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Editorial: Ecology and evolution of host-plant relations in gall-inducing arthropods

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Editorial on the Research Topic
Ecology and evolution of host-plant relations in gall-inducing arthropods

The Tephritidae, or true fruit flies (Diptera), are an economically important group comprising about 5000 described species, of which 400-450 are known gall-inducers. Also known as "peacock flies," the charismatic adults have maculated wings and eye-catching behaviors to match, such as the prominent wing-waving rituals associated with courtship. One of the best known tephritids in the scientific world is *Eurosta solidaginis*, which induces galls on goldenrods (*Solidago* spp.) and has served as a model organism for community ecology (Abrahamson and Weis, 1997).

For the last four decades, Korneyev has been a recognized authority on tephritids, especially those inducing galls. In the first article in the present volume, he provides an update to the systematics of the group, applying a global, biogeographical approach towards advancing the state of our knowledge of this remarkable taxon. Korneyev combines current systematics using traditional morphological and current molecular-based methods to illuminate a richly structured tephritid phylogeny revealing multiple origins of gall induction.

In fact the eponymous fruit flies are ecologically diverse: larval stages attack not only fruits in various stages of ripeness, but also act as saprophages under tree bark, as parasitoids of other insects, and as borers and seed eaters. Gall-inducers in this group exploit principally the Asteraceae, feeding on floral heads, stems, and (subterranean) rhizomes; a smaller number induce galls on plants in the Fabaceae and Goodeniaceae. In his comprehensive review, Korneyev advances a host-plant shift hypothesis in the context of climatic change towards increasing aridification and the appearance of extensive New- and Old-World grassland biomes during the late Miocene and Pliocene epochs. Indeed, this is suggestive of the hypothesis that galls serve an adaptive function in xeric environments generally (Wilson Fernandes and Price, 1992).

The formation of galls is almost always beneficial to the arthropods inducing them but disadvantageous to the host plants by reducing their productivity. Hence insect-induced galls are considered to be an adaptation of the inducers, acting as parasites of the host plants. However, the relationship between fig wasps (Hymenoptera: Chalcidoidea) and their host plants, figs (*Ficus* spp.) (Moraceae) is exceptional as it constitutes a mutualism, as elaborated by Borges in the second article of this volume. Typically, figs (a rich flora numbering 874 species described to date) depend exclusively on the highly specialized fig wasps for pollination, and larvae of fig wasps develop in the fig fruit by inducing galls. Exceptions to this rule include those non-pollinating fig wasps acting purely as parasites of figs. Nevertheless, this system is one of the best-known examples of mutualisms between insects and plants as well as an illustrative example of coevolution and co-speciation between plants and herbivores.

Borges investigates fig/fig wasp systems especially for chemically-mediated host location mechanisms of galling and parasitoid wasps. She makes a strong case for regarding the fig syconium (inflorescence) as a model system for exploring the evolutionary dynamics between host plant and phytophagous insect. In this volume, she summarizes the latest research on gall induction by fig wasps, and concludes by highlighting eleven outstanding questions. These include identifying the mechanisms underlying sanctions imposed by *Ficus* plants on cheating (non-pollinating) fig wasps, the ability of wasps to sense plant volatiles with their ovipositors, and identifying the factors modulating sexual selection in these bizarrely dimorphic, minute arthropods.

Galls are conspicuous structures formed on plant organs by insects and other biological agents, and their presence is evident in the fossil record as well. Paleobotanists and entomologists have long been interested in these formations, occurring not only as body fossils, but also ichnofossils (trace-fossils). Labandeira is an outstanding authority on paleobiology especially focusing on the plant-herbivore interactions revealed in the fossil record. In the third article in this volume, Labandeira provides a sweeping, scholarly review of fossil galls organized by damage types caused by gall inducers ranging from the Paleozoic (the Middle Devonian Period) to the Cenozoic Era (the Neogene Period). Drawing on extensive information from the fossil record, he explores 17 important ecological and evolutionary themes: these include major geologic and climatic events such as the End-Permian extinctions, the spectacular expansion of plant-insect interactions concomitant with the initial diversification of the angiosperms, and the survival of many gall arthropods through the Paleocene-Eocene Thermal Maximum, when land temperatures are thought to have climbed 5-7 degrees Celsius and atmospheric carbon dioxide pressures tripled or even quadrupled from their previous levels.

Labandeira provides an elaborate discussion on the cycles of diversification and decline experienced by gall-inducing arthropods in accordance with the fossil evidence. Illustrations in the article include a rich set of drawings of fossil galls, resembling fine woodcuts, rendered by the author. The review shows that, as in other taxa represented in the fossil record, gall inducers have a long history of radiations and extinctions, with only a small proportion of survivors eventually becoming extant species. Throughout, Labandeira emphasizes the massive gaps in the fossil record, exemplified by the 60-million-year gap following the earliest known gall found on a foliose liverwort fossil dating back 385 million years. Ironically, the most recent 3 million years of the fossil record are impoverished, apparently because the hothouse-icehouse dynamics of glaciation and de-glaciation have not provided suitable conditions for the deposition of fossils.

Global warming affects a wide range of organisms. Insects, in particular, may be more susceptible to climate change than endothermic animals, as their growth and developmental rates are temperature dependent. The Asian chestnut gall wasp, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae), is an invasive pest of the chestnut industry and now causes serious damage to European chestnut (*Castanea sativa*) on the European subcontinent. *Torymus sinensis* (Hymenoptera: Torymidae), a natural enemy of *D. kuriphilus*, is a parasitoid native to China, which was introduced to Japan in the 1980s and made a significant contribution to the control of *D. kuriphilus*. Currently, classical biological control of *D. kuriphilus* using *T. sinensis* is being attempted in Europe.

Aguirrebengoa et al. have investigated the seasonal occurrence of *T. sinensis* in Spain and have found that the southernmost European populations (in Malaga, Spain) have evolved bivoltinism from a univoltine ancestral state, apparently mediated by temperature and gall traits. One potential factor favoring bivoltinism under these conditions is that larger galls may provide some refuge from *T. sinensis*, implying more *D. kuriphilus* hosts may be available for additional generations of the parasitoid. Their results will have implications not only for researchers of pests and introduced natural enemies, but also those working on environmental adaptation in various insects under climate change.

Since the time of Theophrastus, a student of Aristotle in ancient Greece, plant galls have fascinated natural historians and scientists globally. The contributors to this volume have made significant advances in our understanding of these distinctive and ubiquitous features of ecological landscapes. It is hoped this body of work will inspire further exploration into this still-mysterious realm of plant-animal interactions.

Author contributions

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Conflict of interest

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