreau, 1999). However, we are far from being able to recommend the local introduction of certain control agents based on their ability to provide synergistic effects with the existing food web. In fact, the widespread focus of food-web research on parasitoid-host webs for logistical reasons has limited moves in this direction by focusing on only a subset of the agroecosystem (only parasitoids). Thus, the addition into pest-based food-web research of generalist predators, which may eat parasitoids as well as herbivores, will add complexity but much-needed realism when viewing biological control as a food-web phenomenon. Ongoing advances in gut-content analysis of arthropods (Hoogendoorn and Heimpel, 2001; Juen and Traugott, 2005) may alleviate some of the practical constraints that have hindered the quantification of arthropod predator-prey food webs in the past. In fact, recent work has even begun to quantify food webs involving predators, parasitoids and pathogens of aphids (Van Veen et al., 2008), which paves the way for inclusion of other prey species and quantification of intraguild predation, as well as indirect effects across taxa.
A related advance will be the merging of other types of interaction network with predator-prey or parasitoid-host webs, which would account for their non-independence and provide deeper understanding of the ecological and evolutionary dynamics of communities (Fontaine et al., 2011). For example, interactions between plants and pollinators form mutualist networks, and linking pollination networks with food webs could provide significant insights into how the full spectrum of provisioning services in crop systems are affected by environmental changes or different management regimes. Ecologically, such an approach would also allow quantification of the indirect relationships between, for example, pollinators and herbivores that feed on the same plant, or parasitoids that compete with pollinators for nectar but control larval herbivores that pollinate the food plant in their adult stage, or even compete with the larvae of pollinators (such as syrphids) for food. This area is almost entirely unexplored, but a recent paper by Pocock et al. (2012) has pushed new boundaries by quantifying multiple, connected interaction networks from the same farm site (i.e. networks involving parasitoids of aphids, seed-feeding insects, and leafminers, as well as several networks of seed predators and pollinators). The authors found a lack of congruence between the structure and robustness (to simulated extinction) of different network types, though a few plant species that were disproportionately involved in linkages across all the networks may make a useful target for future work trying to restore ecosystem functioning or engineer stable interaction networks.

Finally, the adaptation and resilience of biological control to changing environmental conditions will depend to a large extent on rapid evolutionary changes in pest and natural enemy populations. Work on plants and animals has demonstrated rapid changes in population genetics under climate change (Franks et al., 2007; Parmesan, 2006), and it is likely that other environmental change drivers will exert similar selective pressures. The rapid evolution of pesticide resistance in pest insects (Roush and McKenzie, 1987) is testament to the speed at which they can evolve, and symbiotic bacteria (e.g. *Buchnera*) can also confer tolerance to, for example, extreme temperatures (Dunbar et al., 2007). Therefore, pests may have a large pool of genetic resources (both their own and that of their symbionts) from which
environmental drivers can select. However, in addition to these environmental
effects, food-web interactions can also impose selective pressures (Ings et al., 2009;
Thompson, 1994), which may be orthogonal such that food-web interactions do not
affect adaptation to environmental forces (Harmon et al., 2009). Alternatively,
environmental drivers may alter the coevolutionary process between interacting
species, or similarly species interactions may limit their ability to evolve with
changing environmental conditions (Tylianakis, 2009). It remains largely unexplored
whether the selective pressures of food-web interactions and environmental
stressors generally operate additively, synergistically, or antagonistically, and future
work merging evolution with changes to, and selective pressures of, species
interactions will be critical for understanding the long-term resilience of biological
control in changing environments.

As a first step, a recent study examined food-web interactions among individual
parasitoids of a single species (*Aphelinus mali* (Hymenoptera: Aphelinidae)) and its
aphid host (*Eriosoma lanigerum* (Hemiptera: Aphididae)). Food webs typically treat
species as nodes linked by feeding interactions, whereas evolution operates within
species by changing gene frequencies. Therefore, by treating individuals (rather than
species) as nodes in a food web, Lavandero and Tylianakis (2013) were able to
examine the tendency of certain parasitoid genotypes to attack certain host
genotypes, while simultaneously measuring whether host genotype frequencies
changed along a climatic gradient. Congruence in the within-species phylogenies of
hosts and parasitoids (i.e. related parasitoids attacking related hosts) can be a signal
of host-race formation or coevolution (Legendre et al., 2002), and the authors found
stronger congruence with increasing temperature (Lavandero and Tylianakis, 2013).
Future work using this approach could provide substantial insights into the value of
alternative hosts in conservation biological control, i.e. whether parasitoid
genotypes will specialize on one or other host, and whether this specialization
changes with environmental drivers. Similarly, the finding that some host genotypes
resist parasitism better than others (Ferrari et al., 2001) suggests that host
genotypes can evolve better resistance to parasitoids, and this could in theory be
easier when there are fewer different parasitoid genotypes against which to adapt.
Therefore, parasitoid genetic diversity and connectivity in genotypic food webs may be important for preventing such resistance, in the same way that connectivity in multispecies food webs can affect attack rates. Yet, the ability of any host genotypes to evolve resistance to parasitoids will depend on the overall fitness of those genotypes, which may be primarily determined by environmental changes, parasitoid-induced mortality, or both (Tylianakis, 2009). Therefore, the interplay of environmental change with food-web interactions and fitness differences among individuals and species, will ultimately determine the long-term sustainability of biological control in agricultural food webs. By coupling the holistic understanding generated using food-web approaches with ever-advancing technologies in the study of evolution, in the future we may be able to develop new tools for maximizing biological control in a changing environment.

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**Figure 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.