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IN FOCUS
Natural history matters: how biological constraints shape diversified interactions in pollination networks

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Species-specific traits and life-history characteristics constrain the ways organisms interact in nature. For example, gape-limited predators are constrained in the sizes of prey they can handle and efficiently consume. When we consider the ubiquity of such constrains it is evident how hard it can be to be a generalist partner in ecological interactions: a free living animal or plant can't simply interact with every available partner it encounters. Some pairwise interactions among coexisting species simply do not occur; they are impossible to observe despite the fact that partners coexist in the same place. Sazatornil *et al.* (1) explore the nature of such constraints in the mutualisms among hawkmoths and the plants they pollinate. In this iconic interacion, used by Darwin and Wallace to vividly illustrate the power of natural selection in shaping evolutionary change, both pollinators and plants are sharply constrained in their interaction modes and outcomes.

Keywords: complex networks, forbidden links, long-tubed flowers, mutualism, pollination, Sphingidae

Size-limited foragers show clear restrictions on the size of prey items they can efficiently handle. In the case of plant-pollinator interactions, size uncoupling between pollinator bodies and flower sizes or structure are specially relevant in filtering out a range of potential partners (2). The idea, when applied to the bizarre flowers of some plants pollinated by sphingid moths (Lepidoptera: Sphingidae), was seminal in Darwinian evolutionary theory to support the potential of natural selection in shaping adaptations (3). Wallace (4) in his book, *Creation by law*, vividly uses the famous example of the Malagasy orchid and its sphingid pollinator to refute the arguments of the Duke of Argyll against natural selection and Darwinism:

> "There is a Madagascar Orchis–the *Angrœcum sesquipedale*–with an immensely long and deep nectary. How did such an extraordinary organ come to be developed? Mr. Darwin's [[p. 475]] explanation is this. The pollen of this flower can only be removed by the proboscis of some very large moths trying to get at the nectar at the bottom of the vessel. The moths with the longest proboscis would do this most effectually; they would be rewarded for their long noses by getting the most nectar; whilst on the other hand, the flowers with the deepest nectaries would be the best fertilized by the largest moths preferring them. Consequently, the deepest nectaried Orchids and the longest nosed moths would each confer on the other a great advantage in the 'battle of life.' This would tend to their respective perpetuation and to the constant lengthening of nectar and noses."

Phenotypic fitting of corolla length and shape and the pollinators' feeding apparatus and body sizes are important because the better the fit, the better the consequences in terms of fitness outcomes for the interaction partners (5). Yet the expectation of perfect trait matching across populations or communities is too simplistic (6): "arms races" as initially suggested by Darwin and Wallace are frequently asymmetric, originating pollinator shifts rather than tight phenotypic trait matching (Fig. 1). Extensive local variation in phenotypic mismatch exists in different plant-pollinator systems (e.g., 2; 6; 7), with pollinator-mediated selection geographic mosaics of locally coevolved partners.

Recent work by Sazatornil *et al.* (1) provides evidences that the types of trait mismatching outlined in Fig. 1 limit the ranges of host plants for sphingid pollinators, and ultimately shape their complex plant-pollinator networks. By using a comparative analysis of five different hawkmoth/flower assemblages across four South American biotas (Atlantic rainforest and Cerrado in Brazil, Chaco, and the Chaco-Yungas transition in Argentina) they tested the contributions of phenotypic matching to explain observed patterns of moth-flower interactions.

Yet Sazatornil *et al.* did not include the morphological difference for parameter estimation when interactions were not recorded. Thus the test of the mismatch hypothesis implicitly includes forbidden links effects: a full mismatch of corolla tube/proboscis lengths actually means a forbidden link. In any case the mismatch hypothesis somehow captures the fact that a fraction of the unobserved interactions in these hawkmoth/flower assemblages is due to extreme phenotypic mismatch (i.e., size-related forbidden links).

Proper tests of coevolutionary hypotheses in hawkmoth/flower assemblages (and plant-animal mutualisms in general) should use Sazatornil et al. approach: assessing match/mismatch patterns for every possible pairwise interaction among partners within complex webs of interaction where multiple life-history attributes may contribute biological reasons to expect forbidden links.

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Figures

Fig. 1 Morphological mismatches set important biological constraints for size-limited foragers, including e.g., predators, pollinators, and frugivores. In plant-animal mutualisms, a morphological mismatch between partners sets size limits that filter out a range of phenotypes that otherwise could eventually interact. Other reasons for forbidden links include, e.g., phenological differences (8). Thus, a number of the potential interactions that could take place in a given mutualistic assemblage simply cannot occur because of biological reasons: these are forbidden interactions. Photo: Andrea Cocucci. An sphingid moth, *Agrius cingulata*, visiting a flower of *Bauhinia mollis* (Fabaceae), Las Yungas, Argentina.