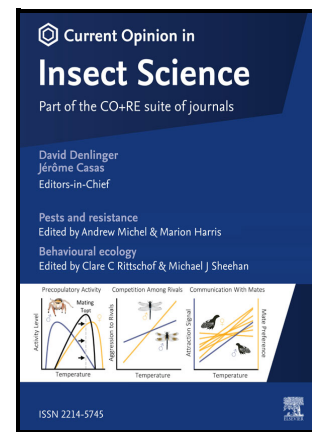


Parasitoid biology in the Anthropocene: It is getting harder to make a living from parasitism

Renee M. Borges
Radhika Venkatesan
Saskya van Nouhuys



PII: S2214-5745(25)00031-8

DOI: <https://doi.org/10.1016/j.cois.2025.101361>

Reference: COIS101361

To appear in: *Current Opinion in Insect Science*

Please cite this article as: Renee M. Borges, Radhika Venkatesan and Saskya van Nouhuys, Parasitoid biology in the Anthropocene: It is getting harder to make a living from parasitism, *Current Opinion in Insect Science*, (2025)
doi:<https://doi.org/10.1016/j.cois.2025.101361>

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Editorial Overview:**Parasitoid biology in the Anthropocene: It is getting harder to make a living from parasitism**

Renee M. Borges^{1,*}, Radhika Venkatesan² and Saskya van Nouhuys¹

¹Centre for Ecological Sciences, Indian Institute of Science, Bengaluru 560012, India

²Department of Biological Sciences, Indian Institute of Science Education and Research, Kolkata, Mohanpur, West Bengal 741246, India

*Correspondence: renee@iisc.ac.in

Parasitoids play a ubiquitous role in multitrophic interactions and structuring of communities involving arthropods [1]. They are essential for top-down regulation of herbivorous insect populations, and thus central to biological control programs [2]. Changes in the environment can both directly and indirectly alter parasitoid biology. For instance, increased pesticide usage not only reduces host populations but also can repel parasitoids, reduce their fitness and alter their host acceptance behavior. New associations due to accidental or intentional introduction of new parasitoids or hosts alter community composition. Further, variation in temperature and humidity affect both hosts and parasitoids, subsequently influencing their coupled population dynamics.

Most insect parasitoids belong to the major insect orders Diptera [3] and Hymenoptera [4]. While some of them show specific host preference, others have a broader host range. The ability of a parasitoid to find and successfully use a host for reproduction is influenced by factors such as host species, developmental stage, densities, intraguild predation and host plant species. Varying environmental conditions affect all of these parameters that in turn affect parasitoid biology. Since host-parasitoid interactions are necessarily matched in time and space, any mismatch resulting from environmental changes, such as early host pupation or late larval development, could cause decline or even breakdown of these interactions [5]. Further, these changes could differ depending on parasitoid life history traits. For instance, ectoparasitoids develop externally on the host, while endoparasitoids develop within it, exposing them to different ecological pressures. The insect host, on the other hand, could be ecto- or endophagous where the insect host larva develops externally on plants or within plant tissues respectively, thereby exposed or shielded from external environmental variation. As a result of all these factors, the outcome of host-parasitoid interactions is highly context-dependent, varying according to the specific traits of both the host and the parasitoid in response to changing environmental conditions.

The major consequences of the Anthropocene are the following:

1. Increase in stochasticity of warming, cooling and precipitation
2. Increased levels of herbicides, pesticides and pollutants
3. Changes in phenology of plants, host insects, and parasitoids

4. Changes in spatial distribution of host plants and host insects due to climatic factors, habitat fragmentation, and species invasions

These factors can affect parasitoids in many ways:

1. Range shift, decline or local extinction because of limited heat or cold tolerance
2. Mortality or increased costs of immunity due to exposure to pesticides, herbicides and pollutants
3. Mismatch in phenology with the plant–host insect complex
4. Mismatch in physiological range with the plant–host insect complex
5. Range shift or local extinctions of plant–host insect complexes impairing host finding and host accessibility
6. Shifts in community composition due to invasion by other parasitoids as competitors, presence of hyperparasitoids, predators and disease as well as the availability of alternate hosts as resources.

This Special Issue aims to bring together contributions from experts exploring the impacts of the Anthropocene on parasitoid biology which includes behavior and ecology. It also seeks to address how parasitoids have evolved in response to environmental changes, offering insights into their future survival and adaptability.

Parasitoids are mega-diverse and probably represent the most speciose group of animals present today. What are the features and evolutionary processes that have given rise to such diversity? In this Special Issue Hambäck et al. [6] examine a range of possibilities, e.g. the escape and radiate hypothesis, and key innovations, such as ovipositor adaptations, that may have been responsible for speciation in parasitoids. The tolerance for sib-mating and the haplodiploid breeding system may also have been contributory factors to local speciation processes. The very mechanisms that may have fuelled parasitoid diversity could be beneficial to parasitoids in dealing with the exigencies of the Anthropocene; however, will they also contribute to more specialisation, and thus lead to faster extinction? These are certainly valuable ideas to be addressed within the constraints of parasitoid biology.

Malinski et al. [7] focus on high-temperature events (HTEs) that are becoming increasingly common during the Anthropocene. The particular focus of this review is on HTEs that are above the temperature optima for either a species or a population. More importantly, this review is crafted as a set of Lessons Learned and Opportunities for Research that will enhance our understanding of how the relationship between parasitoid development biology, parasitoid venom, parasitoid polyDNA viruses that aid in host immunosuppression, and parasitoid host development can be affected by HTEs. This important review focuses on research gaps and calls for research in critical areas.

Yadav and Borges [8] deal with the difficulties that parasitoids have with oviposition decisions under Anthropocene conditions. Pesticides affect associative learning and memory in parasitoids such that females may not remember patches in which they have oviposited, resulting in superparasitism of hosts with negative impacts on offspring survival. Infection by *Wolbachia* is also affected by temperatures and may cause altered oviposition behaviour. Water deficits in host plants and artificial light at night (ALAN) also affect oviposition

behaviour and success. This review highlights the point that while the impact of these environmental factors has been examined individually, their combined effects have not been investigated.

While considerable research has evaluated the effect of climate change, especially high temperatures on parasitoids, hyperparasitoids that are parasitoids of parasitoids have scarcely been examined from this perspective. Segoli et al. [9] investigate the direct and indirect effects of temperature on hyperparasitoids, and the subsequent impacts on these complex interactions between host plants, insect hosts, parasitoids and hyperparasitoids. They call for more research on this valuable trophic group of predators, especially in the context of biological control.

The impact of pesticides on biological pest control is far reaching and is a pervasive feature of the Anthropocene often resulting in the over application of a variety of pesticides especially in developing nations. Theenoor et al. [10] provide a comprehensive review of the impact of pesticides on the life history traits of parasitoids including host-mediated effects. The review highlights the complex and often unintended consequences of pesticide use, emphasizing that sublethal doses can also significantly impact parasitoid populations and their ecological roles. The authors call for sustainable pest management strategies that reduce pesticide use, incorporate biological control agents, and prioritize ecological balance to enhance pest suppression.

Once a parasitoid has oviposited on or in a host, its offspring must contend with the immune response of the host. Ghosh et al. [11] detail the impact of anthropogenic factors on the functioning of the immune system of herbivorous insects that serve as parasitoid hosts. They schematise the relationship of plant secondary metabolites (PSMs), temperature rise, and community composition with parasitoid performance through the lens of host immune response. An important dimension is the likely trade-off by both herbivores and their parasitoids with respect to host range and specialized PSMs; these PSMs are energetically expensive to detoxify but can also secondarily be used as defence. In addition to mounting an immune response and dealing with plant chemical defences, hosts also used endosymbionts to resist parasitoids. Based on literature from other insect groups such as aphids and flies, Hudson et al. [12] hypothesise that increased temperature might affect defensive endosymbionts that confer resistance against parasitoids in their hosts. Considering the limited literature on parasitoids in this regard, the speculations and hypotheses raised in this paper are valuable as new research questions.

Many plants have indirect defence mechanisms in which they elicit the service of parasitoids to prey upon their chewing and cutting herbivores. Herbivore-induced plant volatiles (HIPVs) may signal to parasitoids about the presence of herbivores that learn to respond to these signals which provide information about the availability of parasitoid hosts. However, climate changes such as heat and drought stresses may induce plants to release HIPVs such as green leaf volatiles (GLVs) in response to membrane damage caused by abiotic stress rather than herbivore damage. Thus, parasitoids could be confronted with false signals. Climate change could also result in broken or altered signals wherein the HIPVs released by plants are altered due to oxidising atmospheric pollutants or when atmospheric pollutants occlude the olfactory receptors and prevent signal recognition by parasitoids. The excellent review by Pinto-

Zevallos and Blande [13] highlights the false, broken and unperceived signals between host plant and parasitoids in response to combined abiotic and biotic stresses.

The rest of the papers in this Special Issue scale up to the population and the community level emphasizing agricultural settings and biological control. Shameer and Hardy [14] examine parasitoid–herbivore–plant food webs in agroecosystems, and provide a clear overview on how effects of agricultural practices can be assessed using food web metrics. Kumaraswamy et al. [15] provide a comprehensive review of the deployment of parasitoids in agricultural pest control in India. They emphasise the challenges of mass rearing of parasitoids for effective biological pest control, problems that are likely to be exacerbated under climate and land use changes. Khamis and Ajene [16] document the use of parasitoids for pest control in Africa and propose important research agendas in the future. Oil palm plantations are extremely common in south-east Asia and represent a dominant land use conversion from pre-existing species-rich rain forests. Rizali et al. [17] review parasitoid food webs in oil palm plantation of different ages and also show that the presence of nectar plants is important for the stable presence of parasitoids within these plantations. They advocate the cultivation of native nectar plants over invasive exotics to support sustainable parasitoid populations within these plantations.

Invasive species are another signature of the Anthropocene with global trade and movement of commodities increasing the possibilities of adventive species (plants and insects) becoming invasive under release from their native enemies (herbivores and parasitoids/hyperparasitoids). How might invasive plants and invasive or adventive parasitoids affect community structure? Duan et al. [18] examine this important question and provide examples which strike cautionary notes for the import of exotic or adventive biological control agents.

Another globally important agricultural ecosystem consists of drylands, e.g. in Israel, Oman, and the Sahel. While parasitoids are important in these areas as in any other agricultural landscape, little is known about vital aspects of their biology in such systems and their strategies to cope with harsh, arid conditions. Saabna and Keasar [19] point out the unique nature of dryland agriculture and indicate the many gaps in knowledge about parasitoid food webs and their basic biology.

The reviews in this Special Issue approach the effects of anthropogenic change on parasitoids from diverse perspectives that range from physiology to landscape composition, but still do not address all aspects necessary for a complete understanding of parasitoid biology in the Anthropocene. Many knowledge gaps remain. However, the reviews raise critical questions that can help shape future research, guiding efforts to explore the intricate ways in which environmental changes influence parasitoid ecology, behavior, and evolution.

Declarations of Interest

The authors declare no competing interests.

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Biographies



Radhika Venkatesan is an Associate Professor at the Department of Biological Sciences, Indian Institute of Science, Education and Research, Kolkata, India. Her lab primarily works on understanding chemically mediated interactions between plants and insects in the broad area of chemical ecology. She is particularly interested in insect immune responses, herbivore-induced plant volatiles, and their role in shaping host-parasitoid interactions. Additionally, her lab explores plant-derived bioactive peptides. She combines research on chemistry, ecology and entomology to enhance understanding of plant-insect interactions while also exploring practical applications in sustainable agriculture and medicine.



Renee M. Borges is Professor at the Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India. She is particularly interested in inter-species interactions and has worked on mutualisms and parasitisms in model systems such as interactions between figs and fig wasps, plants and pollinators, ants and ant-plants, termites and their fungus farms, crab spiders and their prey and more recently on potter and mud dauber wasps. She takes a mechanistic approach to behavioural ecology and focuses mainly on vision and olfaction. She has worked on life histories and ovipositor adaptations in fig wasp parasitoids.

**CV:**

Saskya van Nouhuys is a Professor at the Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India. Before joining there she worked for many years in the Department of Biological Sciences at the University of Helsinki. She is a population and community ecologist, especially interested in spatial population dynamics, and in the roles of species interactions in explaining dynamics of populations. She works mostly on parasitoid wasps, and on multitrophic interactions between plants, herbivorous insects and their parasitoids in natural and in agricultural settings.