COIS Editorial

Section Editors: Antonino Cusumano & Nina Fatouros

Short CV and photo – Antonino Cusumano

University of Palermo, Department of Agricultural, Food and Forest Sciences, Palermo, 90127 Italy. e-mail: antonino.cusumano@unipa.it

Antonino Cusumano is an assistant professor of entomology in the Department of Agricultural, Food and Forest Sciences at the University of Palermo in Italy. He has broad interest for insect ecology, plant-insect interactions, chemical ecology and biological pest control. He is particularly interested in understanding how microorganisms affect plant-insect interactions as well as parasitoid foraging behavior.

Short CV and photo – Nina Fatouros

Wageningen University, Biosystematics Group, Wageningen, The Netherlands. E-mail: nina.fatouros@wur.nl

Nina Fatouros is an associate professor of evolution of species interactions at Biosystematics Group, Wageningen University. She is interested in the evolutionary pathways that give rise to intricate interactions between plants, herbivorous insects, symbiotic microbes and hymenopteran parasitoids. Besides a fundamental interest in the chemical, molecular and genetic mechanism of these biotic interactions, she aims to transfer the gained knowledge to the plant breeding and biological control industry.

Volume title: Ecology * Parasites/Parasitoids/Biological control

Section Title: Understanding parasitoid ecology and evolution to advance biological control programs

Insect parasitoids are ubiquitous components of terrestrial food webs and play a key role in terms of biodiversity, ecological impact and economic importance. In the framework of sustainable crop protection, parasitoids play a pivotal role in biological control since many species are effective natural enemies of agricultural pests. Insect parasitoids represent excellent model organisms for ecology and evolution. In addition, because of the intimate relationship with their hosts, parasitoids are also seen as models for studies on climate change. Recent developments in insect evolution have highlighted that hymenopteran parasitoids might be now considered to be the most diverse group of insects. Remarkable progress has been made in some area of parasitoid ecology, particularly towards unravelling which cues parasitoids use to locate hosts. Yet, we still have an incomplete understanding of parasitoid ecology. For example, evidence showing that microorganisms may act as hidden players in parasitoid interactions is rapidly accumulating. In this issue we attempted to fill some gaps on parasitoid ecology and evolution which we believe are relevant for optimizing the use of parasitoids in biological pest control.

It is suggested that parasitoids comprise more than half of the diversity of Hymenoptera (and most of the unknown species diversity) making the Hymenoptera and not Coleoptera the most speciose insect order [1]. The review by **Polaszek and Vilhemsen** highlights recent advances in the diversity of phylogenetic relationships of hymenopteran parasitoids. In the Hymenoptera, a parasitoid lifestyle arose once in the ancestor of the Orussidae and Apocrita more than 200 Mya. From a simple lifestyle, probably an idiobiont wasp parasitizing wood-living beetle larvae, Hymenoptera diversified and evolved to parasitize an enormous diversity of hosts and different lifestyles. The Ichneumonidae and Braconidae are among the most diverse and abundant wasps. One reason of their success is seen in the co-option of so-called polyDNA viruses that help them to overcome the hosts' immune response. Polaszek and Vilhemsen provide a summary of the evolutionary history of the parasitoid Hymenoptera as well as outline the intriguing strategies that parasitoids evolved, such as hyperparasitoidism or phoresy.

Phoresy, the transport of one species by another for dispersal, is a strategy frequently used by parasitoids to forage for hosts [2]. Already since the early 70s, seminal reviews by Vinson [3] and Lewis [4], stimulated the research on parasitoid ecology and the focus on host location behavior of parasitoids. Two reviews in the present issue followed up on this still timely and important topic. **Greenberg et al** discuss recent advances on the strategy adopted by egg parasitoids when foraging for hosts in complex environments. Because of their size, low mobility and challenges connected to finding a small and inconspicuous host stage, egg parasitoids are known to use an interplay of long- and short-range cues emitted by (adult) hosts and host plants to find eggs to parasitize. In their review, the authors discuss the most recent research on the chemical ecology of egg parasitoid host-finding and how dynamic host-finding strategies can be within and between individuals, populations and species. They conclude that a better understanding of this variability in host-finding strategies especially under natural conditions will also aid in disentangling the underlying genetic mechanisms and eventually help to further improve biological control. The review by **Benrey** focuses more on parasitoid preferences and performances taking in consideration the role of plant domestication. In particular she incorporates how plant domestication may affect the classical hierarchical steps of parasitoids' host location originally proposed by Vinson [3,5]. Because of artificial selection, cultivated plants are expected to disrupt the co-evolutionary history of parasitoids and their hosts. Alterations in plant morphology, physical characteristics, or chemical defenses due to domestication can affect host-parasitoid relationships and impact parasitoid fitness. Benrey's review highlights the need for more research on parasitoid ecology and evolution also to better control insect pests.

More recently, an increasing number of studies demonstrates that microorganisms are important hidden players that must be considered in order to fully understand parasitoid ecology. In this editorial we use the term “host” to indicate the organism in which parasitoid larvae develop while we avoid using this terminology to indicate the insect that harbors a microbial symbiont for the sake of clarity. Three reviews of the issue show how microbes can influence the foraging behavior, species interactions and reproduction of insect parasitoids. The review by **Frago and Zytynska** discusses how herbivore symbionts can affect parasitoids’ host location. The starting point is a revisitation of seminal work on parasitoid foraging behavior [5,6] updated to incorporate microbe-mediated effects. The key message of this review is that herbivore-associated microorganisms can have opposite effects on parasitoids: 1) on one hand, microbes can protect their herbivore partners by attenuating indirect plant defenses that lead to reduced parasitoid recruitment; 2) on the other hand, microbes can betray their herbivore partners by altering host cues such as frass or honeydew which signal herbivore presence to insect parasitoids. The authors point out that most of the information available about the role of herbivore-associated microbes on parasitoids’ host location is largely based on hemipteran insects. More research is needed on other taxa to recognize how widespread microbe-mediated effects are. Microbes are also the topic of the review by **Pekas et al** but the focus here is on parasitoid interactions. The authors take a tritrophic perspective and discuss how parasitoid competition can be modulated by microorganisms associated with parasitoids, their herbivore hosts or the host-food plants of the herbivores. Microorganisms affect the competitive traits of parasitoids as well as the “fighting arena” (i.e. the herbivore host and its food plant), in which competition occurs. Overall, Pekas et al make a compelling case for the idea that incorporating microbial symbionts is crucial in order to unravel the strength of intra- and inter-specific interactions in insect parasitoids. The third review on parasitoid-microbe relationships by **Verhulst et al** discusses how parasitoid endosymbionts - which are maternally transmitted through the egg cytoplasm - act as reproductive manipulators. The authors focus on the underlying genetic mechanisms that allow endosymbionts to manipulate parasitoid sex determination via cytoplasmic incompatibility (CI) or parthenogenesis induction (PI). Having a strongly female biased sex ratio in parasitoid species that are used as biological control agents is beneficial for pest management programs. Therefore, knowledge on the presence of CI- or PI endosymbionts and their mechanisms is not only relevant for fundamental research but has also implications for biological pest control.

Biological pest control is also covered by **Zaviezo and Muñoz** but the focus of their review is on conservation biological control; a strategy aimed at enhancing the activity of resident natural enemies associated with arthropod pests. By increasing the vegetation diversity within agroecosystems, it is possible to supplement parasitoids with additional resources (shelter, nectar and pollen, alternative hosts) compared to what the crop alone can provide. The exploitation of additional resources is then expected to improve parasitoid performance as biological control agents. Zaviezo and Muñoz highlight the advantages of using native plants, over non-native plants, in conservation biological control. Future research efforts should be carried out to better understand under which circumstances embedding native plants into agroecosystems translates in successful biological control. To fill this gap, mechanistic investigations are particularly welcome. For example, parasitoids need to locate flowering plants within the agroecosystems in order to feed on floral nectar, yet how parasitoids forage for food resources has received little attention compared to how parasitoids forage for hosts.

According to the trophic-rank hypothesis, higher trophic level organisms suffer more from environmental changes because of cascading effects [7]. Indeed, just like with effects of plant domestication, the tightly co-evolved interactions between parasitoids and their hosts can be disrupted, especially when both partners express asymmetric responses to abiotic factors such as temperature or precipitation. The review by **van Baaren et al** discusses how climate change could challenge ecosystem functioning and services exerted by parasitoid wasps and how the use of geographical gradients help to understand those effects. They outline that life history and physiological traits of parasitoids are directly affected by temperatures along gradients as well as indirectly through their hosts. Yet the use of geographic gradients is limited as they can mismatch climatic gradients or microclimate which may explain failures in understanding phenotypic variation among parasitoid populations. Finally, the authors draw attention to the increase of extreme weather events such as heat waves that might exert strong impact on these fragile host-parasitoid interactions.

The collection of eight reviews in this issue covers some recent developments and missing gaps in the field of ecology and evolution of insect parasitoids. Parasitoids are largely used as biological control agents, yet their efficiency in terms of pest suppression is still rather variable and difficult to predict. Among the factors that play a role in parasitoid efficiency, plant domestication and climate change cannot be overlooked anymore as both impact the tightly linked co-evolutionary interactions between parasitoids and their hosts with consequences for functioning in biological control. We also foresee that more and more efforts will be made to comprehend how microbes affect parasitoid ecology, particularly how they modulate parasitoids' foraging decisions, competitive interactions and reproduction. A better understanding of parasitoid ecology eventually helps to disentangle the underlying genetics, which could be implemented into selective breeding programs to improve parasitoid performances in pest control. Furthermore, parasitoid evolution has a direct link with pest control since the continuous discovery of new species can help to find more suitable candidates for biological control programs. In the long term, a deeper understanding of parasitoid ecology and evolution is likely to be the key to advance the efficiency of parasitoid-based biological control programs.

References

1. Forbes AA, Bagley RK, Beer MA, Hippee AC, Widmayer HA: **Quantifying the unquantifiable: why Hymenoptera, not Coleoptera, is the most speciose animal order**. *BMC Ecol* 2018, **18**:21.
2. Clausen CP: **Phoresy among entomophagous insects**. *Annual Reviews in Entomology* 1976, **21**:343-368.
3. Vinson SB: **Host selection by insect parasitoids**. *Annual Review of Entomology* 1976, **21**:109-133.
4. Lewis WJ, Jones RL, Gross HR, Nordlund DA: **The role of kairomones and other behavioral chemicals in host finding by parasitic insects**. *Behavioral Biology* 1976, **16**:267-289.
5. Vinson SB: **The general host selection behavior of parasitoid hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species**. 1998:79-96.
6. Godfray HCJ: *Parasitoids: behavioral and evolutionary ecology*. Princeton: Princeton University Press; 1994.
7. Holt RD, Lawton JH, Polis GA, Martinez ND: **Trophic rank and the species-area relationship**. *Ecology* 1999, **80**:1495-1504.