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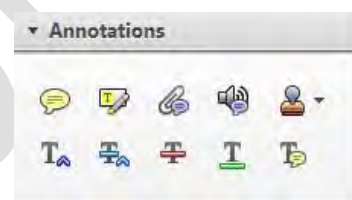


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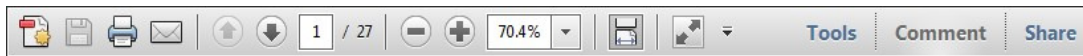


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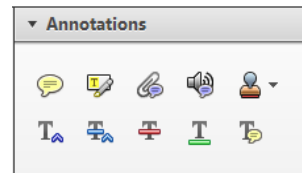
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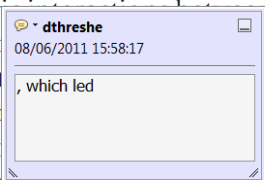


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standard framework for the analysis of microeconomic activity. Nevertheless, it also led to the development of a number of strategic approaches. The number of competitors in an industry is that the structure of the industry is a main component. At the industry level, are externalities important? (Mankiw henceforth) we open the 'black b



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there is no room for extra profits as mark-ups are zero and the number of firms (net) values are not determined by market clearing. Blanchard ~~and Kiyotaki~~ (1987), perfect competition in general equilibrium. The effects of aggregate demand and supply shocks in a classical framework assuming monopolistic competition and an exogenous number of firms

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dynamic responses of mark-ups consistent with the VAR evidence

satisfactory. Many studies have found that the number of competitors and the impact of demand



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and supply shocks. Most of the literature on the effects of demand and supply shocks in a classical framework assuming monopolistic competition and an exogenous number of firms is that the structure of the sector



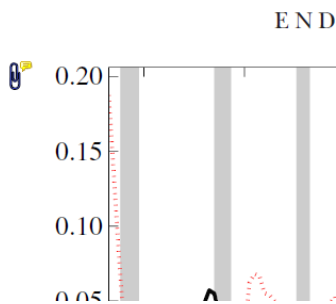
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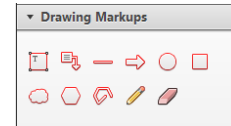
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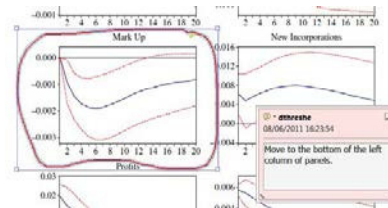


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# Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks

Federico D. Sazatornil<sup>1\*</sup>, Marcela Moré<sup>1</sup>, Santiago Benitez-Vieyra<sup>1</sup>, Andrea A. Cocucci<sup>1</sup>, Ian J. Kitching<sup>2</sup>, Boris O. Schlumberger<sup>3</sup>, Paulo E. Oliveira<sup>4</sup>, Marlies Sazima<sup>5</sup> and

Felipe W. Amorim<sup>6</sup>

<sup>1</sup>Instituto Multidisciplinario de Biología Vegetal (CONICET - Universidad Nacional de Córdoba), Córdoba, Argentina;

<sup>2</sup>Department of Life Sciences, Natural History Museum, Cromwell Road, London, UK; <sup>3</sup>Herrenhausen Gardens, Hannover, Germany; <sup>4</sup>Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil;

<sup>5</sup>Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil; and <sup>6</sup>Departamento de Botânica, Instituto de Biociências, Universidade Estadual Paulista 'Júlio de Mesquita Filho', Botucatu, São Paulo, Brazil

## Summary

1. A major challenge in evolutionary ecology is to understand how co-evolutionary processes shape patterns of interactions between species at community level. Pollination of flowers with long corolla tubes by long-tongued hawkmoths has been invoked as a showcase model of co-evolution. Recently, optimal foraging models have predicted that there might be a close association between mouthparts' length and the corolla depth of the visited flowers, thus favouring trait convergence and specialization at community level.

2. Here, we assessed whether hawkmoths more frequently pollinate plants with floral tube lengths similar to their proboscis lengths (morphological match hypothesis) against abundance-based processes (neutral hypothesis) and ecological trait mismatches constraints (forbidden links hypothesis), in structuring hawkmoth–plant mutualistic networks from five communities in four biogeographical regions of South America.

3. We found convergence in morphological traits across the five communities and that the distribution of morphological differences between hawkmoths and plants is consistent with expectations under the morphological match hypothesis in three of the five communities. In the two remaining communities, which are ecotones between two distinct biogeographical areas, interactions are better predicted by the neutral hypothesis.

4. Our findings are consistent with the idea that diffuse co-evolution drives the evolution of extremely long proboscises and flower tubes, and highlight the importance of morphological traits, beyond the forbidden links hypothesis, in structuring interactions between mutualistic partners, revealing that the role of niche-based processes can be much more complex than previously known.

**3, 4** **Key-words:** co-evolution, morphological forbidden link hypothesis, morphological match hypothesis, neutral hypothesis, plant–pollinator networks

## Introduction

A major challenge in evolutionary ecology is to understand how co-evolutionary processes shape patterns of interactions in biological communities (Guimarães,

Jordano & Thompson 2011). At the community level, reciprocal selection between free-living species could favour convergence and specialization on a core set of mutualistic traits (Thompson 2005). In the last two decades, different network approaches have generated important insights into the organization of plant–pollinator interactions at the community level, for example the nested and modular organization, the pervasive

\*Correspondence author. E-mail: federicosaza@gmail.com

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1 asymmetry in species dependencies and strength of inter-  
 2 actions between partners (Bascompte *et al.* 2003; Vázquez  
 3 & Aizen 2004; Bascompte, Jordano & Olesen 2006; Olesen  
 4 *et al.* 2007; Vázquez, Chacoff & Cagnolo 2009b; Jordano  
 5 2010). A number of factors have been proposed to explain  
 6 these network patterns, such as species abundance, com-  
 7 plementarity in spatio-temporal distribution, phylogenetic  
 8 relationships and matching of phenotypic traits of inter-  
 9 acting species. However, their relative importance contin-  
 10 ues to be debated (Stang *et al.* 2009; Vázquez *et al.*  
 11 2009a; Maruyama *et al.* 2014; Vizentin-Bugoni, Mar-  
 12 uyama & Sazima 2014).

13 Two main hypotheses, related to species abundance and  
 14 flower–pollinator trait-matching, have been postulated as  
 15 the main factors modulating the occurrence of plant–polli-  
 16 nator interactions. On the one hand, the ‘neutral hypothe-  
 17 sis’ postulates that individuals interact randomly. Hence,  
 18 network interaction patterns are mainly dependent on spe-  
 19 cies abundances; that is, abundant species interact more  
 20 frequently and with more species than rare species  
 21 (Dupont, Hansen & Olesen 2003; Ollerton *et al.* 2003;  
 22 Vázquez 2005; Vázquez *et al.* 2009a). On the other hand,  
 23 the ‘forbidden links hypothesis’, also known as ‘barrier  
 24 models’, postulates that interactions are constrained by  
 25 morphological plant–pollinator trait-matching and/or phe-  
 26 nological coupling between mutualistic partners (Santam-  
 27 aría & Rodríguez-Gironés 2007; Olesen *et al.* 2011;  
 28 Maruyama *et al.* 2014; Vizentin-Bugoni, Maruyama &  
 29 Sazima 2014). Specifically for flower–pollinator morpho-  
 30 logical matching, this hypothesis assumes that interactions  
 31 occur only if the length of the pollinator’s mouthparts is  
 32 equal to or greater than flower length (Dupont, Hansen &  
 33 Olesen 2003; Jordano, Bascompte & Olesen 2003;  
 34 Vázquez 2005; Stang *et al.* 2009; Vizentin-Bugoni, Mar-  
 35 uyama & Sazima 2014). Thus, morphological forbidden  
 36 links are represented by the impossibility of interactions  
 37 between pollinator species with short mouthparts and  
 38 long-flowered plant species. Although the forbidden link  
 39 hypothesis associated with species morphology has fre-  
 40 quently been invoked (Jordano, Bascompte & Olesen  
 41 2003), few studies have actually tested whether it plays a  
 42 more important role than other determinants, for example  
 43 species abundance, in determining patterns of interaction  
 44 networks (*e.g.* Stang *et al.* 2009; Maruyama *et al.* 2014;  
 45 Vizentin-Bugoni, Maruyama & Sazima 2014).

46 Finally, optimal foraging models assume that for every  
 47 species there is a trade-off between the suitability of a  
 48 resource and its availability. These models predict that  
 49 there is a close association between mouthparts’ length  
 50 and the corolla depth of the visited flowers, thus favour-  
 51 ing trait convergence and specialization at community  
 52 level, which assumes that for every species there is a  
 53 trade-off between the suitability of a resource and avail-  
 54 ability, have predicted that there might be a close associa-  
 55 tion between mouthparts’ length and the corolla depth of  
 56 the visited flowers (Rodríguez-Gironés & Santamaría  
 57 2006, 2007; Rodríguez-Gironés & Llandres 2008).

According to this hypothesis, resource competition may  
 trigger the co-evolution of long mouthparts and deep  
 flower tubes depending on the context of a given commu-  
 nity. Thus, a given pollinator could be either a poor or an  
 effective pollinator of a particular flower type depending  
 on the distributions of corolla tube depths and mouthpart  
 lengths in the community. Because reciprocal selection  
 acting on mutualistic partners favours convergence and  
 specialization (Thompson 2005; Rodríguez-Gironés &  
 Santamaría 2010), the distribution of characters involved  
 in trait-matching, such as mouthparts and flower lengths,  
 should converge at the community level (see Johnson &  
 Raguso 2015). These patterns have been observed in  
 hawkmoth–plant communities in tropical regions (Agosta  
 & Janzen 2005; Martins & Johnson 2013), but have not  
 been analysed from a network perspective.

In this context, we here evaluate a third (but not mutu-  
 ally exclusive) ‘Morphological match hypothesis’, in which  
 the probability of an interaction depends on the frequency  
 of all possible differences between mouthpart and flower  
 lengths in a given community. Under this hypothesis,  
 hawkmoths, especially those long-tongued species, should  
 preferentially visit flowers similar in length to their pro-  
 boscises (Agosta & Janzen 2005; Rodríguez-Gironés &  
 Llandres 2008). Previous studies have shown that hawk-  
 moth-pollinated species with extremely long corolla tubes  
 offer larger amounts of nectar than those species with  
 short corolla tubes (Haber & Frankie 1989; Martins &  
 Johnson 2013; Johnson & Raguso 2015). Thus, if flowers  
 were too short, the energetic reward would be insufficient  
 to compensate for the high foraging costs of long-tongued  
 hawkmoths. In addition, by foraging at long-tubed flow-  
 ers, the long-tongued hawkmoths are released from com-  
 petition with all other short-tongued flower visitors  
 (Agosta & Janzen 2005). On the other hand, if flowers are  
 too long, a situation arises similar to that under the for-  
 bidden links hypothesis; that is, short-tongued pollinators  
 cannot access the nectar and may learn to avoid such  
 flowers (Balkenius, Kelber & Balkenius 2004).

Since the seminal publication of the subject by Darwin  
 (1862), pollination of long flowers by long-tongued noc-  
 turnal hawkmoths (Lepidoptera: Sphingidae) has been  
 invoked as a showcase model of co-evolution because this  
 interaction implies reciprocal selection between proboscis  
 and flower tube length for successful pollination (Darwin  
 1862; Nilsson *et al.* 1987; Arditti *et al.* 2012). However,  
 diffuse community level rather than paired co-evolution-  
 ary processes is supposed to drive the evolution of pro-  
 boscis and flower lengths, because one-to-one interactions  
 are rare in plant–pollinator systems and when multiple  
 species interact selection pressures imposed by one species  
 are not independent of the selection pressures imposed by  
 a second species (Nilsson *et al.* 1987; Haber & Frankie  
 1989; Hougén-Eitzman & Rausher 1994; Agosta & Janzen  
 2005; Moré *et al.* 2012; Martins & Johnson 2013). Here,  
 we analysed the role of the neutral, forbidden links and  
 morphological match hypotheses in structuring

mutualistic hawkmoth–plant networks. To this end, we collected data from five communities in four South American biogeographical regions including a wide range of proboscis and flower tube lengths. Then, we tested whether the pattern of morphological differences between proboscises and flowers in each community departed from expectations under the neutral, forbidden links or morphological match hypotheses. Evidence supporting the morphological match hypothesis would provide insights into how diffuse co-evolution shapes interaction patterns in specialized plant–pollinator networks.

## Materials and methods

### STUDY AREA AND HAWKMOTH–PLANT NETWORKS

Field work was carried out in five communities in South America (Fig. S1, Supporting information) corresponding to four different biogeographical regions: Atlantic Rain forest (AF), Cerrado (CE), transition zone between western Chaco woodland and Yungas montane rain forest (CY1 and CY2) and Chaco montane dry woodland (CM). In each community, we determined the hawkmoth assemblage by sampling all the individuals attracted to vertical sheet light traps (480 h in AF, 168 h in CE, 20 h in CY1, 24 h in CY2 and 80 h in CM). Captured hawkmoths were kept in individual entomological envelopes to avoid pollen contamination among individuals. For general details of the moth collecting method, see Amorim, Wyatt & Sazima (2014) for AF, Amorim *et al.* (2009) for CE and Moré (2008) for CE, CY1 and CY2 communities. Hawkmoths are present throughout the year in the Brazilian communities (see Amorim *et al.* 2009; Amorim, Wyatt & Sazima 2014) while in Argentina they show a markedly seasonality flying mostly from October to March (Moré 2008). Thus, we sampled monthly in AF and CE and during spring and summer in CY1, CY2 and CM communities. Sampling effort was greater in Brazilian (AF and CE) than in Argentine (CM, CY1 and CY2) communities because the flowering period extends throughout the year and hawkmoth species richness was higher (Moré, Kitching & Cocucci 2005; Amorim *et al.* 2009). Captured hawkmoths in each community ranged from 321 to 577 individuals with a mean of 388. Rarefaction species and interactions curves were performed using the *iNEXT package* (Chao *et al.* 2014; Hsieh, Ma & Chao 2015) in R software (R Development Core Team 2014). We carefully inspected captured hawkmoths under a stereo microscope to locate pollen loads and identified pollen types by comparison with reference samples taken from flowering plants in each community (Kislev, Kraviz & Lorch 1972; Haber & Frankie 1989) or with pollen identification guides (Markgraf & D'Antoni 1978). This animal-centred survey allows exposure of an important number of interactions that would be undetected in a plant-centred approach (Bosch *et al.* 2009; Chacoff *et al.* 2012). This method is especially appropriate for our system because it allows for recording of actual hawkmoth visits to a given plant species (Alarcón, Davidowitz & Bronstein 2008). In addition, hawkmoth–plant interactions usually have low frequencies (see Oliveira, Gibbs & Barbosa 2004; Amorim, Wyatt & Sazima 2014) and are difficult to record as they occur at night. Also, hawkmoths are long-distance flying insects with flight capacity of over 15 km (see Amorim, Wyatt & Sazima 2014), thus making inappropriate the use of independent estimation of

plant abundances. Hence, in order to build the quantitative interaction matrices, we assigned to each cell the number of individual hawkmoths carrying pollen from a given plant species. Individuals not carrying pollen were not included in the interaction matrices but were included in trait distribution analyses. We excluded from matrices those pollen types belonging to anemophilous or non-nectariferous species because these pollen grains could become passively attached to hawkmoths' bodies when resting or flying near these plants (Alarcón, Davidowitz & Bronstein 2008). Excluded pollen types represent less than 1% of the total interactions recorded.

### FLOWER AND PROBOSCIS LENGTHS

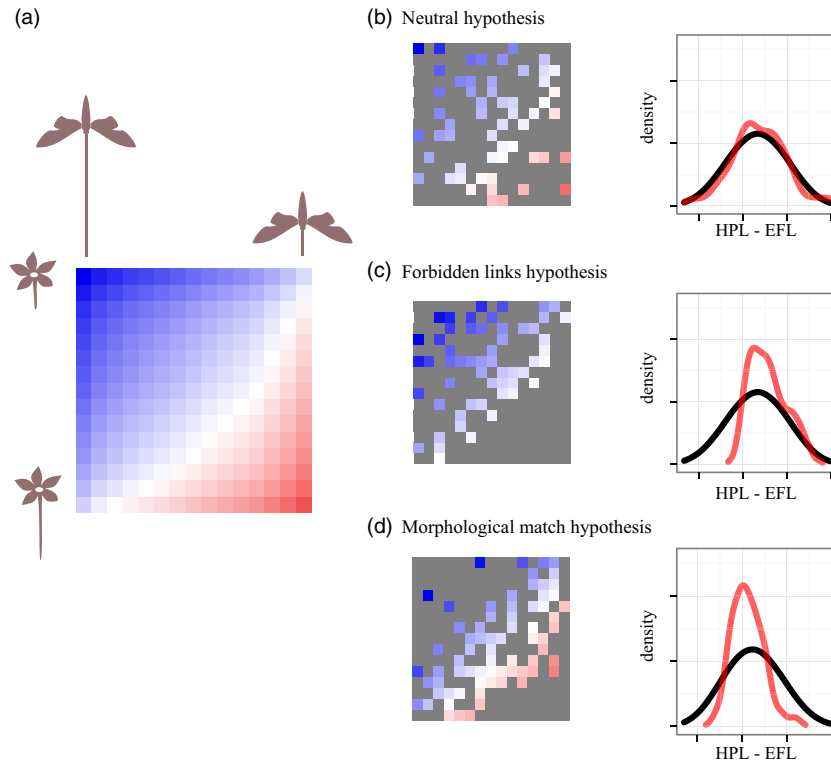
We considered flower tube length as the main constraint determining nectar accessibility to hawkmoths (Haber & Frankie 1989; Martins & Johnson 2013; Amorim, Wyatt & Sazima 2014; Johnson & Raguso 2015). We measured hawkmoth proboscis lengths (HPLs) and effective flower lengths (EFLs) with a digital calliper (0.1 mm accuracy). EFL was measured in ten plants per species when their abundances allowed it. We measured EFL as corolla tube length in tubular and salverform flowers or as stamen length in brush-type and funnel-shape flowers. In the case of unidentified pollen types, we assumed an effective flower length of 15 mm because we previously identified most plant species present in each community with typical moth-pollinated flowers, and all species have flower tube lengths longer than 15 mm (Amorim 2008, 2012; Moré 2008).

### DISTRIBUTION OF MORPHOLOGICAL TRAIT-MATCHING IN HAWKMOTH–PLANT NETWORKS

We assumed that co-evolutionary processes favour convergence between proboscis and flower lengths at the community level, so we used the morphological difference between HPL and EFL as a continuous variable to assess trait-matching in hawkmoth–plant networks. We estimated the weighted mean and standard deviation of the observed morphological differences for each community. To estimate these parameters, all possible pairwise differences were weighted by their respective interaction frequency. For example, in the CM community, the morphological difference between *Lintneria maura* (Burmeister, 1879) and *Cestrum parqui* Benth. was 28.91 mm, and there were seven interactions between these species. When an interaction between two species did not occur, the morphological difference was not taken into account for parameter estimation. We followed this approach to maintain the connectance value of each network and to avoid disproportional influence of rare hawkmoth species in the mean value (see Hypothesis testing below).

### HYPOTHESES TESTING

For each community, we simulated the distributions of morphological differences under the three hypotheses. These simulations considered all the possible pairwise morphological differences and the expected frequency of interactions under a given hypothesis, that is neutral, forbidden links and morphological match hypotheses (Fig. 1). Under the neutral hypothesis, the individuals of the community interact according to their abundances (Vázquez *et al.* 2007). Thus, the weighted mean and standard deviation of observed differences should not differ from those of



**Fig. 1.** Possible scenarios of trait-matching as determinant of the species assembly in hawkmoth–plant networks. (a) Idealized matrix representing all possible pairwise differences in trait-matching between hawkmoth proboscis length (HPL) and effective flower length (EFL). Pollinator and plant species are sorted according to their average HPL and EFL, respectively. Blue cells indicate positive differences (HPL > EFL), red cells indicate negative differences (HPL < EFL) and white cells indicate equal lengths. (b–d) Hypotheses concerning the influence of trait-matching on plant–pollinator assemblages. Left panel: simulated interaction matrices under each hypothesis; cell colours correspond to the descriptions above, and grey cells indicate non-existing interactions. Right panel: Distribution of all possible pairwise trait-matching differences (HPL – EFL, black line) and of the predicted combinations (red line) under each hypothesis. (b) Neutral hypothesis, where interactions are independent of trait-matching. Notice that under this hypothesis distribution parameters (mean and standard deviation) must be the same for both distributions. (c) Forbidden links hypothesis, where interactions occurred only if HPL is equal to or greater than EFL. Notice the absence of interactions below the diagonal of the interaction matrix and that distribution parameters differ. (d) morphological match hypothesis, where the probability of occurrence of an interaction depends on the frequency of possible pairwise differences between HPL and EFL. Notice the absence of interactions both above and below the diagonal and that both distributions have the same mean but differ in standard deviation.

all possible pairwise differences, simply because under neutral hypothesis interactions occur at random and their frequency depends on species abundances (Fig. 1b). Under the forbidden links hypothesis (Fig. 1c), hawkmoths interact with flowers only when morphological difference is equal to or greater than zero, that is HPL is equal or longer than EFL (Dupont, Hansen & Olesen 2003; Jordano, Bascompte & Olesen 2003; Stang *et al.* 2009; Maruyama *et al.* 2014; Vizentin-Bugoni, Maruyama & Sazima 2014). Thus, the weighted mean of morphological differences should be greater than the mean of all possible pairwise differences, since the absence of negative morphological differences corresponds to forbidden interactions. Likewise, the standard deviation should be smaller (Fig. 1c). Finally, under the morphological match hypothesis, the weighted mean of morphological differences should be the same as the mean of all possible pairwise differences, but the standard deviation should be smaller, because those interactions involving both extremes, positive or negative morphological differences, should not occur.

Simulations were performed using the original and modified versions of the *vaznull* function of the BIPARTITE v. 2.04 package (Vázquez *et al.* 2007; Dormann, Gruber & Fründ 2008) in R

software (R Development Core Team 2014). To test the neutral hypothesis we used the original *vaznull* function. In the case of the forbidden links hypothesis, we used a modified version of the *vaznull* function (see Data S1, Supporting information) in which we multiplied the binary matrix that assigns interactions according to species abundances by a second matrix in which possible links were assigned a value of one and forbidden links of zero, in order to constrain the probability of occurrence of a particular interaction, so that

$$p_{ij} = \begin{cases} 1 & \text{for } (\text{HPL}_j - \text{EFL}_i) \geq 0 \\ 0 & \text{else,} \end{cases} \quad \text{eqn 1}$$

where  $p_{ij}$  is the probability of occurrence of a given interaction, taking into account both proboscis length (HPL) and flower length (EFL).

Finally, in the morphological match hypothesis, we multiplied the binary matrix by an interaction probability matrix. In each cell of this matrix, the probability ( $p_{ij}$ ) of any given interaction depends on the absolute morphological difference value (|HPL–EFL|) and the maximum absolute difference such that

$$p_{ij} = 1 - \frac{|\text{HPL}_j - i|}{\max |\text{HPL}_j - i|}, \quad \text{eqn 2}$$

6 thus, when the difference attains its maximum value, the probability of occurrence is zero, and when the difference is zero (*i.e.* perfect match), the probability of occurrence is one. In all simulations, the marginal totals and the connectance of the observed matrix were preserved.

Finally, for each community, we tested whether the observed weighted mean and standard deviation of morphological differences lay within the respective 95% confidence intervals obtained from 5000 simulations runs under the three hypotheses.

## Results

### NETWORK DESCRIPTION AND TRAIT DISTRIBUTIONS

We recorded an average of 23 plant species (ranging from 17 in CY1 up to 34 in AF) pollinated by an average of 23 hawkmoth species (ranging from 8 in CM up to 40 in CE) per community. The more representative

hawkmoth-pollinated plant families were Fabaceae ( $n = 9$ ), Rubiaceae ( $n = 8$ ), Apocynaceae ( $n = 6$ ) and Solanaceae ( $n = 6$ ). A total of 353 interactions were observed in average per community, ranging from 270 in AF to 429 in CM (Tables S1–S3, Supporting information). Rarefaction analyses of light trapped hawkmoths showed a tendency to stabilization indicating an adequate sampling effort. Rarefaction curves of interactions also tended to stabilization in three of the five communities (CM, CY1 and CY2, with values of sample coverage of 0.90, 0.92 and 0.90 respectively), while in the other two more diverse and larger ones (CE and AF), sampled interactions involved 0.70 and 0.56 of sample coverage, respectively (Fig. S2, Supporting information).

Community mean HPL ranged from 43.24 to 52.89 mm, and mean EFL ranged from 31.26 to 35.48 mm (Fig. 2). Mean HPL in each community was consistently greater than the respective EFL. Frequency distributions of HPL and EFL in each community were in general right-skewed, ranging from 0.89 to 1.75 in

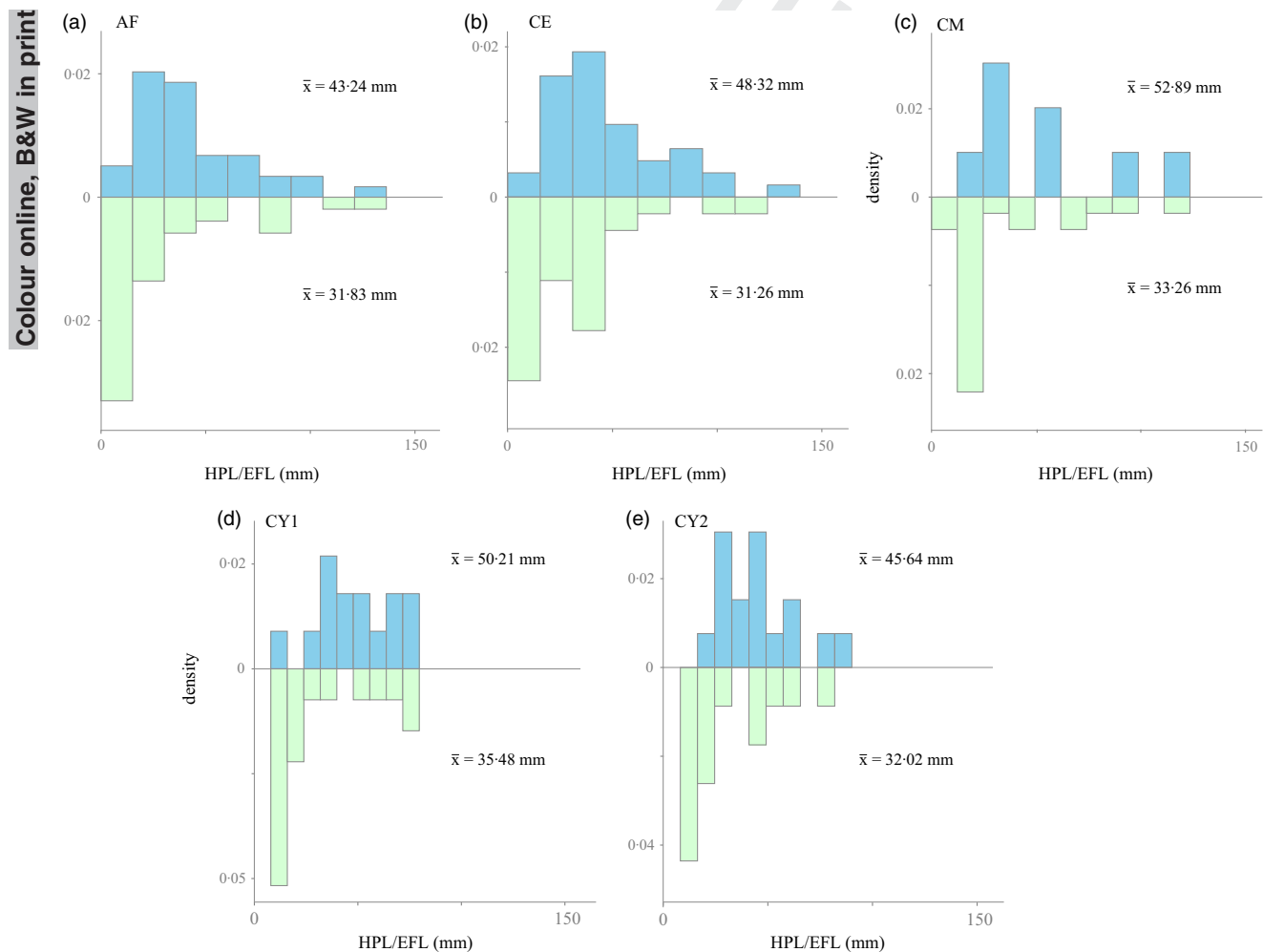


Fig. 2. Trait distributions per community. Hawkmoth proboscis length (HPL) distribution of captured individuals using light traps (upper histograms). Effective flower length (EFL) distributions (lower histograms) of plants species. a) Atlantic Rain forest (AF), b) Cerrado (CE), c) Chaco Montane dry woodland (CM), d) Chaco–Yungas transition 1 (CY1) and e) Chaco–Yungas transition 2 (CY2).



1 flower length and from 0.04 to 1.41 in proboscis length  
2 (Fig. 2).

3 Mean weighted morphological difference per community  
4 ( $\pm$  SD) were  $-2.06 \pm 34.33$  mm in AF,  $12.27 \pm 33.77$  mm  
5 in CE,  $5.75 \pm 32.1$  mm in CM,  $19.33 \pm 26.11$  in CY1 and  
6  $18.99 \pm 25.72$  in CY2 (red lines in Fig. 3). Additionally,  
7 the distributions of both the observed morphological dif-  
8 ferences and all possible pairwise differences are shown in  
9 Fig. S3 (Supporting information).

#### 10 HYPOTHESIS TESTING

11 In three communities (CM, CE and AF), the observed  
12 values of both mean and standard deviation of morpho-  
13 logical differences supported the morphological match  
14 hypothesis (Fig. 3a–c, centre and right panels). In those  
15 communities the mean difference is low, fitting with the  
16 predictions of either the neutral or morphological match  
17 hypotheses. Standard deviations were lower than pre-  
18 dicted under the neutral hypothesis and interactions  
19 involving extreme positive or negative differences rarely  
20 occurred.

21 In the other two communities (CY1 and CY2) both  
22 mean and standard deviations were not consistent with  
23 the morphological match hypothesis (Fig. 3b,c, centre and  
24 right panels). Observed means lay within the predictions  
25 of the neutral hypothesis. In community CY2, the  
26 observed standard deviations were significantly lower than  
27 expected under the neutral hypothesis. Inspection of the  
28 observed morphological differences showed that these two  
29 communities are characterized by higher frequency of  
30 interactions where  $HPL \gg EFL$  (Fig. S3, Supporting  
31 information).

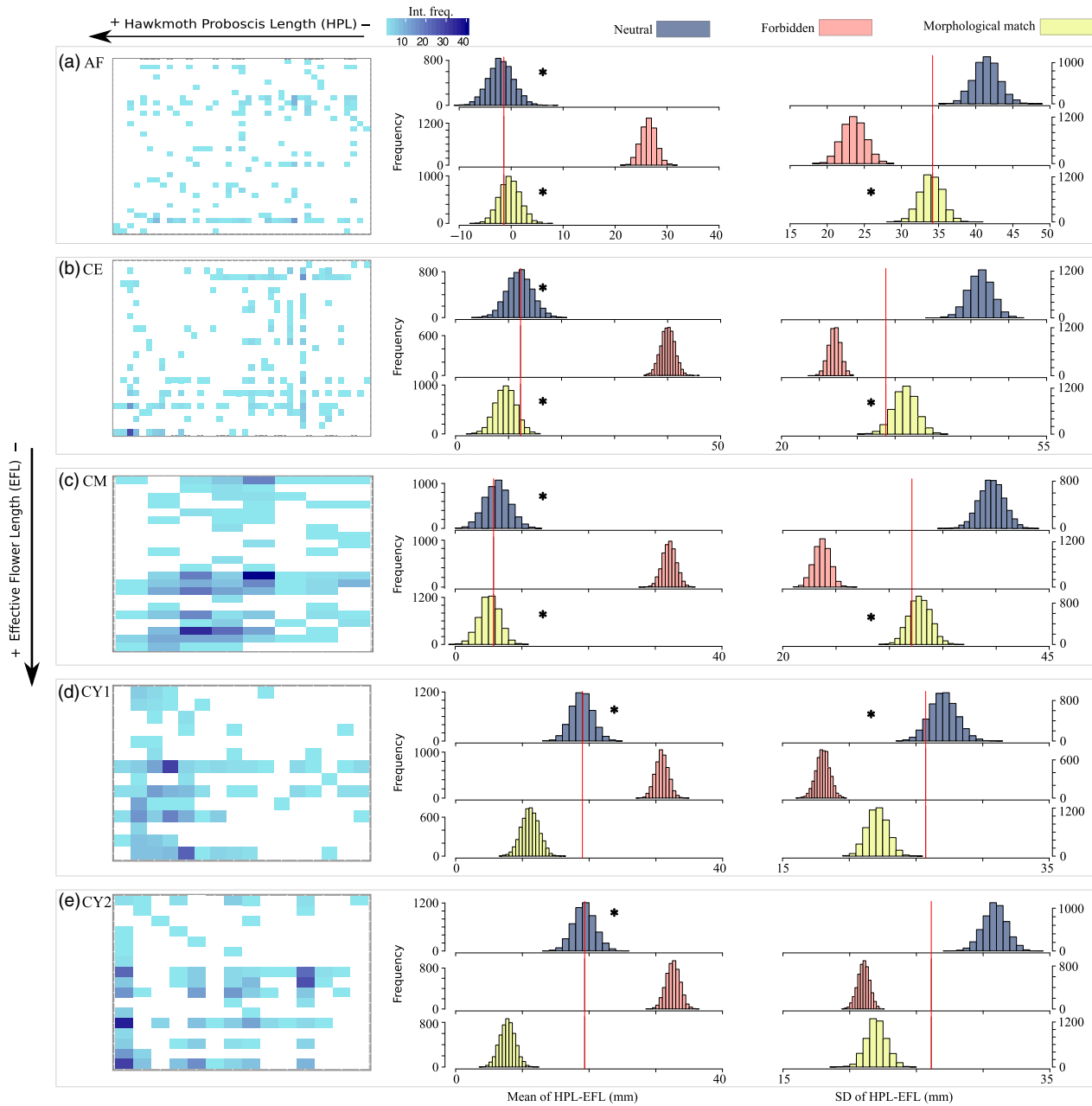
#### 32 Discussion

33 Co-evolutionary selection is a key process that shapes  
34 trait distributions, interaction patterns and even the net-  
35 work structure of free-living mutualists across land-  
36 scapes (Thompson 2005; Nuismer, Jordano &  
37 Bascompte 2012). Here we found right-skewed proboscis  
38 and flower length distributions in five communities from  
39 four contrasting biogeographical areas in South Amer-  
40 ica. These patterns are similar to those observed in  
41 other hawkmoth–plant communities from Costa Rica  
42 and Madagascar (Agosta & Janzen 2005). Hence, con-  
43 vergence in morphological traits across landscapes sup-  
44 ports the idea that diffuse co-evolution is the process  
45 driving the evolution of plant–pollinator traits within  
46 communities (Agosta & Janzen 2005; Vázquez 2005;  
47 Rodríguez-Gironés & Llandres 2008; Pauw, Stofberg &  
48 Waterman 2009). Our findings highlight the importance  
49 of morphological traits in structuring plant–pollinator  
50 interactions reported for other specialized systems such as  
51 plant–hummingbird communities (Maglianesi *et al.* 2014;  
52 Maruyama *et al.* 2014; Vizentin-Bugoni, Maruyama &  
53 Sazima 2014).

54 However, beyond the agreement that niche-based pro-  
55 cesses are important in structuring plant–pollinator net-  
56 works, we also showed that for three of the five studied  
57 communities, the distribution of morphological differences  
between plant and pollinator interacting traits is consis-  
tent with the expectations under the morphological match  
hypothesis. These results suggest that hawkmoths, despite  
being able to access the flowers over a broader spectrum  
of plants in the communities, may preferentially visit  
those species in which flowers are similar in length to their  
proboscises. In these three communities, long-tongued  
hawkmoths are much less abundant than their short-ton-  
gued counterparts (Moré, Sérsic and Cocucci 2007; **7**  
Amorim *et al.* 2009; Amorim, Wyatt & Sazima 2014)  
making nectar access in short-tubed flowers less profitable  
than in long-tubed flowers. On the other hand, the two  
communities where the interaction patterns were not consis-  
tent with the morphological match hypothesis presented  
similar abundances of long- and short-tongued hawk-  
moths (Fig. 2), leading to a higher frequency of oppor-  
tunistic interactions between long-tongued hawkmoths  
and short-tube flowers (Fig. S3, Supporting information).  
The high abundance of long-tongued hawkmoth individu-  
als may lead to competition for the relatively scarce  
long-tubed flowers, and shifts to other nectar sources. In  
addition, some of the long-tubed flowers in these commu-  
nities (e.g. *Echinopsis ancistrophora* Speg.) bloom  
synchronously and thus are available only a few days per  
season (Schlumpberger *et al.* 2009).

Even though, is worth to mention that our animal-  
centred approach may lead to an underestimation of neu-  
tral-based processes, since the nature of our system makes  
independent sampling of plant abundance unfeasible.  
However, our findings are consistent with the predictions  
of optimal foraging models, which propose that resource  
competition between short- and long-tongued floral visi-  
tors leads to resource partitioning and trigger the co-evo-  
lution or adjustment between flower and proboscis  
lengths (Rodríguez-Gironés & Santamaría 2006, 2007;  
Rodríguez-Gironés & Llandres 2008). Additionally, as  
long-tongued hawkmoths require higher amounts of  
energy to sustain the cost of foraging (Heinrich 1983;  
Agosta & Janzen 2005), long-tubed flowers represent the  
best foraging choices for long-tongued hawkmoths  
because they commonly offer larger amounts of nectar  
and reduce competition from short-tongued counterparts  
(Haber & Frankie 1989; Martins & Johnson 2013; John-  
son & Raguso 2015; Amorim F.W. unpublished results,  
but see also Ornelas *et al.* (2007) for a similar pattern in  
hummingbird-pollinated plants).

Although we did not test if phenology determined tem-  
poral matches among interacting species, resulting in for-  
bidden links (Olesen *et al.* 2011; Maruyama *et al.* 2014;  
Vizentin-Bugoni, Maruyama & Sazima 2014), our work  
highlights that hawkmoths more frequently visit plants  
with floral tube lengths similar to their proboscis in most  
of the studied communities. In this scenario, our study



**Fig. 3.** Observed hawkmoth–plant networks of five communities and parameter simulations for the three hypotheses of interaction occurrence. The five communities are arranged in rows. Columns, from left to right, show the observed interaction networks, and the frequency distributions of mean and SD of trait-matching. In the observed hawkmoth–plant networks, hawkmoth species are sorted in columns from left to right by decreasing HPL. Plant species are sorted in rows, from top to bottom, by increasing EFL. Cell colour intensity corresponds to interaction frequency as indicated in the scale at the top of the figure. The centre and right panels show the frequency distributions of 5000 simulated mismatch means and standard deviations, respectively, under the neutral (blue), forbidden links (pale red) and morphological match (yellow) hypotheses. Vertical red lines correspond to the observed mismatch distribution parameters and asterisk indicate if observed value laid within the predictions of the different hypotheses. Studied communities, a) Atlantic Rain forest (AF), b) Cerrado (CE), c) Chaco Montane dry woodland (CM), d) Chaco–Yungas transition 1 (CY1) and e) Chaco–Yungas transition 2 (CY2).

supports the hypothesis that diffuse co-evolution could be the process driving the adjustment of hawkmoth–plant morphological traits across different environments. Probably, behavioural decisions driven by optimal foraging strategy and other niche-based processes are more important than simple abundance or morphological barriers in

defining interactions and network structure. Nevertheless, the approach of morphological match does not exclude other factors, such as phenology, from contributing towards explaining the observed patterns of interactions. Other flower traits such as flower scent, visual signals and nectar energetic content, may also influence the

interaction pattern between mutualistic species (Gómez, Perfectti & Lorite 2015; Larue, Raguso & Junker 2015). Future studies will help to clarify the relative contributions to and importance of these traits for the structure and assembly of hawkmoth–plant communities.

Our results highlight the role that co-evolutionary dynamics may play in shaping trait distribution and interaction patterns in mutualistic systems in different ecological areas of South America. Hawkmoth–plant networks, a system in which interactions are mainly constrained by morphological matches, differ from generalist plant–pollinator networks, where interactions could be affected by multidimensional traits (e.g. flower architecture, flower signals, flower rewards and pollinator behaviour). While we have found that the morphological match hypothesis is not the only mechanism to explain patterns of hawkmoth–plant interactions, additional studies are needed to evaluate whether this hypothesis is applicable to others mutualistic networks, both specialized and generalist.

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## Data accessibility

Raw data of interaction networks, hawkmoth proboscis lengths and effective flower lengths are available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.qn83r> (Sazatornil *et al.* 2016).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Figure S1.** Studied hawkmoth–plant networks.

**Figure S2.** Rarefactions curves of species and interaction number.

**Figure S3.** Distribution of morphological differences in the studied communities.

**Table S1.** Hawkmoth species.

**Table S2.** Plant species.

**Table S3.** Summary of the studied networks.

**Data S1.** R code to perform the simulations.

# Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main.



- 14** The authors assessed whether hawkmoths more frequently visit plants with floral tube lengths similar to their proboscis lengths beyond abundance-based processes and ecological trait mismatches constraints. The findings highlight the importance of morphological traits matching, revealing that the role of niche-based processes can be much more complex than previously known.

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