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6 **IN FOCUS**
7 **Natural history matters: how biological**
8 **constraints shape diversified interactions in**
9 **pollination networks**

10 **Pedro Jordano¹**

11 *1. Integrative Ecology Group, Estación Biológica de Doñana, Consejo Superior*
12 *de Investigaciones Científicas (EBD-CSIC), Avenida Americo Vespucio s/n,*
13 *E-41092 Sevilla, Spain*

14 *Correspondence author. jordano@ebd.csic.es

15 IN FOCUS: Sazatornil, F.D., Moré, M., Benitez-Vieyra, S., Cocucci, A.A.,
16 Kitching, I.J., Schlumpberger, B.O., Oliveira, P.E., Sazima, M. & Amorim,
17 F.W. (2016) Beyond neutral and forbidden links: morphological matches
18 and the assembly of mutualistic hawkmoth-plant networks. *Journal of An-*
19 *imal Ecology*, 00, 000–000. doi:10.1111/1365-2656.12509

20
21 **Species-specific traits and life-history characteristics constrain**
22 **the ways organisms interact in nature. For example, gape-limited**
23 **predators are constrained in the sizes of prey they can handle and**
24 **efficiently consume. When we consider the ubiquity of such con-**
25 **straints it is evident how hard it can be to be a generalist partner**
26 **in ecological interactions: a free living animal or plant can't simply**
27 **interact with every available partner it encounters. Some pairwise**
28 **interactions among coexisting species simply do not occur; they**
29 **are impossible to observe despite the fact that partners coexist in**
30 **the same place. Sazatornil *et al.* (1) explore the nature of such**
31 **constraints in the mutualisms among hawkmoths and the plants**
32 **they pollinate. In this iconic interaction, used by Darwin and Wal-**
33 **lace to vividly illustrate the power of natural selection in shaping**
34 **evolutionary change, both pollinators and plants are sharply con-**
35 **strained in their interaction modes and outcomes.**

36
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38 **ism, pollination, Sphingidae**

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

49 "There is a Madagascar Orchis—the *Angræcum sesquipedale*—
50 with an immensely long and deep nectary. How did such an
51 extraordinary organ come to be developed? Mr. Darwin's [[p.
52 475]] explanation is this. The pollen of this flower can only be
53 removed by the proboscis of some very large moths trying to get
54 at the nectar at the bottom of the vessel. The moths with the
55 longest proboscis would do this most effectually; they would be
56 rewarded for their long noses by getting the most nectar; whilst
57 on the other hand, the flowers with the deepest nectaries would
58 be the best fertilized by the largest moths preferring them. Con-
59 sequently, the deepest nectaried Orchids and the longest nosed
60 moths would each confer on the other a great advantage in the
61 'battle of life.' This would tend to their respective perpetuation
62 and to the constant lengthening of nectar and noses."

63 Phenotypic fitting of corolla length and shape and the pollinators' feeding
64 apparatus and body sizes are important because the better the fit, the better
65 the consequences in terms of fitness outcomes for the interaction partners
66 (5). Yet the expectation of perfect trait matching across populations or com-
67 munities is too simplistic (6): "arms races" as initially suggested by Darwin
68 and Wallace are frequently asymmetric, originating pollinator shifts rather

69 than tight phenotypic trait matching (Fig. 1). Extensive local variation
70 in phenotypic mismatch exists in different plant-pollinator systems (e.g.,
71 2; 6; 7), with pollinator-mediated selection geographic mosaics of locally
72 coevolved partners.

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

81 Yet Sazatornil *et al.* do not include unobserved interactions in their quan-
82 tifications of mismatches, so the test of the mismatch hypothesis actually in-
83 cludes also forbidden links effects: a full mismatch of corolla tube/proboscis
84 lengths actually meaning a forbidden link.

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90 long-tubed flowers.

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Pedro Jordano

*Integrative Ecology Group, Estación Biológica de Doñana,
Consejo Superior de Investigaciones Científicas (EBD-CSIC),
Avenida Americo Vespucio s/n,
E-41092 Sevilla, Spain*

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.

