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Editorial: Evolutionary ecology of plant defenses and herbivore interactions in the tropics: from molecules to communities

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Editorial on the Research Topic

Evolutionary ecology of plant defenses and herbivore interactions in the tropics: from molecules to communities

In tropical forests, the high diversity of plants and their associated insect herbivores has resulted in a variety of plant defenses and herbivore counteradaptations. In these habitats, their interactions have been invoked as one of the main drivers of trait diversification, arms race coevolution and ecological coexistence for both groups of organisms (Janzen, 1970; Fine et al., 2004; Kursar et al., 2009; Coley and Kursar, 2014; Endara et al., 2017; Forrister et al., 2019). These relationships play a critical role in ecosystem functioning, affecting every organism inhabiting this species-rich biome. This Research Topic represents an effort to bring focus to the study of the ecology and evolution of plant-herbivore interactions in the tropics (still poorly represented in the literature; Crespo-Pérez et al., 2020). Since the early days of the study of plant defenses, much of the research has focused on temperate ecosystems, and has been summarized in previous efforts (e.g. Fritz and Simms, 1992; Karban and Baldwin, 1997; Herrera and Pellmyr, 2002). Filling this gap was the first goal of this special feature.

The second goal was to stimulate debate and future research. The development of new analytical methods has greatly improved our ability to test classical hypotheses in plant-insect interactions. For example, thanks to recent advancements in chemical analytical techniques and mass spectrometry we can now perform full characterizations of chemical defensive profiles. It has also allowed us to finally estimate chemical similarity and diversity in order to answer questions across large taxonomic and geographic scales. One such question concerns the role of geographic variation in chemically mediated plant-herbivore associations (Thompson, 2005). Specifically, ecological and evolutionary theory suggests that the magnitude and direction of selection between plants and herbivores differ between localities resulting in variation on reciprocal selection and trait remixing across environments. A thorough study of this hypothesis requires not only data on host plant and herbivore populations at different sites, but also a comprehensive characterization of chemical phenotypes mediating the interaction. In this Research Topic, using metabolomic methods, two studies offer answers at different scales. Fine et al. integrates data on secondary metabolites and associated herbivores for the tropical genus of trees *Protium* (Burseraceae) in two rainforest sites separated by 1500 km in Peru and Brazil. Although high phylogenetic beta-diversity in herbivore insects between sites was found, no significant variation in chemical phenotypes was present. Gene flow across sites (Dexter et al., 2017) may prevent *Protium* populations to diverge in chemotypes. On the contrary, in a multi-site transplant experiment with clones of *Piper arboreum* in the Cerrado gallery forests in central Brazil, Serejo Rabelo et al. found high plasticity in secondary metabolite expression between populations before and after transplanting. Contrasting results in both studies probably reflect resource gradients and the different scales at which both studies were carried out. Interestingly, chemical diversity and similarity influence herbivore diversity and composition in both studies, supporting the defensive nature of secondary metabolites.

Although secondary metabolites have been notoriously identified as the most relevant plant traits for herbivore host choice and specialization, the relative importance of these vs other host traits is not fully understood. With the development of new phylogenetic tools and analytical methods, it is possible now to combine host phylogeny and trait information to test the relative contribution of different plant traits to host selection. Segar et al. ask the simple question: what factors drive host specialization of caterpillars associated with four species-rich tropical plant genera *(Ficus, Macaranga, Syzygium and Psychotria)* in Papua New Guinea? Using phylogenetic comparative methods, their analyses find that host specialization is better explained by host phylogeny and to a lesser degree by polyphenol content. Mechanical traits played a small role. High herbivore beta-diversity across the four plant genera suggests that, in this tropical forest each lineage can be seen as a host island. This pattern might be driven by the differential expression of host plant traits conserved at the genus level, such as lineage specific chemicals. Thus, host traits appear to play a crucial role in shaping the high levels of host specialization observed in tropical forests.

Besides contend with their host plants, herbivores are also confronted with attack by the third trophic level. Recruitment of predators and parasitoids by plants are recognized as indirect defenses against herbivory (Johnson, 2011). However, the significance of interactions with the third trophic level as effective defenses has been the subject of much debate (Dicke and Baldwin, 2010). Corozo-Quiñonez et al. studied whether the resistance of several species and genotypes of *Capsicum* (Solanaceae) to *Phytophthora capsici* (Peronosporaceae) and *Bemisia tabaci* (Hemiptera: Aleyrodidae) could be complemented by interactions with the third trophic level. After a greenhouse experiment, the authors concluded that the presence of natural enemies contributed to the resistance of *Capsicum* spp. to an aerial herbivore and a soil-borne pathogen. This resistance varied with the different genotypes, suggesting the potential for the development of genetic lines that are resistant to pathogens. These results provide the basis for environmentally friendly biological control programs for crops.

In this Research Topic, studies carried out at large geographic and taxonomic scales, as well as in experimental settings, have illustrated the tight relationship that exists between plant defenses and herbivores and their susceptibility to the third trophic level. Multi-site studies have contributed to determine the factors shaping community assembly and phenotypic variation. The inclusion of metabolomics and phylogenetics has allowed us to collect trait data at large scales permitting the exploration of ecological relevant traits for host selection. We argue that other host traits, such as flowering time and growth rate, or the ontogenetic stage of leaves as well as trees (Cobo-Quinche et al., 2019; Sedio et al., 2019), should be also evaluated in parallel to the defensive chemistry at macroevolutionary timescales to better understand coevolutionary outcomes in both plants and their pathogens (Carmona et al., 2011). Nevertheless, there is an evident lack of long-term studies, as well as of global change research on species interactions in the tropics. Thus, we need studies that include plants, insects, phenological species traits and the effect of multiple drivers of global environmental change if we want to make reliable predictions of the future of these species-rich habitats, where the diversity of insect herbivores and their host plants are among the biggest in the terrestrial world.

Author contributions

RC: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. KA: Writing – review & editing. M-JE: Conceptualization, Investigation, Writing – original draft, Writing – review & editing.

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Conflict of interest

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