Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

Community ecology of the ‘other’ parasitoids

John O Stireman III

The study of parasitoid communities is an active and dynamic field. Most studies, however, are focused primarily on parasitic wasps, despite the thousands of other insect parasitoids distributed across many lineages. Although questions in parasitoid community ecology are much the same for different groups, answers to these questions may not be due to differing biological traits. The ecology of non-hymenopteran (‘NH’) parasitoid communities is poorly known, but recent work indicates that habitat and host traits have strong impacts on the size and composition of these parasitoid assemblages. Recent food-web analyses indicate that host ranges vary widely within and among taxa and associations are shaped by host ecology and defenses. Evidence is also accumulating for strong ‘bottom-up’ and ‘top-down’ multi-trophic interactions between NH-parasitoids and nonadjacent trophic levels, as well as trait-mediated indirect effects on communities. Recent technical and conceptual advances in characterizing and comparing food webs, consideration of phylogenetic history, and increasing anthropogenic impacts provide many new and stimulating areas of research on parasitoid communities.

Address
Department of Biological Sciences, Wright State University, Dayton, OH, USA

Corresponding author: Stireman, John O (john.stireman@wright.edu)

Current Opinion in Insect Science 2016, **14**:87–93

This review comes from a themed issue on **Parasites/Parasitoids/Biological control**

Edited by **Paul Ode** and **George Heimpel**

http://dx.doi.org/10.1016/j.cois.2016.02.002

Introduction

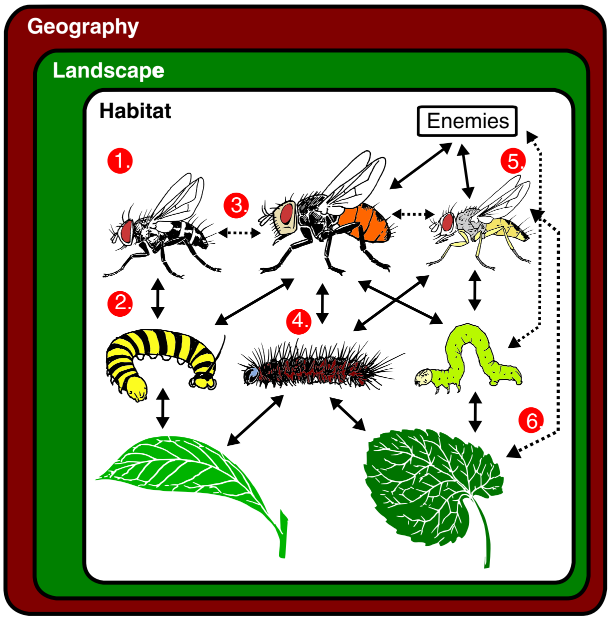
The great diversity and ecological importance of insect parasitoids is well established with thousands of published studies focused on parasitoids and their relationships with hosts. The vast majority of these have focused on hymenopteran parasitoids, that is, the parasitic wasps. Indeed, the term ‘parasitoid’ is often used synonymously with parasitoid wasp. Yet, there exist many other groups of insect parasitoids belonging to an array of different insect orders and families [1]. Emphasis on hymenopteran parasitoids is warranted due to their incredible diversity, the broad range of hosts they attack, and their frequent use of economically important pests as hosts. But, what is true for one lineage of parasitoids may not be true for them all. Differences in behavior, physiology, morphology and life history at the species level are likely to translate into differences in structure, dynamics, and stability at the community level. Here, I focus on the understudied parasitoid cousins of the Hymenoptera, briefly reviewing our knowledge of their communities based on recent studies, where major gaps in our knowledge lie, and what areas of future research might be most promising. Given the paucity of research on most other taxa, I primarily focus on parasitoids in the order Diptera, which comprise the majority of the ‘other’ parasitoids.

At least 21 families of Diptera [1] and 11 families of Coleoptera [2] contain species with parasitoid lifestyles. Unlike the Hymenoptera, in which the parasitoid habit appears to have evolved only once [3], ‘parasitoidism’ has evolved dozens of times in these orders from a variety of ancestral feeding niches. In the Diptera alone it is estimated that parasitoids may have evolved in over 100 lineages [1]. With so many varied origins and histories, it is difficult to characterize these communities and their interactions with hosts as a group. It is easier to characterize them by traits they collectively lack relative to hymenopteran parasitoids than the many varied adaptations of particular taxa. Primary among these is the absence of a piercing, appendicular ovipositor by which to insert eggs into the bodies of their hosts or drill through substrates to attack concealed hosts (e.g. wood, soil, plant tissues). Associated with this is the lack of accessory glands containing paralytic venoms, viral particles, or other substances to subdue hosts or their immune defenses. The absence of these tools has resulted in rare use of certain types of hosts (e.g. gall-forming insects, leafminers) as well as novel adaptive strategies for attacking others (e.g. host-seeking planidial/triungulin larval forms in several fly and beetle families and microtype eggs that are ingested by hosts in Tachinidae [4,5]). In addition, parasitism of quiescent stages such as eggs or pupae is unusual in most NH-parasitoids (with notable exceptions), hyperparasitism is virtually unknown, and aphids and their ilk (Sternorrhyncha) are rarely attacked. These differences in host location and attack strategies likely have consequences for parasitoid host ranges, parasitism rates, the types of hosts they attack, defenses of their hosts and other aspects of the structure and dynamics of their communities.

Community size and structure

Among the most fundamental topics of community ecology is how species diversity is distributed in space and time and what factors shape this distribution (Figure 1). For most

Figure 1



Current Opinion in Insect Science

An illustration of some of the major areas of research in parasitoid community ecology. **(1)** Diversity and composition of parasitoid communities, **(2)** Host range and food-web structure of parasitoids, **(3)** Competition and indirect interactions between parasitoids, **(4)** Parasitoid assemblage size and parasitism frequency of hosts, **(5)** Direct and indirect interactions with predators/hyper-parasitoids, **(6)** Top-down and bottom-up interactions between parasitoids and non-adjacent trophic levels. The surrounding boxes represent that all of these patterns and processes may vary across multiple environmental scales. Understanding this variation and its causes is one of the major areas of current research on parasitoid communities.

groups of NH-parasitoids we have little information on what or how many species occur in communities, let alone how they vary across habitats and what underlying factors determine their richness. Thus, basic descriptive studies based on field sampling or host-rearing are needed to establish baseline data on the composition of NH-parasitoid communities. However, there has been progress in understanding diversity of some NH-parasitoid communities. For tachinid flies, sampling studies have examined how community composition and diversity varies across microhabitats [6], between forest canopy and the understory [7], relative to size and isolation of habitat fragments [8••], and in relation to agricultural habitats and the landscapes that surround them [9•,10,11,12••] (see below). Some general conclusions that can be taken from these studies are that, firstly, Tachinid parasitoid communities vary substantially with habitat, despite strong dispersal abilities, secondly, local communities are strongly affected by the surrounding landscape matrix, and thirdly, effects of habitat can be complex and include interactions between local habitats and surrounding landscapes [9•,10]. Work on other NH-parasitoid groups is limited. Studies of ant-parasitizing phorid fly communities have found that parasitoid diversity is positively related to host diversity and abundance and that habitat features can influence community composition [13,14]. Habitat associations of sciomyzid flies, many of which are parasitoids, have also received some attention from researchers due to their dependence on particular wetland habitats where their snail hosts are found (e.g. [15]).

At the level of host species, richness of NH-parasitoid assemblages and parasitism frequencies have been found to depend on host abundance, gregariousness, feeding niche, and defensive strategies [16–18,19••]. Strengths of these effects vary among parasitoid groups. Tachinid flies dominate the parasitoid assemblages of exposed caterpillar hosts, whereas assemblages on concealed caterpillars are dominated by Hymenoptera [18,19••]. As might be expected, indirectly ovipositing Tachinidae are more likely to attack concealed hosts than those directly laying eggs on hosts [19••]. Observations of increased richness of tachinid assemblages with polyphagy of caterpillar hosts has been attributed to the relative polyphagy of tachinids, allowing them to opportunistically attack hosts occurring in a variety of habitats [18]. The few studies of other NH-parasitoid communities on hosts have also found that parasitoid assemblage size varies with host traits. For example, larger bumblebee species tend to harbor greater numbers and diversity of conopid parasitoids [20,21]. Host plant identity can also have dramatic effects on susceptibility to parasitoids (see Section 'Indirect Interactions'). At somewhat larger scales, landscape structure can influence parasitism risk, as exemplified by Roland and Taylor's [22] classic study demonstrating that parasitism of forest tent caterpillars by four dipteran parasitoid species was strongly and differentially influenced by landscape structure in a fragmented landscape.

Many documented examples exist of interspecific parasitoid competition (e.g. [23]). However, there is limited evidence that this is a major factor in determining NH-parasitoid assemblage sizes on hosts [24,25]. This relative lack of evidence may be due to the lack of community-level analyses evaluating if and how intraguild competition has shaped patterns of host use in parasitoids, and this may be a promising area for future research. Observations that parasitoid guilds appear to partition hosts according to ontogeny (Hymenoptera: young hosts, Diptera: late instars [26]) hint at possible character displacement, but it is unclear if this might be the result of past competition.

Geographic patterns in NH-parasitoid diversity are not well understood. Some hymenopteran parasitoids do not exhibit typical negative latitudinal gradients in species richness

[27], but see [28], and it has been inferred that this may be a general pattern for parasitoids [29]. Hypotheses to explain this pattern include the resource fragmentation hypothesis (i.e. low host resource density makes specialized parasitoid lifestyles unviable), and the 'nasty host' hypothesis (i.e. potential hosts in the tropics are chemically defended against parasitoids [29]). Although explicit tests of latitudinal patterns have not been conducted, anecdotal evidence from sampling regimes and rearing programs, suggest that at least some NH-parasitoid communities are as rich or richer in the tropics than at temperate latitudes [30].

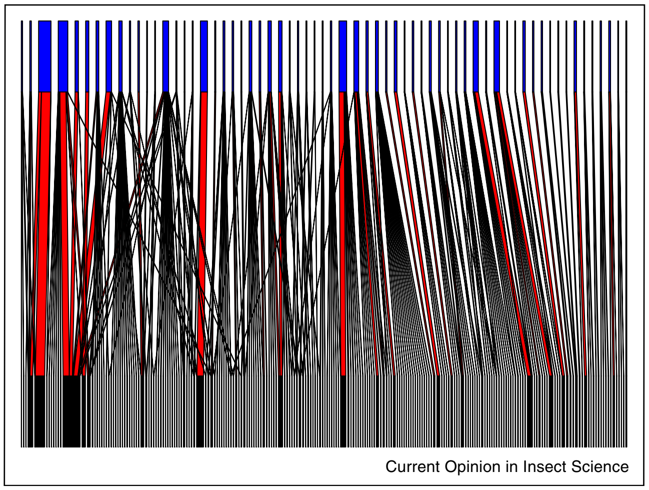
More research focused on patterns of parasitoid community structure relative to host traits, habitats and geography is needed. Only a handful of studies have investigated these issues in NH-parasitoids, and those that have are focused mostly on tachinids due to their frequent attack of caterpillars. Most hosts of other NH-parasitoids are rarely reared (e.g. ants, plant-hoppers, beetles, spiders) and thus host associations are spotty at best and little quantitative sampling of adults has been conducted. In addition, few studies have moved beyond these patterns to test hypotheses for their underlying causes, examine how they vary across ecological communities (though see [16]), and explore the implications for the population and community dynamics of their hosts.

Interaction structure: host specialization

Most of what we know about NH-parasitoid–host community structure is derived from large scale rearing projects of caterpillars (e.g. [31]). Of particular interest has been the degree of parasitoid specificity and the determinants of their host ranges. High levels of specialization may lead to lower connectance of parasitoid–host interaction webs, greater compartmentalization, lower redundancy, and decreased nestedness, which can influence dynamics, stability, and energy flow of communities [32,33••]. Host range in NH-parasitoids has received attention because, unlike most Hymenoptera, some groups are thought to possess relatively broad host ranges. Indeed, the dichotomy of parasitoids as either relatively specialized koinobionts or more generalized idiobionts does not apply to other parasitoids as nearly all would be classified as koinobionts, yet they range widely in level of host specificity.

Although the notion that tachinid parasitoids are relatively polyphagous is supported by rearing studies [34,35], when molecular data has been employed to differentiate cryptic species, the number and degree of specialized taxa has been found to increase dramatically [35]. A recent study by Hrcek *et al.* [19••] failed to find any differences in host range between tachinid and hymenopteran parasitoids of a community of tropical caterpillars, and analyses of caterpillar-tachinid food-webs from Ecuador suggest that host range is extremely variable, with both polyphagous and highly specific taxa (Figure 2).

Figure 2


Current Opinion in Insect Science

A semi-quantitative food-web of tachinid-caterpillar associations from an Ecuadorian cloud forest based on a long term rearing study. Widths of top (tachinids, blue) and bottom (host caterpillars) bars are proportional to the number of tachinids reared or hosts attacked (respectively), and widths of connectors (red) indicates frequency of host use. Data are shown for tachinid morphospecies reared on ≥5 occasions. Names of taxa are omitted for clarity.

One hypothesized reason for why tachinids and many other NH-parasitoids exhibit relatively broad host ranges is that they possess 'indirect' oviposition strategies, that is, adult females do not deposit offspring directly on the host but rather in environments frequented by the host. However, comparisons of direct and indirect oviposition strategies have generally not found strong differences in host range [19••,34,36]. Interestingly, Hrcek *et al.* [19••] found that tachinids were both more specific and more generalized than hymenopteran parasitoids (more extreme host ranges), suggesting the existence of additional behavioral or physiological strategies.

Host ranges in other NH-parasitoid taxa are relatively poorly known. Phorid parasitoids of ants are often exceptionally specialized, as they typically use species specific pheromones to locate their hosts [37]. Such specificity is also found in other parasitoid taxa that utilize specific host-derived cues (e.g. [4,38]). In other NH-parasitoid lineages host ranges can be broad or highly variable (e.g. [39]).

The determinants of host range in NH-parasitoids are not well known, but it appears that host-habitat plays a prominent role in determining host associations in many taxa (e.g. [30,34,40]), perhaps more so than in the Hymenoptera. Recent work on conopid parasitoids indicates the strength of immune response is an important determinant of bumblebee host use [41]. Such physiological constraints need to be explored more widely in NH-parasitoids. One intriguing pattern emerging from analyses of parasitoid–host communities is that the parasitoid richness and attack rates are higher in hosts that are well-defended from predators [17,18]. It has been proposed that such hosts offer 'enemy free space' [42] for parasitoids, an argument recently elaborated by Murphy *et al.* [43••]. These studies have also found that host traits that predispose or protect hosts from parasitism by hymenopteran parasitoids, often do not have the same effects on other parasitoids, hinting at differences in how they interact with hosts.

Interaction structure: food webs

Parasitoid–host interaction webs offer excellent opportunities to understand food-web structure. They are easier to quantify than predator–prey webs and may be simpler in structure due to greater compartmentalization. In recent decades they have been the subject of many food web studies (see [44]). However, few of these have involved NH-parasitoids, and those that have rarely consider how parasitoid groups differ in their interaction structure. This lack of attention is due in part to the focus on highly tractable systems in which NH-parasitoids are rare or absent (e.g. leaf-miners, gallers, aphids) and the tendency to treat parasitoids as a group regardless of disparities in phylogeny and life history.

The failure to consider differences among parasitoid groups may obscure important variation in food-web structure and its larger effects. For example, Morris *et al.*'s [45•] innovative comparative study of parasitoid food webs concluded that the general structure of these networks does not vary latitudinally. However, only six of 28 food webs included hosts likely to host NH-parasitoids (i.e. leaf chewers), and five of these were temperate (the other being Hawaii). Clearly, little can be concluded from this analysis about how leaf-chewer-parasitoid webs vary with latitude, let alone how NH-parasitoid food webs vary. This is not to criticize the approaches used by this and other studies, but to point out the weakness in our knowledge and understanding of NH-parasitoid food webs.

Recent improvements in the characterization, analysis and comparison of parasitoid–host interaction networks promises to bring new insight into our understanding of food web structure and stability, and at least some recent studies have included NH-parasitoids. For example, Peralta *et al.* [46] compared replicate food webs of caterpillars across a habitat gradient in New Zealand and found that greater complementarity (resource partitioning) leads to higher parasitism, greater redundancy stabilizes parasitism over space, and greater connectance increases variability in parasitism rates. Approximately 25% of the parasitoids in this study were not Hymenoptera, though they were not considered separately. Studies such as this and those of Tylianakis *et al.* [47] that not only characterize food webs, but compare replicate food webs across environments or gradients are particularly likely to lead to insights into how communities are assembled, how they function and why they vary. Consideration of variation among parasitoid clades will improve this insight.

Indirect interactions

In addition to direct interactions among species, indirect interactions can have powerful and disproportionate effects on communities (e.g. [48]). For parasitoid–host communities there are several potentially consequential avenues of indirect effects. One such indirect interaction is apparent competition, that is, when hosts indirectly compete by hosting enemies of one another [49]. For example Barbosa *et al.* [50] found that numerically dominant and subdominant herbivore species were strongly linked through shared parasitoids, and they hypothesized that these indirect interactions were responsible for population suppression of the subdominant herbivores. Such interactions may be important in both determining the richness and abundance of herbivore communities and driving diversification of host–parasitoid systems.

Another interesting and important type of indirect interaction is the non-lethal effect of phorid parasitoids on behavior of their ant hosts [51•,51•]. These strong, indirect effects have been harnessed for biological control of invasive ant species, with the prediction that non-lethal effects of reduced ant foraging may equalize the balance of competition between the invasive and native ants [53]. Such phorid-ant systems provide some of the clearest and most fascinating examples of trait-mediated indirect interactions in terrestrial ecosystems (e.g. [54,55•]).

Multi-trophic effects on non-adjacent trophic levels are common indirect interactions in parasitoid communities and form the basis of many biological control programs. Parasitoid communities can affect host–plants or prey of their hosts and be affected by these lower trophic levels (Figure 1). Strong effects of host plants on attack rates of parasitoids of herbivorous hosts have been observed in multiple studies, particularly for NH-parasitoids (e.g. [19••,40,56••]). Such effects are likely mediated by varying olfactory and visual cues among plant taxa that are used in parasitoid host finding [56••]. Plants can also affect parasitoids by altering host quality or defenses [57]. For example, experimental studies have shown that tachinid parasitoids can be adversely affected by host-plant diets of their hosts (e.g. [58,59]). Despite a growing number of studies investigating how secondary chemistry of host–plants affects parasitoid survival and development (directly or via effects on immune responses [60]), very few systems have been studied in depth. Investigation of the 'bottom-up' indirect effects of secondary plant metabolites on parasitoids is a compelling area for future research.

Parasitoid communities in a changing world

It is increasingly difficult to study ecological communities without considering how they are influenced by anthropogenic environmental changes. Recognition of anthropogenic effects is not new to parasitoid researchers due to the long history of research in agricultural systems, but relatively little of this work has been focused on communities of NH-parasitoids. Recently, several studies have examined how tachinid parasitoid communities respond to landscape fragmentation and composition in anthropogenically modified systems. Inclán and colleagues [9•] observed strong effects of local habitat and landscape on tachinid communities in an orchard agro-ecosystem. They also demonstrated benefits of organic agriculture on tachinid diversity at local and landscape levels (Inclán *et al.* [10]). Similar research by Letourneau *et al.* [11,12••] found that in organic farms embedded in landscapes with higher proportions of semi-natural vegetation relative to cropland exhibited greater tachinid richness, abundance, and parasitism rates.

The response of NH-parasitoid communities to habitat changes in non-agricultural habitats has also received some attention (e.g. [22]). Inclán *et al.* [8••] found that tachinid parasitoid communities respond to both fragment area and isolation in remnant grassland fragments consistent with island biogeographic theory. One revealing study of the effects of habitat fragmentation focused on a community associated with bracket fungi in an old growth boreal forest [61]. These authors found that the primary parasitoid in the system (a tachinid fly) was completely lost from forest fragments isolated for more than 12 years. Negative effects of fragmentation have also been found in tropical forest inhabiting phorids [62], a notable exception to the paucity of such studies on other parasitoid groups.

The significant patterns revealed by initial studies of anthropogenic effects on parasitoid communities demonstrate the insight that can be gained inexpensively with taxonomic knowledge, creative ecological questions, and fieldwork. Still, there are few studies asking how NH-parasitoids might respond to climatic warming or other types of climate change (though see [31]), how they are affected by invasive species and biotic homogenization, or how their community structure is altered in urbanized landscapes. These are promising and relatively open areas for future research [63•].

Future research directions

Perhaps the most pressing need for research on NH-parasitoids is simply to acquire more basic ecological data for more taxa. We know virtually nothing about communities of most non-hymenopteran parasitoids. For example, the carabid genus *Lebia* (parasitoids of Chrysomelidae) contains 450 described species, but only four species have known hosts [63]. Likewise, in the Neotropical region, only 2% of species of leafhopper-attacking 'big-headed' flies (Pipunculidae) have known hosts [64]. Even for the relatively well studied Tachinidae, host associations are unknown for the majority of species. We cannot hope to understand the structure and dynamics of these communities if we don't even know what hosts they interact with. Furthermore, ecological studies of 'parasitoids' should distinguish between different guilds and clades of parasitoids to assess if and how they differ in interaction structure and relationships with hosts (e.g. [19••]).

As mentioned above, effects of anthropogenic change on parasitoid communities is another rich source of research opportunities. Due to their relatively high trophic position and specificity, parasitoids are ideal 'indicator' species of environmental stress and change. They are highly dependent on the existence of viable populations of their hosts and are prone to local extinction to due relatively small population sizes. Thus parasitoid communities can both reflect changes at lower trophic levels and serve as harbingers of changes to come. Understanding how anthropogenic environmental change affects parasitoid communities is a rich, if alarming, area for future study (e.g. [50,63•]).

One research area that promises to dramatically improve our understanding of parasitoid–host associations and interaction webs is the use of molecular tools to identify taxa. Not only have such tools altered our understanding of the specificity and diversity of parasitoids [33••,34], sensitive high-throughput sequencing techniques have opened up whole new possibilities for understanding both the realized and potential (unsuccessful) interactions between parasitoids and hosts [47].

Finally, a fascinating recent research area is attempting to understand not just how parasitoid communities function and are structured, but why; i.e. how do communities form over evolutionary time scales, and how do interactions shape the evolution of the constituents? Studies of parasitoid community phylogenetics have harnessed increasingly available and powerful genetic/genomic tools to assess phylogenetic diversity of communities, signals of coevolution and the processes of community development and change (e.g. [65]). Unfortunately, exploration of these questions and application of these techniques to dipteran or other parasitoids has lagged behind hymenopteran parasitoid–host systems that are more amenable to study. These are just a few examples of the many areas of parasitoid community ecology that are in need of exploration, particularly for non-hymenopteran parasitoids. In some ways this review has been more about what we do not know that what we do know, because we know so little about most NH-parasitoid groups. This can be viewed as a disheartening lack of attention or as an exciting void in our knowledge awaiting exploration.

Acknowledgements

I would like to thank Paul Ode and George Heimpel for the invitation to write this review. I was supported by NSF DEB 1442134, and data for Figure 2 was made possible by NSF DEB 1020571.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Eggleton P, Belshaw R: **Insect parasitoids an evolutionary overview**. *Philos Trans R Soc Lon B* 1992, **337**:1-20.

2. Weber DC, Saska P, Chaboo CS: **Carabid beetles (Coleoptera: Carabidae) as parasitoids**. In *Encyclopedia of Entomology*. Edited by Capinera JL. Springer; 2008:719-721.

3. Whitfield JB: **Phylogeny and evolution of host–parasitoid interactions in hymenoptera**. *Annu Rev Enomol* 1998, **43**: 129-151.

4. Goubert C, Josso C, Louapre P, Cortesero AM, Poinsot D: **Short- and long-range cues used by ground-dwelling parasitoids to find their host**. *Naturwissenschaften* 2013, **100**:177-184.

5. Stireman JO III, O'Hara JE, Wood DM: **Tachinidae: evolution, behavior, and ecology**. *Annu Rev Entomol* 2006, **51**:525-555.

6. Stireman JO III: **Alpha and beta diversity of a tachinid parasitoid community over space and time**. *Ann Entomol Soc Am* 2008, **101**:362-370.

7. Stireman JO III, Cerretti P, Whitmore D, Hardersen S, Gianelle D: **Composition and stratification of a tachinid (Diptera: Tachinidae) parasitoid community in a European temperate plain forest**. *Insect Conserv Diver* 2012, **5**:346-357.

8. •• Inclán DJ, Cerretti P, Marini L: **Interactive effects of area and connectivity on the diversity of tachinid parasitoids in highly fragmented landscapes**. *Landscape Ecol* 2014, **29**:879-889.

One of the few studies to examine effects of area and isolation on a community of NH-parasitoids. As the title suggests, the authors find significant effects of both aspects of habitat fragmentation despite high vagility of tachinid flies and, consistent with Island Biogeographic Theory, they find that connectivity of fragments dampens negative effects of decreasing fragment size. High levels of polyphagy in many species may further reduce effects of habitat fragmentation.

9. • Inclán DJ, Cerretti P, Gabriel D, Benton TG, Sait SM, Kunin WE, Gillespie MAK, Marini L: **Organic farming enhances parasitoid diversity at the local and landscape scales**. *J Appl Ecol* 2015, **52**:1102-1109.

An example of the complex interplay between local habitats and landscapes on NH-parasitoid community composition and diversity. This study observed positive effects of organic farming on tachinid parasitoid diversity both at the local farm level and at the landscape level. However, this effect depended on the type of farming system: effects of organic management were much stronger for arable fields than for pastures. Small scale location effects on parasitoid diversity (field margins versus centers) were also observed.

10. Inclán DJ, Cerretti P, Marini L: **Landscape composition affects parasitoid spillover**. *Agric Ecosyst Environ* 2015, **208**:48-54.

11. Letourneau DK, Allen SGB, Stireman JO III: **Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops**. *J Appl Ecol* 2012, **49**:1405-1416.

12. •• Letourneau DK, Kula RR, Sharkey MJ, Stireman JO III: **Habitat eradication and cropland intensification may reduce parasitoid diversity and natural pest control services in annual crop fields**. *Elementa* 2015, **3**:000069.

This study shows that diversity and parasitism rates by tachinid flies is enhanced in organic farm fields surrounded by semi-natural habitat versus those surrounded by cropland. Effects of particular natural vegetation types are also observed and comparisons are made with hymenopteran parasitoids. This is one of several recent studies that have demonstrated significant landscape effects on local parasitoid communities. Also see Letourneau *et al.*, 2012.

13. Folgarait PJ, Patrock RJW, Gilbert LE: **Associations of fire ant phorids and microhabitats**. *Environ Entomol* 2007, **36**:731-742.

14. Elizalde L, Folgarait PJ: **Host diversity and environmental variables as determinants of the species richness of the parasitoids of leaf-cutting ants**. *J Biogeogr* 2010, **37**:2305-2316.

15. Maher C, Gormally M, Williams C, Skefington MS: **Atlantic floodplain meadows: influence of hydrological gradients and management on sciomyzid (Diptera) assemblages**. *J Insect Conserv* 2014, **18**:267-282.

16. Hawkins BA: *Pattern and Process in Host–Parasitoid Interactions*. Cambridge University Press; 1994.

17. Gentry G, Dyer L: **On the conditional, nature of neotropical caterpillar defenses against their natural enemies**. *Ecology* 2002, **83**:3108-3119.

18. Stireman JO III, Singer MS: **Determinants of parasitoid–host associations: insights from a natural tachinid-lepidopteran community**. *Ecology* 2003, **84**:296-310.

19. •• Hrcek J, Miller SE, Whitfield JB, Shima H, Novotny V: **Parasitism rate, parasitoid community composition and host specificity on exposed and semi-concealed caterpillars from a tropical rainforest**. *Oecologia* 2013, **173**:521-532.

An analysis of parasitism frequency and parasitoid assemblage size of a New Guinean tropical caterpillar community. The authors find significant variation in responses of hymenopteran and tachinid parasitoids to host feeding niche (exposed or concealed), as well as differences in host specificity (see text), and effects of host plants on parasitism. They also find that oviposition strategies of tachinids vary significantly according to host feeding niche. This is one of the few recently published studies that explicitly examines and compares hymenopteran and dipteran parasitoid communities.

20. Otterstatter M: **Patterns of parasitism among conopid flies parasitizing bumblebees**. *Entomol Exp Appl* 2004, **111**:133-139.

21. Malfi RL, Roulston TH: **Patterns of parasite infection in bumble bees (*Bombus* spp.) of Northern Virginia**. *Ecol Entomol* 2014:39.

22. Roland J, Taylor PD: **Insect parasitoid species respond to forest structure at different spatial scales**. *Nature* 1997, **386**:710-713.

23. Harvey JA, Poelman EH, Tanaka T: **Intrinsic inter- and intraspecific competition in parasitoid wasps**. *Annu Rev Entomol* 2013, **58**:333-351.

24. LeBrun EG, Plowes RM, Gilbert LE: **Indirect competition facilitates widespread displacement of one naturalized parasitoid of imported fire ants by another**. *Ecology* 2009, **90**:1184-1194.

25. Porter SD, Calcaterra LA: **Dispersal and competitive impacts of a third fire ant decapitating fly (*Pseudacteon obtusus*) established in North Central Florida**. *Biol Control* 2013, **64**: 66-74.

26. Murphy SM, Stoepler TM, Grenis K, Lill JT: **Host ontogeny determines parasitoid use of a forest caterpillar**. *Entomol Exp Appl* 2014, **150**:217-225.

27. Janzen DH: **The peak in North-American ichneumonid species richness lies between 38-degrees and 42-degrees-N**. *Ecology* 1981, **62**:532-537.

28. Quicke DLJ: **We know too little about parasitoid wasp distributions to draw any conclusions about latitudinal trends in species richness, body size and biology**. *PLoS ONE* 2012, **7**:e32101.

29. Gauld ID, Gaston KJ: **Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis**. *Oikos* 1992, **65**: 353-357.

30. Feener DH Jr, Brown BV: **Diptera as parasitoids**. *Annu Rev Entomol* 1997, **42**:73-97.

31. Stireman JO III, Dyer LA, Janzen DH, Singer MS, Lill JT, Marquis RJ, Ricklefs RE, Gentry GL, Hallwachs W, Coley PD *et al.*: **Climatic unpredictability and parasitism of caterpillars: implications of global warming**. *Proc Natl Acad Sci U S A* 2005, **102**:17384-17387.

32. Thebault E, Fontaine C: **Stability of ecological communities and the architecture of mutualistic and trophic networks**. *Science* 2010, **329**:853-856.

33. Wirta HK, Hebert PDN, Kaartinen R, Prosser SW, Varkonyi G,
•• Roslin T: **Complementary molecular information changes our perception of food web structure**. *Proc Natl Acad Sci U S A* 2014, **111**:1885-1890.
This is an excellent example of the insight that can be gained when employing molecular methods in addition to host-rearing to understand parasitoid–host food-webs. Using a relatively depauperate caterpillar–parasitoid community in Greenland, the authors sequence hosts and adult parasitoids and find three times as many interactions using the combined data rather than rearing alone. Differences in interaction structure obtained by inclusion of molecular methods dramatically affected estimates of food-web metrics as well as species diversity.

34. Stireman JO, Singer MS: **What determines host range in parasitoids? An analysis of a tachinid parasitoid community**. *Oecologia* 2003, **135**:629-638.

35. Smith MA, Wood DM, Janzen DH, Hallwachs W, Hebert PDN: **DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera, Tachinidae) are not all generalists**. *Proc Natl Acad Sci U S A* 2007, **104**:4967-4972.

36. Belshaw R: **Life history characteristics of Tachinidae (Diptera) and their effect on polyphagy**. In *Parasitoid Community Ecology*. Edited by Hawkins BA, Sheehan W. Oxford University Press; 1994:145-162.

37. Mathis KA, Philpott SM: **Current understanding and future prospects of host selection, acceptance, discrimination, and regulation of phorid fly parasitoids that attack ants**. *Psyche* 2012:1-9.

38. Lakes-Harlan R, de Vries T: **Experimental infection of a periodical cicada (*Magicicada cassinii*) with a parasitoid (*Emblemasoma auditrix*) of a proto-periodical cicada (*Okanagana rimosa*)**. *BMC Ecol* 2014, **14**:31.

39. Boesi R, Polidori C, Andrietti F: **Searching for the right target: oviposition and feeding behavior in *Bombylius* bee flies (Diptera: Bombyliidae)**. *Zool Stud* 2009, **48**:141-150.

40. Lill JT, Marquis RJ, Ricklefs RE: **Host plants influence parasitism of forest caterpillars**. *Nature* 2002, **417**:170-173.

41. Davis SE, Malfi RL, Roulston TH: **Species differences in bumblebee immune response predict developmental success of a parasitoid fly**. *Oecologia* 2015, **178**:1017-1032.

42. Jeffries MJ, Lawton JH: **Enemy-free space and the structure of ecological communities**. *Biol J Linn Soc* 1984, **23**:269-286.

43. Murphy SM, Lill JT, Bowers MD, Singer MS: **Enemy-free space**
•• **for parasitoids**. *Environ Entomol* 2014, **43**:1465-1474.
This paper formalizes and evaluates the argument that 'enemy free space' (EFS) may be an important determinant of host use by parasitoids. Using results from several case studies, the authors provide evidence that parasitoids gain some degree of EFS through physical, chemical, and host–plant associated defenses of their hosts. Although not focused solely on NH-parasitoids, the authors use several examples involving tachinid flies, contrasting them with Hymenoptera.

44. Hrcek J, Godfray HCJ: **What do molecular methods bring to host–parasitoid food webs?** *Trends Parasitol* 2015, **31**:30-35.

45. Morris RJ, Gripenberg S, Lewis OT, Roslin T: **Antagonistic**
• **interaction networks are structured independently of latitude and host guild**. *Ecol Lett* 2014, **17**:340-349.

46. Peralta G, Frost CM, Rand TA, Didham RK, Tylianakis JM: **Complementarity and redundancy of interactions enhance attack rates and spatial stability in host–parasitoid food webs**. *Ecology* 2014, **95**:1888-1896.

47. Tylianakis JM, Tscharntke T, Lewis OT: **Habitat modification alters the structure of tropical host–parasitoid food webs**. *Nature* 2007, **445**:202-205.

48. Eubanks MD, Finke DL: **Interaction webs in agroecosystems: beyond who eats who**. *Curr Opin Insect Sci* 2014, **2**:1-6.

49. Holt RD, Lawton JH: **The ecological consequences of shared natural enemies**. *Annu Rev Ecol Syst* 1994, **25**:495-520.

50. Barbosa P, Caldas A, Godfray HCJ: **Comparative food web structure of larval macrolepidoptera and their parasitoids on two riparian tree species**. *Ecol Res* 2007, **22**:756-766.

51. Pardee GL, Philpott SM: **Cascading indirect effects in a coffee**
• **agroecosystem: effects of parasitic phorid flies on ants and the coffee berry borer in a high-shade and low-shade habitat**. *Environ Entomol* 2011, **40**:581-588.

52. Guillade AC, Folgarait PJ: **Effect of phorid fly density on the**
• **foraging of Atta vollenweideri leafcutter ants in the field**. *Entomol Exp Appl* 2015, **154**:53-61.

53. Feener DJ: **Is the assembly of ant communities mediated by parasitoids?** *Oikos* 2000, **90**:79-88.

54. Hsieh H, Liere H, Soto EJ, Perfecto I: **Cascading trait-mediated interactions induced by ant pheromones**. *Ecol Evol* 2012, **2**:2181-2191.

55. Perfecto I, Vandermeer J, Philpott SM: **Complex ecological**
• **interactions in the coffee agroecosystem**. *Annu Rev Ecol Evol Syst* 2014, **45**:137-158.
This is a general overview many types of interactions, however of particular interest are the indirect trait–mediated interactions between phorid parasitoids and ant hosts that cascade to lower trophic levels. In general, phorids discourage ant foraging which permits scale-eating beetles to reproduce more quickly. They also release pressure on coffee-berry borers, but enable synergistic interactions among ant species in controlling herbivores. This review provides an overview of the many interesting previous papers on this system by Perfecto, Philpott and colleagues (see [56] above).

56. Farkas TE, Singer MS: **Can caterpillar density or host–plant**
•• **quality explain host–plant-related parasitism of a generalist forest caterpillar assemblage?** *Oecologia* 2013, **173**:971-983.
Parasitism of temperate forest caterpillar communities is found to be strongly related to host tree identity. This pattern is stronger for dipteran parasitoids that dominate this system and appears to be independent of host density or host–plant quality. The authors suggest the host–plant effects are most likely a function of apparency and/or interactions with caterpillar predators.

57. Ode P: **Plant chemistry and natural enemy fitness: effects on herbivore and natural enemy interactions**. *Annu Rev Entomol* 2006, **51**:163-185.

58. Singer MS, Stireman JO III: **Does anti-parasitoid defense explain host–plant selection by a polyphagous caterpillar?** *Oikos* 2003, **100**:554-562.

59. Ichiki RT, Tabata J, Nakahara Y, Kainoh Y, Nakamura S: **Effects of food plants of host herbivores on development of a midgut-resident tachinid parasitoid, *Compsilura concinnata* (Diptera: Tachinidae), and two hemocoel-resident parasitoids**. *Ann Entomol Soc Am* 2014, **107**:461-467.

60. Singer MS, Mason PA, Smilanich AM: **Ecological immunology mediated by diet in herbivorous insects**. *Integr Comp Biol* 2014, **54**:913-921.

61. Komonen A, Penttila R, Lindgren M, Hanski I: **Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus**. *Oikos* 2000, **90**:119-126.

62. Elizalde L, Queiroz JM: **Parasitoids of acromyrmex (Hymenoptera: Formicidae) leaf-cutting ants in continuous and fragmented Atlantic Forest**. *Sociobiology* 2013, **60**:397-404.

63. Tylianakis JM, Binzer A: **Effects of global environmental**
• **changes on parasitoid–host food webs and biological control**. *Biol Control* 2014, **75**:77-86.

64. Virla EG, Moya-Raygoza G, Rafael JA: **First record of *Eudorylas schreiteri* (Shannon) (Diptera: Pipunculidae) as a parasitoid of the corn leafhopper (Hemiptera: Cicadellidae) in Argentina, with a table of pipunculid-host associations in the Neotropical Region**. *Neotrop Entomol* 2009, **38**:152-154.

65. Nyman T, Leppanen SA, Varkonyi G, Shaw MR, Koivisto R, Elling Barstad T, Vikberg V, oininein H: **Determinants of parasitoid communities of willow-galling sawflies: habitat overrides physiology, host plant and space**. *Mol Ecol* 2015, **24**:5059-5074.