REVIEW AND SYNTHESIS

A quantitative review of pollination syndromes: do floral traits predict effective pollinators?

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Abstract

The idea of pollination syndromes has been largely discussed but no formal quantitative evaluation has yet been conducted across angiosperms. We present the first systematic review of pollination syndromes that quantitatively tests whether the most effective pollinators for a species can be inferred from suites of floral traits for 417 plant species. Our results support the syndrome concept, indicating that convergent floral evolution is driven by adaptation to the most effective pollinator group. The predictability of pollination syndromes is greater in pollinator-dependent species and in plants from tropical regions. Many plant species also have secondary pollinators that generally correspond to the ancestral pollinators documented in evolutionary studies. We discuss the utility and limitations of pollination syndromes and the role of secondary pollinators to understand floral ecology and evolution.

Keywords

Floral evolution, floral syndromes, meta-analysis, plant breeding systems, plant reproduction, pollination efficiency, pollination networks, specialisation, tropical ecology.

INTRODUCTION

Since Darwin (1862), pollinator-mediated selection on floral traits has been considered an important evolutionary force underlying the diversification of flowering plants. Different pollinators may drive floral divergence, whereas similar pollinators shared by different plant species might drive convergence of floral traits (Fenster *et al.* 2004). These integrated sets of floral traits (e.g. morphology, colour, odour, size, rewards, phenology) associated with particular pollinator groups are known as floral or pollination syndromes (Faegri & van der Pijl 1979). The pollination syndrome concept implies that plants specialise on particular functional groups of pollinators that exert similar selective pressures on floral traits (Fenster *et al.* 2004). However, the association of particular sets of floral traits with specific pollinators has been questioned given the apparent widespread generalisation in pollination systems found in various studies (Waser *et al.* 1996; Petanidou *et al.* 2008).

It has long been documented that flowers of particular plant species are often visited by various taxonomic groups of pollinators (Robertson 1928). However, pollination ability differs among floral visitors and interactions may span from mutualistic to antagonistic (Thomson 2003). Stebbins (1970) proposed that floral traits reflect selection mediated by the pollinators

that visit flowers most frequently and effectively. Thus, while pollination syndromes are expected to reflect adaptation to primary pollinators, syndrome traits may not preclude visits by less efficient floral visitors, i.e. secondary pollinators (*sensu* Stebbins 1970), which may also play a role in floral evolution. Particular floral traits may exclude only certain groups of secondary pollinators, while allowing pollination by other groups. For example, bat flowers with highly exerted stamens may allow pollination by birds but not by bees (e.g. *Gesneria pedunculosa*; Martén-Rodríguez & Fenster 2008). Therefore, we may expect pollination syndromes to be non-randomly associated with certain groups of secondary pollinators. For a thorough understanding of the role of plant–pollinator interactions on floral syndrome evolution, it is important to consider the entire pollinator assemblages and to assess the relative efficiency of all floral visitors.

Several studies based on pollination efficiency data have found support for pollination syndromes (e.g. Lazaro *et al.* 2008; Martén-Rodríguez *et al.* 2009; Reynolds *et al.* 2009; Armbruster *et al.* 2011; Danieli-Silva *et al.* 2012); others have found the opposite, concluding that pollination syndromes are an unreliable tool for predicting the effective pollinators of flowering plants (e.g. Waser *et al.* 1996; Valdivia & Niemeyer 2006; Smith *et al.* 2008; Li & Huang 2009; Ollerton *et al.* 2009). One of the few global evaluations of pollination syndromes,

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using several communities around the world, found support for pollination syndromes only for around 30% of the species in the communities (Ollerton *et al.* 2009). A few studies have evaluated syndromes by differentiating ineffective floral visitors from effective pollinators using phylogenetically independent statistical analyses (i.e. Smith *et al.* 2008; Martén-Rodríguez *et al.* 2010). Without the empirical determination of floral visitor effectiveness, generalisation in plant–pollinator interactions is likely to be overestimated (Rosas-Guerrero *et al.* 2011). Furthermore, for a general understanding of the role of pollinators as selective agents on floral traits, the influence of shared evolutionary history and ecological factors on floral traits needs to be clearly established.

Despite the strong debate about the reliability of pollination syndromes, several authors have used them to infer floral evolution or pollination systems of plant species in the absence of empirical evidence of pollinators (e.g. Machado & Lopes 2004; Knapp 2010). As valuable as these approaches are, it is crucial to know the strengths and limitations of pollination syndromes, particularly when these are used to address questions of community ecology, comparative biology and floral evolution. Even when many studies of individual species have tested the validity of pollination syndromes, a quantitative literature review of pollination syndromes across species and world regions has not been conducted. Such an approach would allow synthesising the results of detailed pollination studies that have quantified the efficiency of the entire pollinator assemblages of plant species throughout the world.

In the context of pollination syndromes various traits might influence the association between pollinators and floral traits. For example, reproductive systems are directly associated to pollination and plant fitness. Thus, dioecious, monoecious and self-incompatible hermaphrodite animal-pollinated plants, which are highly dependent on pollinators, should experience more consistent selection on floral traits and greater predictability of pollination syndromes than self-compatible species. Geographical distribution may also influence the relationship between plants and pollinators. The latitudinal gradient in species diversity has been associated with a greater strength of biotic interactions at lower than at higher latitudes (Schemske *et al.* 2009). Under this scenario, stronger biotic interactions should lead to increased niche space and greater species diversification and coexistence in tropical regions (Schemske *et al.* 2009; Moya-Laraño 2010). In the tropics the frequency of animal-pollinated plants is greater than in temperate regions (Schemske *et al.* 2009). Therefore, the predictability of pollination systems should be greater in the tropics than in extratropical regions.

Here, by means of phylogenetic meta-analysis, we assess whether floral traits predict the most effective pollinators of plants and whether the predictability of pollination syndromes is associated with breeding system, geographic distribution, and pollinator functional group. We further explore the relationships between plants and their primary and secondary pollinators by looking at current patterns of interactions through plant–pollinator networks. We also document potential evolutionary relationships between plants and pollinators by synthesising the current information available on pollinator evolutionary transitions and appearance of plant and pollina-

tor groups along the evolutionary history of life on earth. Finally, we discuss the several implications of pollination syndromes on the ecology and conservation of plant–pollinator interactions.

MATERIALS AND METHODS

Literature search and effect size estimation

We carried out an extensive literature search in the ISI Web of Knowledge database from 1900 to 2013 using the following keyword combinations: 'pollinat* effic*' or 'effic* pollinat*' or 'pollinat* effectiv*' or 'effectiv* pollinat*' or 'pollination syndrom*' or 'floral syndrom*' in the topic field. We also included our own published and unpublished data. Pollinator efficiency or effectiveness has been evaluated by many different methods, which may not be all equally good at measuring the performance of pollinators and their influence on plant reproductive success (Ne'eman *et al.* 2010). We only considered studies conducted under natural conditions that quantitatively assessed pollination effectiveness of all floral visitors of plants by at least one of the following methodologies: (1) pollen on pollinator's body, (2) contact of pollinator with the flower's reproductive organs, (3) pollen deposited on stigmas, (4) pollen removed from anthers, (5) fruit and (6) seed production by specific functional groups. Since pollination effectiveness may vary depending on the method (Ne'eman *et al.* 2010), we statistically compared effect sizes among these measures of effectiveness.

We followed mainly the descriptions of Faegri & van der Pijl (1979), Proctor *et al.* (1996), Ollerton *et al.* (2009) and Willmer (2011) to characterise 11 pollination syndromes (Table S1). We assigned pollination syndromes to each plant species based exclusively on the presence or absence of each character state for each floral trait (Table S2).

By means of both ordinary and phylogenetic meta-analysis, we tested whether pollination syndromes can predict the most effective pollinator of plants. All the analyses were conducted using the standardised unbiased mean difference (Hedges′ *d*) as a measure of effect size (Appendix S1 in supporting information for formulas). This effect size expresses the difference in pollination effectiveness between pollinator species or genera belonging to the functional group expected by the floral syndrome and the species or genera not expected by the floral syndrome of the plant species. To calculate Hedges′ *d,* each study had to provide mean values, standard deviations and sample sizes of any measure of pollination effectiveness. These parameters were obtained from text, tables and figures. Data from graphs were obtained using Datathief II software (B. Tummers, available online: http://www.nikhef.nl/˜keeshu/datathief/). When any of these parameters were not provided, we contacted the authors to obtain them.

In cases where we could not obtain mean values, standard deviations and/or sample sizes, we calculated a different effect size (Odds Ratio) based on binary data by computing the number of events and non-events in two groups (Cooper *et al.* 2009). To do this, we constructed 2 × 2 contingency tables, with columns indicating the pollinator functional group (expected and non-expected by the syndrome) and rows corre-

sponding to effective or ineffective pollination (Appendix S1). Odds Ratios (OR) were then transformed to Log (OR). Previous to running the analyses, we converted all Log (OR) and its variance into Hedges′ d and its corresponding variance to unify the effect size metric for all studies (Cooper *et al.* 2009, formula not shown). Positive values of effect sizes d implied that pollinators expected by the syndrome were more efficient (i.e. support for the pollination syndrome hypothesis), whereas negative d values mean that pollinators not matching the syndrome were more efficient.

Traditional and phylogenetic meta-analyses

When a plant species was effectively pollinated by more than two pollinator functional groups, we included separated calculations of effect size for each alternative group of the same plant species for the traditional meta-analysis. As a result, the traditional meta-analysis was performed on a total of 517 data points. However, for the phylogenetic meta-analysis we pooled these multiple effect sizes per species using a traditional meta-analysis with a fixed effects model (Koricheva *et al.* 2013). Phylogenetic meta-analysis was performed on 417 unique plant species.

We used MetaWin 2.0 (Rosenberg *et al.* 2000) and Phylo-Meta 1.3 (Lajeunesse 2009) to run ordinal and phylogenetic meta-analyses respectively. Confidence intervals of effect sizes were calculated using bootstrap re-sampling procedures (Adams *et al.* 1997). An effect was considered significant (either in positive or negative direction indicating support or rejection of the pollination syndrome hypothesis respectively) if the 95% biased-corrected bootstrap confidence intervals (CI) of the effect size (d) did not overlap zero. Data were analysed using random-effect models, which assume that studies differ not only by sampling error (as fixed-effects models do) but also by a random component in effect sizes (Raudenbush 2009). Random-effect models are preferable in ecological data syntheses because their assumptions are more likely to be satisfied (Gurevitch & Hedges 1999).

We additionally analysed whether the following moderator or predictor variables influenced effect sizes: breeding system (self-compatible or self-incompatible/monoeciuos/dioecious) and geographical region (tropical or extra-tropical). To examine the heterogeneity of effect sizes, we used Q statistics, which are weighted sums of squares that follow an approximately asymptotic chi-square distribution. These statistics allow categorical comparisons of moderator variables that may explain structure in the variation of effect sizes. We examined the *P*-values associated with Q-between categories, which describe the variation in effect sizes that can be ascribed to differences between the categories (Cooper *et al.* 2009). Information about each of the moderator variables for each of the species included in this review were obtained either from the same study or from other publications of the same plant species.

To run phylogenetic meta-analyses, we incorporated the phylogenetic relatedness of the species from our dataset following Lajeunesse′s method (Lajeunesse 2009; Koricheva *et al.* 2013). To accomplish this, we constructed a phylogenetic hypothesis of the 417 unique plant species included in our meta-analysis from a modified megatree of all major

plant groups based on Angiosperm Phylogeny Group III (2009) using PHYLOMATIC (Webb & Donoghue 2005). Relationships at family and species level of several genera were resolved with the help of published phylogenetic studies (Figure S1). Species lacking phylogenetic information were placed as polytomies at the root of their family or genus (Koricheva *et al.* 2013) and all branch lengths were transformed to one (Verdú & Traveset 2004). In addition, the branch lengths of our phylogenetic tree were adjusted with the Bladj algorithm of Phylocom 3.34b program (www.phylodiversity.net/phylocom), while calibration points were based on the estimated divergence times of major plant groups (Hedges *et al.* 2006). This ultrametric tree was converted into a phylogenetic correlation matrix (P) that has the standardised shared branch length distance of each species in off-diagonals and ones in the main diagonal (Lajeunesse 2009; Koricheva *et al.* 2013). Phylogenetic tree edition was performed in R (R Development Core Team 2011) and Mesquite v. 2.75 (Maddison & Maddison 2011). To analyse each predictor or moderator variable, we constructed a subset tree to estimate P for each category, which contains only the species present in that particular comparison and retains all the branch length information found in the hypothesised tree (Fig. S1). Because results were similar between traditional and phylogenetic meta-analyses, we interpreted and discussed results of the latter. Results of traditional meta-analysis are provided in Table S3.

Publication bias

An intrinsic problem when conducting quantitative reviews of published studies is the potential of publication bias; i.e. studies showing significant results may have a greater possibility of publication than those showing non-significant results. To explore such possibility, we conducted a Spearman rank correlation test, which examines the relationship between the standardised effect size and the sample size across studies (Cooper *et al.* 2009). A significant correlation indicates a publication bias where larger effect sizes are more likely to be published than smaller effect sizes. We also used the fail-safe number calculator to estimate the number of non-significant, unpublished or missing studies that would need to be added to a meta-analysis to nullify its overall effect size (available online: http://lsweb.la.asu.edu/rosenberg) (Rosenberg 2005). If the fail-safe number is larger than $5n+10$, where n is the number of studies, then publication bias, may be safely ignored (i.e. the results are robust regardless of publication bias) (Rosenberg 2005).

Association of floral syndromes with primary and secondary pollinator functional groups

To evaluate associations between pollination syndromes and primary and secondary pollinator functional groups we built quantitative, standardised, pollination efficiency networks using the bipartite package of R (Dormann *et al.* 2008; R Development Core Team 2011). For each plant species included in the meta-analysis, we computed the relative contribution of each pollinator functional group to the pollination

Table 1 Estimated time of origin and diversification of particular plants and pollinators across geological eras*

Era	Period	Epoch	Age (Ma)	Plant evolution†	Pollinator evolution†	References
Cenozoic	Quaternary	Holocene	0.01	Crop domestication	First report of bumblebee decline and range contraction in North America Honeybee domestication	Doebley et al. 2006; Bloch et al. 2010; Cameron et al. 2011
		Pleistocene	2.6	Radiation of Andean Lupinus		Hughes & Eastwood 2006
	Tertiary	Pliocene	5.3	Radiation of Costus	Radiation of Neotropical bumblebees (3.8) Radiation of yucca-moth pollinators (2–3)	Pellmyr & Leebens-Mack 1999; Kay et al. 2005; Hines 2008
		Miocene	23.0	Diversification of Bromeliaceae Diversification of Cactaceae (5–10) Origin of Yucca (9–18) Origin of Agavaceae (20–26)	Radiation of Nearctic bumblebees (6–8) Origin of nectar-feeding bats (12–28) Bee fossil with orchid pollinaria (15–20) Fossils of Andrenidae, Halictidae, Colletidae Origin of Phyllantheae-moth mutualism	Michener & Poinar 1996; Pellmyr & Leebens-Mack 1999; Danforth et al. 2006; Good-Avila et al. 2006; Ramírez et al. 2007; Hines 2008; Fleming et al. 2009; Kawakita & Kato 2009; Arakaki et al. 2011; Givnish et al. 2011
		Oligocene	33.9	Origin of three clades of fragrance-producing orchids	Oldest fossil of hummingbird in Germany Oldest fossils of members of tribe Apini Divergence of extant bumblebee lineages	Engel 1998; Mayr 2004; Hines 2008; Ramírez et al. 2011
		Eocene	55.8	Origin of Cactaceae (35)	Origin of Euglossine bees (34–38)	Arakaki et al. 2011; Ramírez et al. 2011
		Paleocene	65.5	Beginning of orchid diversification	Diversification of Syrphid flies Origin of fig-wasp obligate mutualism (60)	Ramírez et al. 2007; Lopez-Vaamonde et al. 2009; Bell et al. 2010; Wiegmann et al. 2011
Mesozoic	Cretaceous		146	Origin of oil and resin reward Origin of Orchidaceae (76–84) and Bromeliaceae (100) Origin of Asteridae (101–119), Rosidae (108–121) and Magnoliidae (108–141)	Origin of oil-, and resin-foraging bees Earliest fossil bee (90–110) Diversification of Coleoptera, Hemiptera, Diptera and Lepidoptera Probable Gymnosperm pollination by Thysanoptera (105–110)	Crepet et al. 2004; Langenheim 2003; Danforth et al. 2006; Poinar Jr & Danforth 2006; Ramírez et al. 2007; Hu et al. 2008; Murphy & Breed 2008; Whitfield & Kjer 2008; Wiegmann et al. 2009; Bell et al. 2010; Moore et al. 2010; Renner & Schaefer 2010; Givnish et al. 2011; Peñalver 2012
	Jurassic		202	Monocot–dicot divergence (140–150) Origin of Nymphaeales (145–187) Origin of Angiosperms (167–199)	Diversification of some long-proboscid flies Probable pollination in cycads and conifers by Coleoptera, Diptera and Mecoptera	Labandeira 1998; Crepet et al. 2004; Chaw et al. 2004; Labandeira et al. 2007; Ren et al. 2009; Bell et al. 2010; Moore et al. 2010; Wiegmann et al. 2011
	Triassic		251	Diversification of Conifers	Occurrence of Lepidoptera, Hymenoptera, Trichoptera, Coleoptera and Diptera Earliest record of palynophagy by Coleoptera	Chaw et al. 2004; Whitfield & Kjer 2008; Wiegmann et al. 2009; Labandeira 2010

Table 1. (continued)

Era	Period	Epoch	Age (Ma)	Plant evolution†	Pollinator evolution†	References
Paleozoic	Permian		299	Origin of Conifers and Ginkgoales	Occurrence of Polyneoptera (Phasmathodea, Orthoptera)	Whitfield & Kjer 2008; Zhou 2009; Labandeira 2010
	Carboniferous		359	Origin of Cycadales and Gnetales / Possible origin of nectar-like fluids from the phloem	Occurrence of Neoptera / Earliest pollen consumption by Hemipteroidea and Orthopteroidea	Krassilov & Rasnitsyn 1996; Labandeira 1998; Whitfield & Kjer 2008; Nepi *et al.* 2009; Labandeira 2010
	Devonian		416	Origin of seed plants	Origin of Pterygota (winged insects) / Origin of Collembola	Whitfield & Kjer 2008; Grimaldi 2010; Labandeira 2010
	Silurian		444	Origin of vascular plants	Divergence of Hexapoda from crustaceans / Earliest terrestrial sporivory, probably by myriapods or insects	Edwards *et al.* 1995; Labandeira 1998; Steemans *et al.* 2009; Labandeira 2010
	Ordovician		488	Origin of Bryophytes		Fiz-Palacios *et al.* 2011

*Discontinuous lines indicate mass extinction events (from Cretaceous to Paleocene and from Permian to Triassic).
†Numbers in parentheses indicate estimated dated age in millions of years.

of each plant species. With this information, we constructed a pollination network for each syndrome, whose nodes are plant species and pollinator groups that are joined by weighted links that show the relative efficiency of each pollinator functional group.

In order to understand the potential evolutionary transitions between plants and pollinator functional groups we built an evolutionary history table across geological eras. Table 1 indicates the estimated time of origin and diversification of main plant and main animal groups known to transfer plant sperm and pollen. To accomplish this, we conducted literature searches of studies with molecular and fossil evidence on the origin of these groups. We also compiled a list of all studies conducted to date that assessed pollination syndrome transitions within a phylogenetic framework. We used studies that had resolved phylogenies and inferences of ancestral pollination systems. With this information, we constructed a network of evolutionary transitions that allowed us to determine the most common ancestral pollinator groups recorded for each pollination syndrome.

RESULTS

Characteristics of cumulated research

From an original set of 1990 studies found in the literature search, we found 213 suitable publications involving 370 plant species, which together with 47 species from our published and unpublished data completed a total of 417 unique plant species (Table S2). The rule to include a species was that the pollination efficiency of the entire pollinator assemblage was determined. After systematically assigning flower trait variables to each plant species corresponding to a particular pollination syndrome from Table S1, we observed that 68% of the species corresponded to bee (35%), bird (20%), and bat (11%) syndromes, while fly (9%), wasp (9%), moth (7%), long-tongued fly (2%), beetle (2%), butterfly (2%) carrion fly (1%) and non-flying mammal (1%) syndromes altogether comprised the remaining 32% of all plant species included in our review (Table S2). The vast majority of plant species studied are herbs (52%). Shrubs and trees comprise 19 and 12% respectively. The remaining 17% belong to epiphyte, lianas, vines and woody cacti (Table S2). In general, breeding systems were fairly evenly represented within each syndrome (Table S2). There were, however, some particular associations between pollination syndromes and geographical regions that are worth mentioning. Plant species with bat syndrome were almost exclusive to tropical regions, while species with fly, carrion fly, long-tongued fly, wasp and non-flying mammal syndromes were mostly found in species from extratropical regions. The majority of species with bee and bat syndromes were herbs and woody species (shrubs and trees) respectively.

Spearman rank correlation test between sample size and Hedges′*d* effect sizes was non-significant ($r_s = 0.026$, $d.f. = 418$, $P = 0.590$), indicating absence of publication bias in our meta-data. Furthermore, the weighted fail-safe number calculated was much larger than 5n+10 (2105 < 47837), suggesting that results are robust despite any publication bias.
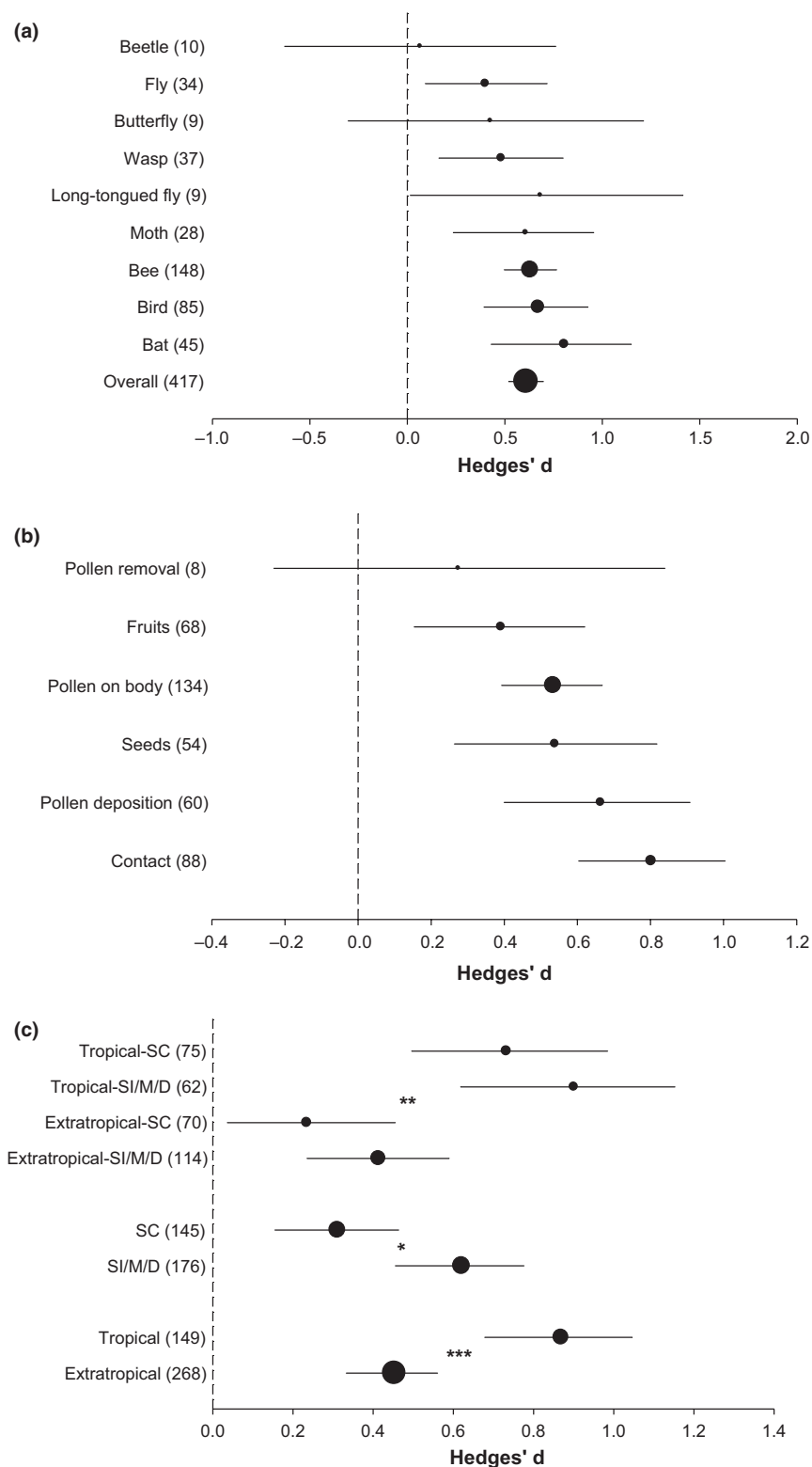
Figure 1 Phylogenetic meta-analyses of the predictability of pollination syndromes on the most effective pollinators showing weighted-mean effect sizes and 95% bias-corrected confidence intervals. (a) Overall effect for a total of 417 plant species and for each pollination syndrome (non-flying mammal and carrion fly are not shown due to their low sample size; Table S3). (b) Weighted mean effect sizes of different methods used to estimate pollinator effectiveness and (c) of plants with traits associated with higher predictability of pollination syndromes. SI/M/D: self-incompatible/monoecious/dioecious, SC: self-compatible. Sample sizes for each category are shown in parentheses. The size of each dot representing each mean effect size is proportional to its weight or contribution to the overall mean calculation. Dotted lines show Hedges' $d = 0$. When confidence intervals overlap zero the effect sizes are not significantly different from zero. Significance level associated with $Q_{between}$-values for group comparisons: *$P < 0.05$; **$P < 0.01$ ***$P < 0.001$.

Quantification of pollination syndrome effects

Both traditional and phylogenetic meta-analyses showed support for pollination syndromes (Fig. 1a, Table S3), indicating that floral syndromes of plants predict the most effective pollinators regardless of breeding system or region. The overall effect after accounting for the phylogenetic history across the species was positive (0.609) and statistically different from zero (Fig. 1a). Pollinators that matched the floral syndrome were significantly more efficient than pollinators that did not match the syndrome. The only exceptions were the beetle, butterfly and carrion fly syndromes, whose effect sizes were not different from zero (Fig. 1a, Table S3). Although all of them had positive mean effect sizes, their relatively small sample sizes precluded powerful testing of their effects. In any case, the lack of significant effects would indicate that expected pollinators of these three syndromes were not more efficient than non-expected pollinators. The rest of the syndromes were all positive and significantly different from zero (Fig. 1a, Table S3), validating the pollination syndrome concept. Effect sizes ranged from 1.25 in non-flying mammals (but very small sample size, Table S3) to 0.065 in beetle (also with small sample size). For pollination syndromes with large sample sizes and better estimations, the bat syndrome had the largest effect size (0.805), followed by bird and bee syndromes, and wasp had the lowest (0.482; Fig. 1a). Pollination effectiveness measures did not significantly differ in their ability to detect differences in pollination syndromes accuracy to predict the effective pollinator functional groups ($Q_{between}$ = 4.21; P = 0.102; Fig. 1b). That is, any of the methods used by the authors was successful at discriminating the most effective pollinator. The only exception was pollen removal, which was underrepresented (n = 8 species) and was not significantly different from zero (Fig. 1b). Regarding the external moderator variables, the effective pollinators were more strongly predicted by floral syndromes in plants from tropical regions and in plants with dioecious, monoecious or self-incompatible systems (Fig. 1c). Accordingly, when comparing species with both of these traits combined, pollination syndromes of pollinator-dependent species from tropical regions were significantly more predictable than any other plant group (Fig. 1c).

The predictability of pollination syndromes was also evident in the pollination networks: the most effective pollinator functional group of plant species was in most cases the expected by their syndrome (Fig. 2). The networks also showed that for all syndromes there was variation in the level of specialisation; there was a group of plant species pollinated exclusively by the expected functional group (to the left of the networks), and another group of plants pollinated by up to three (bat, bird, moth and wasp syndromes), five or six (fly and bee respectively) alternative functional groups of pollinators (Fig. 2). Associations between secondary pollinators and particular pollination syndromes showed a systematic pattern, where the main secondary pollinators were: birds for bat flowers, butterflies and flies for bee flowers, bees for bird and moth flowers, and bees and beetles for fly and wasp flowers (Fig. 2). Most long-tongued fly flowers did not have secondary pollinators (Fig. 2).

Evidence on animal-mediated plant sperm transfer across evolutionary time on earth suggests that plant fertilisation by animals may have occurred as early as the Silurian period (Rosenstiel *et al.* 2012). Evidence from the fossil record and phylogenetic analyses suggests that scorpionflies, beetles and flies might have been the first animal pollinator groups in the Jurassic period. The origin of bees and the diversification of Coleoptera, Diptera, and Lepidoptera occurred in the Cretaceous. Finally, nectar feeding birds and bats originated in the Oligocene and the Miocene respectively; paralleling the origin and diversification of some plant groups, e.g. Bromeliaceae and Cactaceae (Table 1). The pollination network built in our study (Fig. 2) revealed that the main secondary pollinator often corresponds to an evolutionary younger pollinator group. Secondary pollinators generally corresponded to the ancestral pollinators documented in evolutionary studies. The most common evolutionary transitions of pollination systems that have been documented involving 23 plant taxa (Fig. 3) included: bee to bird (43 transitions in 12 studies), bee to other bee group (19 transitions in two studies), bee to moth (14 transitions in two studies), bird to bee (13 transitions in three studies), bird to moth (11 transitions in four studies), bird to generalist insects (six transitions in two studies) and bird to bat (four transitions in three studies).

DISCUSSION

This is the first study that quantitatively syntheses and tests the universal character of pollination syndromes based on empirical evidence obtained from cumulated research throughout the world. Particular suites of floral traits correlated with particular effective functional groups of pollinators across a set of taxonomically widespread angiosperm species. Our findings support Stebbins' principle (Stebbins 1970), suggesting that convergent evolution of floral traits is driven mainly by adaptation to the most effective pollinator functional group. However, secondary pollinators were common and they may play an important role in plant reproduction. We argue that the concept of pollination syndromes does not necessarily imply the absence of other secondary pollinators. Our study also showed that geographical location and plant reproductive system influence the predictive accuracy of pollination syndromes. Interestingly, beyond the syndrome characterisation, we found a non-random association between primary and secondary pollinators, and the latter may often correspond to the ancestral pollinator group.

Traits associated with predictability of pollination syndromes

As we initially expected, pollinators predicted by the syndrome were more effective in dioecious, monoecious and self-incompatible hermaphrodite species than in species less dependent on pollinators; thus, pollinator-mediated selection on suites of floral traits may be stronger in these outcrossing groups of species, where fitness is highly dependent on pollinators. In self-compatible hermaphroditic species, however, autogamy may compensate reproduction in the absence of pollinators and we might expect more relaxed selection by pollinators on floral traits.

Pollination syndromes in species from tropical regions were significantly more adjusted than in species from other regions.
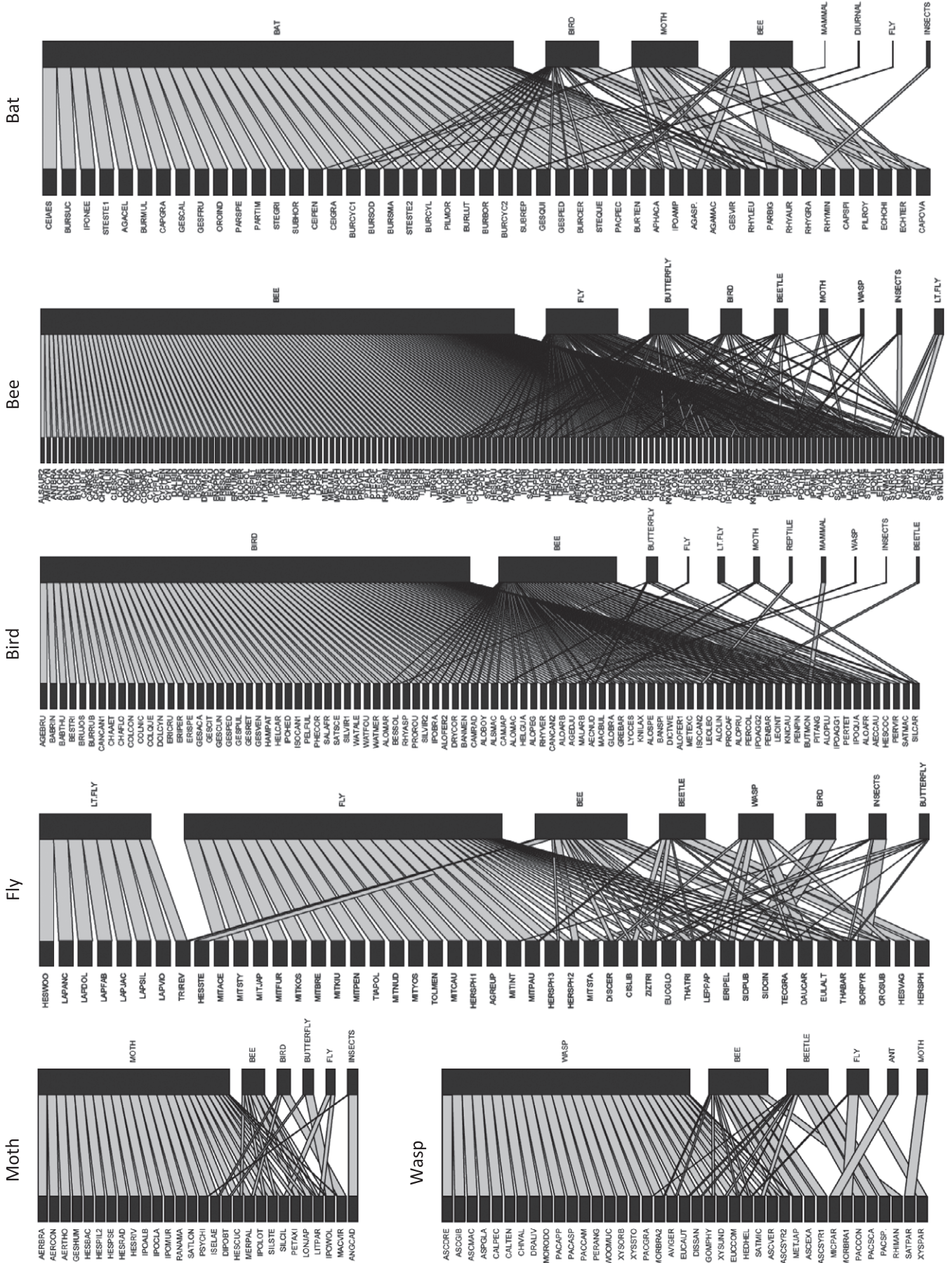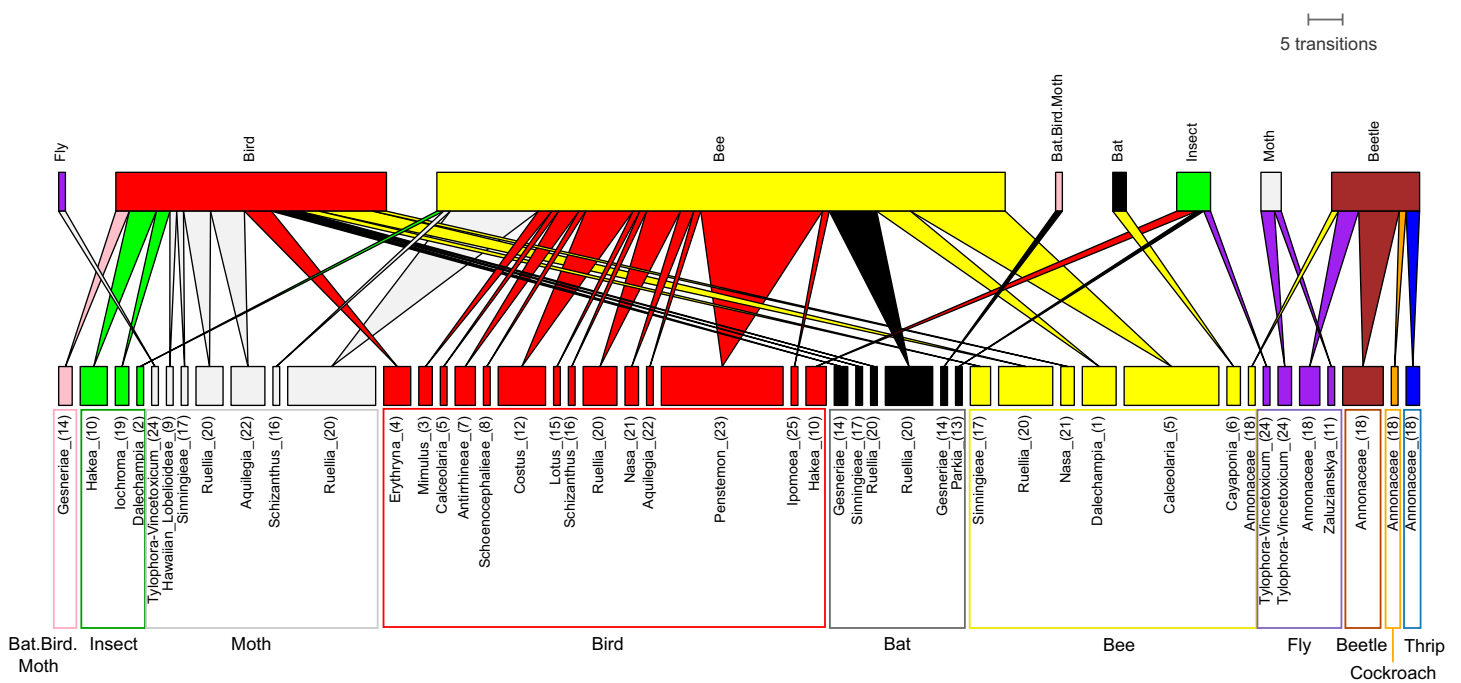
Figure 3 Network of evolutionary transitions of pollination systems. Transitions from ancestral (upper rectangles) to current (lower rectangles) pollination systems are indicated by triangles. The width of the upper rectangles indicates the total number of transitions reported from an ancestral pollination system. The width of the lower rectangles and of the links indicate the number of transitions to a particular pollination system per plant taxa (range: 1–18). Numbers following the plant taxa correspond to references given in Appendix S2.

Stronger biotic interactions in the tropics may generate more and narrower niches (Schemske *et al.* 2009). Tropical plants typically have narrower niches, which are reflected in their non-overlapping flowering phenology patterns. Although individual species have restricted flowering times, flowering at the community level occurs throughout the year (Frankie *et al.* 1974). On the other hand, many pollinator species are present all year round in the tropics, requiring continuous food resources (Lobo *et al.* 2003). A steady supply of floral resources for pollinators can be achieved by the sequential flowering phenologies of plant species constituting a particular resource guild. Some examples are provided by the staggered flowering phenologies of hummingbird-pollinated *Heliconia* species in Costa Rica (Stiles 1975) and bat-pollinated Bombacaceae species in Mesoamerica (Lobo *et al.* 2003). Such phenological patterns may contribute to the selection of suites of floral traits that signal particular resources to particular functional groups of pollinators. The higher predictability of pollination syndromes in the tropics may also be related to the lower population densities of plants and pollinators, associated with high diversity levels (Gentry 1988). If lower densities lead to lower visitation rates and higher pollen limitation in the tropics, we would expect strong selection on floral traits that increase efficiency and precision in pollen transfer. These

hypotheses certainly deserve further exploration. Previous studies that have assessed latitudinal patterns using communities of floral visitors and plants have found no differences in pollination specialisation between geographical regions (Ollerton & Cranmer 2002; Schleuning *et al.* 2012). However, equating floral visitation with effective pollination may be misleading (King *et al.* 2013), since frequent floral visitors are often poor pollinators (reviewed in Fenster *et al.* 2004); therefore, studies based on visitor assemblages are not directly comparable with our review. Our study is the first quantitative review that makes a comparison of tropical and extratropical plant–pollinator interactions using pollinator efficiency data and a phylogenetically corrected statistical analysis, suggesting that interactions with effective pollinators generate strong selection on floral traits in the tropics.

Floral syndromes and the role of secondary pollinators

Pollination networks built across published evidence show that certain functional groups are more commonly found as secondary pollinators of particular syndromes (Fig. 2). Interestingly, some of the most common transitions of pollination systems documented in the literature concur with our observed trends: from bee to moth, from bee to bird and from bird to

Figure 2 Quantitative pollination networks between plant species from all studies included in the meta-analysis and their pollinator functional groups classified as (top to bottom): bat, bee, bird, fly and long-tongued fly, moth and wasp pollination syndromes. Top and bottom rectangles of each network represent pollinator groups and plant species respectively. Line widths indicate the relative effectiveness of each pollinator group on each plant species. The widths of the upper rectangles indicate the summed effectiveness of the respective pollinator group across the plant species of the entire network. Plant species codes are the first three letters of the genus and the first three (four when ambiguous) of the species (from Table S2). Category 'insects' refers to unspecified insects or small diverse insects as ants, true bugs, thrips. L.T. Fly: long-tongued fly.

bat pollination (Fig. 3, van der Niet & Johnson 2012). There-fore, important secondary pollinator groups in our pollination networks may correspond to the ancestral pollinator groups of plant lineages. Whether evolutionary transitions from bee to fly, bee or beetle to wasp and from fly to bee pollination exist, as the networks suggest, is worth exploring.

In some cases, secondary pollinators of plants belong to pollinator groups that originated earlier in evolutionary his-tory than the primary pollinator group predicted by the syn-drome (Fig. 2, Table 1). For example, the main secondary pollinator group of bird-pollinated plants were bees (Fig. 2), whose origin is dated before the diversification of the hum-mingbirds (mid Cretaceous and Oligocene respectively). Simi-larly, the diversification of hummingbirds (birds are the main secondary pollinators of bat flowers) precedes the origin of nectar-feeding bats in the late Miocene. These patterns suggest that transitions from historically older to younger pollinator groups could be a common pattern in the evolutionary history of angiosperms (Table 1, Fig. 3).

It is noteworthy that for most of the plant species where syndromes failed to predict the most effective pollinator, the pollinator predicted by the syndrome was still present within the pollinator assemblage (Fig. 2). In these cases, the most effective pollinator is often the main secondary pollinator of the syndrome and may represent the ancestral pollination sys-tem of the plant lineage (e.g. where bees are the most effective pollinators of bird flowers). Transitions to ancestral groups may be promoted if the quantity or quality of visits by con-temporary pollinators is reduced and if ancestral pollinator groups perform more efficiently. Whether cases where pollina-tion syndromes did not predict the most effective pollinator imply transitions, either back to their ancestral state or to a novel pollination system, should be further explored.

None of the pollination syndromes was entirely effective at filtering secondary functional groups of pollinators. These results suggest that current suites of floral traits in most plant species have the potential for adapting to new conditions under changing selective pollination environments (Kay *et al.* 2005; Whittall & Hodges 2007). Such shifts in pollination sys-tems may occur quite rapidly through novel floral mutations. For instance, Bradshaw & Schemske (2003), demonstrated that a single allele substitution resulted in flower colour change and generated an adaptive shift in pollinator prefer-ence. However, without an increase in the frequency of visita-tion of the secondary pollinator, the new mutation cannot be fixed by selection (Thomson & Wilson 2008). In the current changing world, a decrease in primary pollinators due to human disturbance (Aguilar *et al.* 2006) may result in an increase in the relative frequency of less vulnerable alternative secondary pollinators with potential evolutionary conse-quences to the plants. Reliable pollen transfer by secondary pollinators could provide a potential venue to driving novel evolutionary changes in floral traits, and eventually, lead to modified floral syndromes in novel environments.

Conclusions and future directions

Our results support the view that pollination syndromes reflect patterns of convergent evolution and adaptation to the most efficient pollinator functional group. While our results are robust and support the pollination syndrome theory, we stress the current scarcity of studies on syndromes such as beetle, butterfly, carrion fly, long-tongued fly and non-flying mammal across different regions of the world to better deter-mine their predictability. Our results also suggest that second-ary pollinators may play an important role on plant reproduction, acting as antagonists or ensuring reproduction when primary pollinators are absent or scarce. Thus, second-ary pollinators may provide a potential venue for evolutionary shifts in pollination syndromes.

Future studies of pollinator-mediated selection should consider potential sources of selection, both antagonistic and mutualistic, to understand how convergence of specia-lised floral phenotypes is maintained even in plants that currently show generalised pollination systems. Experimental work that integrates knowledge of the genetic basis of floral trait variation with studies of pollination biology and polli-nator-mediated selection will also provide important insights about the mechanisms underlying the evolution of floral diversity. Moreover, studies of plant–pollinator interactions should explore the role of primary and secondary pollina-tors across space and time, quantifying the respective role of each floral visitor on plant reproductive success. Studies that assess pollination systems and floral traits in a phylo-genetic context will allow determining the importance of secondary pollinators as drivers of evolutionary change. Last, assessing the importance of all pollinator functional groups under different levels of habitat disturbance will be very useful in understanding potential changes in pollination services and floral evolution in our rapidly changing envi-ronment.

AUTHORSHIP

All authors contributed equally to designing the study, collect-ing data and writing the manuscript. RA also performed meta-analyses.

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