

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

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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. explore the nature of such con-**  
31 **straints in the mutualisms among hawkmoths and the plants they**  
32 **pollinate. In this iconic interaction, used by Darwin and Wallace to**  
33 **vividly illustrate the power of natural selection in shaping evolu-**  
34 **tionary change, both pollinators and plants are sharply constrained**  
35 **in their interaction modes and outcomes.**

36  
37 **Keywords:** complex networks, forbidden links, long-tubed flowers, mutual-  
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 (1). 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. Wallace  
46 (2) 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 (3). Yet the expectation of perfect trait matching across populations or com-  
67 munities is too simplistic (4): "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 1; 4; 5), with pollinator-mediated selection geographic mosaics of locally  
72 coevolved partners.

73 Recent work by Sazatornil *et al.* (6) 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.

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82 long-tubed flowers.

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## 111 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 (7). 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.

