ARTICLE ADDENDUM

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Insects on flowers

The unexpectedly high biodiversity of flower-visiting beetles in a tropical rainforest canopy

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Insect biodiversity peaks in tropical rainforest environments where a large but as yet unknown proportion of species are found in the canopy. While there has been a proliferation of insect biodiversity research undertaken in the rainforest canopy, most studies focus solely on insects that inhabit the foliage. In a recent paper, we examined the distribution of canopy insects across five microhabitats (mature leaves, new leaves, flowers, fruit and suspended dead wood) in an Australian tropical rainforest, showing that the density (per dry weight gram of microhabitat) of insects on flowers were ten to ten thousand times higher than on the leaves. Flowers also supported a much higher number of species than expected based on their contribution to total forest biomass. Elsewhere we show that most of these beetle species were specialized to flowers with little overlap in species composition between different canopy microhabitats. Here we expand our discussion of the implications of our results with respect to specialization and the generation of insect biodiversity in the rainforest canopy. Lastly, we identify future directions for research into the biodiversity and specialization of flower-visitors in complex tropical rainforests.

The extraordinary biodiversity of insects in tropical rainforest canopies has been the inspiration and basis for the development of many theories attempting to explain the evolution of plant-animal interactions,[1-4] food web dynamics,[5] and global biodiversity patterns.[6-9] However, almost all of our current hypotheses, predictions and theories have been based on the assumption that the majority of insects are herbivores associated with leaves.[10] Species inhabiting other canopy microhabitats have previously been considered to represent a minor component of insect biodiversity and have subsequently been overlooked or omitted in studies of insect biodiversity (see[6-9]).

In a novel approach, we simultaneously sampled invertebrates from multiple canopy microhabitats in order to make comparisons in the importance of different resources for supporting invertebrate abundance and species richness and to test the assumption that most canopy insects are leaf-associated herbivores. The primary results of our paper[11] was the demonstration that (i) the invertebrate assemblage inhabiting the leaves is *not* representative of the wider canopy community, and (ii) each microhabitat supports a unique assemblage in terms of species composition, species richness, relative abundances, and density. In particular, flowers constitute a very important, but until now under-appreciated, microhabitat for species richness and abundance. Despite constituting a tiny fraction of canopy biomass, flowers supported invertebrate densities that were one to three orders of magnitude greater than on the leaves. Species-level analysis of the beetle fauna estimated that flowers were utilized by ~41% of species, with a high level of microhabitat fidelity resulting in little overlap in species composition between microhabitats.[11]

Further work performed using the same data set, however, also revealed the

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occurrence of unexpectedly high levels of host specialization among flower visiting beetles (Wardhaugh et al. in review). These results suggest that the beetle fauna is under selective pressure to form and maintain strong host-plant associations based on the floral or phenological traits of individual plant species. Furthermore, the occurrence of so many invertebrates on flowers undoubtedly has a significant effect (both positive and negative) on the reproductive possibilities of the host plants.[12,13] Here, we further expand on the possible significance of the interactions between flowering plants and flower-visiting insects in the evolution and diversification of both plants and insects.[14]

The Generation of Flower-Visiting Insect Biodiversity

High levels of host specificity, combined with taxonomic conservatism in microhabitat utilization,[15] suggest that high species richness among flower-visitors has been the result of diversification and adaptation in response to host plant characteristics. For herbivores on leaves, diversification is thought to be in large part the result of coevolutionary responses between herbivores and host plant defenses.[16] We suggest that this is unlikely to be the case on flowers since they are generally less well defended against herbivores than leaves[17] since flowers also must function to attract pollinators, and high levels of defense may hinder reproductive success.[13] We suggest that high species richness and host specificity among flower-visitors could be the result of the requirement to locate unique hosts embedded in a diverse multitude of non-hosts.[18] In most tropical rainforests local plant diversity is typically very high, and, as a consequence, local densities of individual plant species is often very low. In addition, species diversity of plants may also result in high diversity of olfactory and other signals from plants seeking to attract insect pollinators to flowers. Specialising on locating one or a few host plant species may shorten searching and decision times, thus conserving energy and reducing exposure to time-based mortality factors.[18] Under this scenario, the degree of specialization among the flower-visitor community will be positively associated with the species richness of the flowering plant community, a pattern typical of the species richness of herbivores on leaves.[8,9]

The diversification and dominance of modern angiosperms has long been thought to be the result of the interaction between flowering plants and insect pollinators,[19,20] and it has been suggested that pollinating beetles in particular were instrumental in promoting early angiosperm diversification.[20] However, the hypothesis that angiosperm diversification was the result of specialist pollination syndromes remains controversial (see[22,23]), since generalized insect pollination and wind pollinated systems outnumber specialist systems.[1,24] While there has been a large focus on the evolutionary role of pollinators, most insects that visit flowers probably do not carry out pollination.[14] Flowers represent high quality resources to many insects, and while some species inadvertently benefit the host plant by transporting pollen, flower-visiting insects may utilize flowers for a variety of reasons. Independent of whether a species is an active pollinator, flower visitation and the utilization of flowers as a resource in tropical forests may still lead to adaptation, diversification and specialization.[14] For example, pollen feeding is proposed to represent the precursor of foliage feeding in many herbivorous groups.[21] Floral herbivory therefore, rather than pollination per se, may have played a substantial role in both the diversification of insects and the radiation of angiosperms during the Cretaceous.[14,25] This is consistent with our hypothesis that specialization among flower-visitors is independent of the role played by flower-visiting species and is instead a function of local plant diversity.

Future Directions

As our study[11] is one of the few to examine the fauna attracted to flowers in tropical rainforests, it is impossible to know how they generalize to other locations. It seems, however, that there is *prima facie* reason to expect high levels of specialization rather than low levels. For one, our conclusions are not counter-intuitive or contradictory to existing evidence, but are instead logically consistent (e.g.[8,9,14,18]). What is perhaps surprising is that it has been assumed that flower-visitors (or species on other microhabitats) were not likely to display high levels of host specificity or support high species richness (see[5,8,29]). The implications of these results for the evolution and estimation of global biodiversity and food web dynamics will require studies documenting the diversity and specialization of flower-visitors in other rainforest locations.[11] While some information is available for some areas or plant groups,[1,26-29] detailed examinations of flower-visiting insects are scarce for tropical rainforests. For example, although the fauna and flora of the Australian Wet Tropics is very well known, the pollination biology of less than 1% of the plant species has been studied, and the Australian flora is much better known than most tropical rainforest areas.[30] Ultimately, the potential for flower-visitors to significantly alter our current understanding of the extent, influence and generation of biodiversity in tropical rainforests means that flower-visitors, not just pollinators, can no longer be ignored.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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