Chapter 11
Pollination Syndromes: A Global Pattern of Convergent Evolution Driven by the Most Effective Pollinator

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Abstract Convergent evolution of floral traits driven by pollinators has resulted in floral syndromes shared among different plant lineages. However, the flowers of many plant species are often visited by different pollinator groups, which apparently

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contradict the idea of syndromes. Here, we demonstrate that the most efficient pollinators consistently correspond to the ones predicted by the syndrome, and the predictive accuracy of the syndrome tends to be higher for species pollinated exclusively by one functional group than for species pollinated by more than one functional group. Secondary pollinator functional groups affected differentially the relative efficiency of the primary pollinator depending of the syndrome. The most frequent secondary pollinator group of a given syndrome is also the least efficient one. Floral symmetry did not influence predictability of pollination syndromes. Except for the bee-syndrome plants, pollination syndromes were more effective on plants that depend strongly on animal pollination than on less dependent plants. Last, effective pollinators for each floral syndrome were better predicted for plants from tropical regions, particularly for the bat, bee, and bird syndromes. Our results have implications on the effects of global change on floral evolution and suggest that current suites of floral traits in most plant species have the potential to adapt to new conditions under changing selective pollination environments.

11.1   Introduction

Angiosperms are the most diverse group of living plants with more than 350,000 species distributed across all major ecosystems of the earth (The Plant List 2013). This plant group, which rapidly diversified in the Cretaceous period, is characterized by two important features that include a great diversity of flowers and an unparalleled diversity of pollination and reproductive systems. Darwin described the sudden and rapid radiation of the angiosperms as an abominable mystery and recognized Gaston de Saporta's idea that early interactions with pollinating insects favored outcrossing promoting diversification (Friedman 2009). Darwin (1862) also described the great variety of floral traits and breeding systems in the angiosperms as examples of adaptation to promote cross-pollination by animal vectors. Today, pollinator-mediated selection is considered one of the major evolutionary processes underlying floral diversification (Harder and Johnson 2009; van der Niet and Johnson 2012). The specific combinations of floral traits, including flower morphology, color, scent, type, and amount of reward that have independently evolved to attract specific groups of animal pollinators, are known as pollination syndromes.

The idea that floral traits should be associated with particular pollinating agents was first proposed by Delpino (1867) and later elaborated by Kunth (1906), Vogel (1954), and Faegri and van der Pijl (1979). In accordance with this hypothesis, Stebbins (1970) proposed that floral traits reflect adaptation to the pollinators that visit flowers most frequently and effectively, an idea that was later acknowledged as the "most effective pollinator principle." Effective pollinators are differentiated from other floral visitors in their ability to effect fruit set and are expected to have a direct impact on plant fitness. Thus, according to Stebbins´ principle, flowers may receive visits by different pollinator groups, but floral phenotypes should correspond to the

most effective ones. The concept of pollination syndromes was later complemented with the idea that pollinators can be clustered into functional groups that have similar behavior and exert similar selection on flowers (Fenster et al. 2004).

Phenotypic selection exerted by pollinators on single reproductive traits or trait combinations of plants is the main evidence to assert that most flowers reflect specialization for pollination by particular animal groups (Stebbins 1970; Fenster et al. 2015). However, it is also evident that more than one pollinator species visit the flowers of many plant species (Waser et al. 1996). These observations have stimulated discussion in the literature on the premises that most pollination systems are generalized in nature (Waser et al. 1996) and that pollinators do not always correspond to those predicted by floral traits (e.g., Ollerton et al. 2009). However, other studies have shown that floral traits are associated with particular functional groups of pollinators (Fenster et al. 2004), and that pollination syndromes do predict the most important pollinators of plants (Martén-Rodríguez et al. 2009; Reynolds et al. 2009). The most recent comprehensive quantitative review on pollination syndromes demonstrates that syndromes predict the most effective pollinators of plant species even when there are secondary pollinators (i.e., pollinators not according to the syndrome) within the pollinator assemblage of plants (Rosas-Guerrero et al. 2014).

Here, we further analyze the database of Rosas-Guerrero et al. (2014) focusing on testing hypotheses within and across pollination syndromes. In the context of each pollination syndrome, various traits might influence the association between pollinators and floral traits, but not all syndromes may respond identically. In this chapter, we expand our previous findings and test five hypotheses relating the level of specialization, the identity of secondary pollinators, floral morphology, breeding systems, and geographic location to each pollination syndrome.

In the first hypothesis, we consider that the level of pollination specialization should determine the predictability of syndromes. In species with more generalized pollination systems, selection on floral traits may be disruptive or more relaxed (Gómez et al. 2014). Thus, we expect that species pollinated exclusively by one functional group should show greater predictive accuracy of pollination syndromes than species pollinated by more than one functional group.

A second hypothesis proposes that within a syndrome the efficiency of secondary pollinators varies. Therefore, the relative efficiency of the primary pollinator within any given syndrome will be differentially affected depending on the identity of the secondary pollinator group. For example, in bat-syndrome flowers, typically with highly exerted stamens, birds may be more efficient secondary pollinators than bees (e.g., *Gesneria pedunculosa*, Martén-Rodríguez and Fenster 2008). In such case, we might expect birds to exert stronger selection on floral traits than bees, modifying more the relative efficiency of bats.

In a third hypothesis, we propose that floral symmetry may act as a pollinator-filtering agent. Bilateral flowers can restrict the directionality of approach and movement of pollinators within flowers (Sargent 2004), with a consequent decrease in the type of visitors that may access these flowers (Huang and Gong 2009). Indeed, the idea that the origin of bilateral symmetry is a consequence of

strong selection exerted by specialized pollinators has been recently supported by empirical data (Gómez et al. 2006). Therefore, we expect greater predictability of pollination syndromes in plants with bilateral flowers than with radial flowers. Since sensory abilities differ among pollinator functional groups, we explored floral symmetry within each syndrome.

In a fourth hypothesis, we suggest that within each syndrome, pollinator-dependent species should experience more consistent selection on floral traits than species that have the ability to set seeds via autonomous self-pollination. We previously documented that regardless of their syndrome, pollinator-dependent species, such as dioecious, monoecious, and self-incompatible species, show greater predictability of pollination syndromes than self-compatible species (Rosas-Guerrero et al. 2014). Here, we explore whether this finding is consistent within each pollination syndrome.

The fifth hypothesis proposes that within each syndrome, the predictability of pollination syndromes will differ between tropical and extra-tropical plant species. Because the strength of biotic interactions is expected to increase with decreasing latitude, tropical species should have narrower niches, facilitating coexistence and promoting diversification (Schemske et al. 2009; Moya-Laraño 2010). In tropical species, the pollinators expected by the syndrome are more efficient than in extra-tropical species (Rosas-Guerrero et al. 2014). Here, we further explore the relationship between geographic distribution and predictability by making such comparisons within each pollination syndrome.

By means of ordinary and phylogenetic meta-analyses, we previously tested whether pollination syndromes can predict the most effective pollinator of plants (Rosas-Guerrero et al. 2014). The analysis was based on a complete and systematic literature review of detailed pollination studies throughout the world that quantified the efficiency of the entire pollinator assemblages of plant species (Rosas-Guerrero et al. 2014). From a total of 1990 studies in the literature search, we considered 213 suitable publications including 370 plant species, and 47 species of our own studies, that were conducted under natural conditions and quantitatively assessed pollination effectiveness of all floral visitors of plants. Pollination effectiveness measures considered were pollen on pollinator's body, contact of pollinator with the flower's reproductive organs, pollen deposited on stigmas, pollen removed from anthers, or fruit and/or seed production by specific functional groups. These pollination effectiveness measures (Ne'eman et al. 2010) did not significantly differ in their ability to detect differences in pollination syndromes accuracy to predict the effective pollinator functional groups (Rosas-Guerrero et al. 2014).

We assigned one of 11 pollination syndromes to each plant species based on the presence or absence of character states of floral traits (Rosas-Guerrero et al. 2014). Each syndrome was assigned to each plant species without previous knowledge of its assemblage of floral visitors. Pollination syndromes were characterized according to Faegri and van der Pijl (1979), Proctor et al. (1996), Ollerton et al. (2009), and Willmer's (2011) descriptions.

In our previous synthesis, we found that both phylogenetically independent and traditional meta-analyses produced almost identical response patterns

(Rosas-Guerrero et al. 2014). Such homogeneity of responses between both types of meta-analyses implies that calculated effect sizes are not conserved across the phylogeny of the sample of species included in our review, i.e., there is no phylogenetic signal in the relative efficiency of pollinators according and not according to any particular syndrome. When effect sizes are not conserved within the phylogeny (i.e., there is weak or null phylogenetic signal), any phylogenetic correction may have a trivial effect on meta-analytical results, as effect sizes are fundamentally independent across the phylogeny (Chamberlain et al. 2012). Therefore, in this chapter, we only conduct traditional meta-analyses using the entire database to gain power in effect size estimations.

For the meta-analyses, we used the standardized unbiased mean difference (Hedges' d) as a measure of effect size that expresses the difference in pollination effectiveness between two pollinator groups:

$$d = \frac{X_s - X_{ns}}{S_{\text{within}}} J$$

where X_s is the mean value of pollination effectiveness of the expected pollinator functional group according to the syndrome, X_{ns} is the pollination effectiveness of the pollinator functional group not according to the syndrome, S_{within} is the within-groups standard deviation, pooled across groups, and J is a correction factor for small sample sizes (see Gurevitch and Hedges 2001 for calculation details).

In cases where mean values, standard deviations, and/or sample sizes were not provided by a study, we calculated a different effect size; the Odds Ratio (OR, Cooper et al. 2009):

$$\text{OR} = \frac{AD}{BC}$$

where A is the number of effective pollination events of the expected pollinator, B is the number of effective pollination events of the non-expected pollinator, C is the number of ineffective pollination events of the expected pollinator, and D is the number of ineffective pollination events of the non-expected pollinator. When one of the pollinator groups was not observed, we added 0.5 to each cell to be able to calculate OR (Cooper et al. 2009). To unify effect size metrics and be able to run the meta-analyses, we converted log (OR) values and their variance into Hedges' d and its corresponding variance values through mathematical transformations (Cooper et al. 2009).

When effect sizes Hedges' d are positive, it implies that pollinators expected by the syndrome are more efficient (i.e., there is support for the pollination syndrome hypothesis), whereas when effect sizes d are negative, pollinators not matching the syndrome are more efficient. In the cases that a plant species had two or more effective pollinator functional groups besides the one predicted by the syndrome,

we calculated an effect size for each syndrome versus each alternative group combination for that plant species. Due to these situations, we ended up with 517 data points from 417 unique plant species. We used MetaWin 2.0 to run the traditional meta-analyses (Rosenberg et al. 2000). Confidence intervals of effect sizes were calculated using bootstrap resampling procedures (Adams et al. 1997). An effect was considered significant if the 95 % biased-corrected bootstrap confidence intervals (CI) of the effect size (d) did not overlap zero. Data were analyzed 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 (Gurevitch and Hedges 1999), which is the expectation in ecological and evolutionary studies.

To test our hypotheses, we analyzed whether the following moderator or predictor variables influenced differentially the effect sizes within each of the syndromes with large sample sizes (bat, bee, bird, fly, moth, and wasp): breeding system (pollinator-dependent: self-incompatible/monoecious/dioecious species versus non-pollinator-dependent: self-compatible species), floral symmetry (bilateral versus radial flowers), diversity of functional groups (plants pollinated by only one functional group versus pollinated by two or more functional groups), identity of secondary pollinators functional group (expected pollinator´s functional group versus each alternative pollinator functional group), and geographical region (tropical versus extra-tropical plants). To examine whether each of these comparisons were statistically significant, we used Q statistics, examining the P values associated with $Q_{between}$ statistics, which describe the heterogeneity in effect sizes that can be ascribed to differences between each of these categories (Cooper et al. 2009). We found no publication bias in our meta-analysis (Rosas-Guerrero et al. 2014), which implies that studies with significant results were not systematically more published than non-significant studies.

11.2 Overall Prevalence of Pollination Syndromes Across Angiosperms

The 417 plant species of our database represent 217 genera from 81 plant families of angiosperms from all continents around the world except the Antarctica. The most represented pollination syndromes in order of importance were bee, bird, bat, fly, wasp, and moth. The least represented groups were butterfly, long-tongued fly, beetle, carrion fly, and non-flying mammal (Table 11.1; Fig. 11.1).

Most of the studies were conducted in Africa, followed by Mesoamerica (Mexico and Central America), Asia, South America, and North America. The least represented continents were Europe and Oceania (Fig. 11.1). In our sample, the bee syndrome is predominant in North and South America, Asia, and Europe. Bat syndrome predominates only in Mesoamerica. Moreover, in Asia, Africa, and

Table 11.1 Results of
traditional meta-analyses. *K* is
the number of pooled effects;
effect size values (Hedges' *d*)
are given for the overall effect
and for each pollination
syndrome; LCI and UCI are
lower and upper confidence
intervals around effect sizes,
respectively. *Q*between test
evaluates differences in effect
size among pollination
syndromes

|	*k*	Hedges' *d*	LCI	UCI
Overall effect	517	0.5937	0.4964	0.6915
		Qb = 14.53, *d.f.* = 10, *P* = 0.175		
Pollination syndromes	*N*			
Bat	58	0.7173	0.4462	1.079
Bee	184	0.6199	0.4854	0.7444
Beetle	12	0.1189	−0.5199	0.7577
Bird	96	0.6985	0.4466	0.9692
Butterfly	14	0.2297	−0.2426	0.9054
Carrion fly	5	0.3385	−0.9425	0.7096
Fly	58	0.3775	0.0719	0.6302
Long-tongued fly	9	0.6572	−0.2214	1.5326
Moth	33	0.6689	0.3280	0.9868
Non-flying mammal	7	1.2131	0.1302	2.1998
Wasp	41	0.5508	0.2395	0.8634

N = Data points
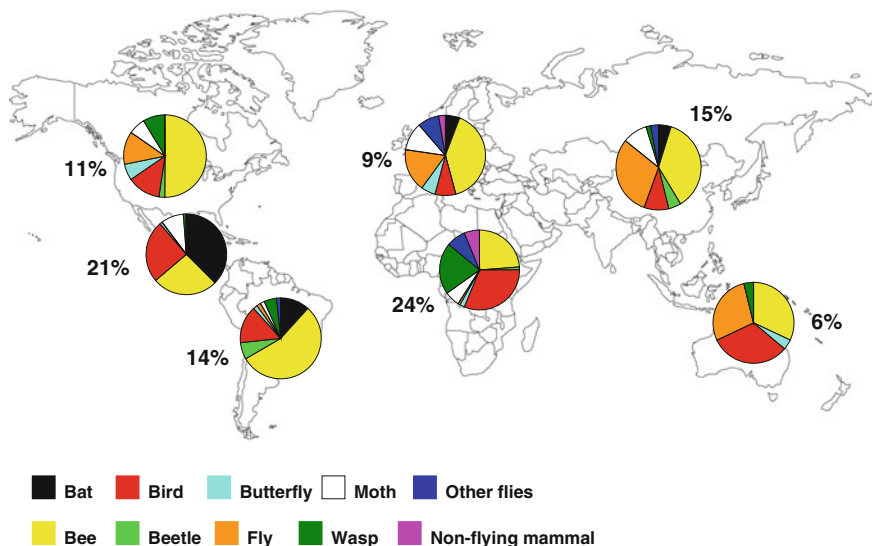
Fig. 11.1 Distribution of studies assessing pollination effectiveness of entire pollination assemblages in 417 plant species throughout the world. Within each circle, we show the relative proportion of pollination syndromes of the plant species studied in each region: North America, Meso America, South America, Europe, Africa, Asia, and Oceania. *Percentages given in numbers* refer to the relative representation of plant species for each region to the total

Oceania, there is no unique dominant syndrome, and two or three syndromes are similarly frequent (bee, bird, fly, and wasp syndromes, Fig. 11.1).

In most of the syndromes, the effect sizes were positive and significantly different from zero (Table 11.1), meaning that pollinators that matched the floral syndrome were significantly more efficient than pollinators that did not match the syndrome. The beetle, butterfly, and carrion fly syndromes had positive effect sizes but were not different from zero, though they had small sample sizes and statistical power. In these syndromes, a non-significant effect indicates at most that pollinators predicted by the syndrome were not more efficient than pollinators not predicted by the syndrome.

Our overall results indicate that particular suites of floral traits do correlate with particular effective functional groups of pollinators across a set of taxonomically widespread angiosperm species. Thus, our results suggest that adaptation to the most effective pollinator functional group drives the convergent evolution of floral traits, supporting Stebbins' most effective pollinator principle (Stebbins 1970). We, however, 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.

11.3 First Hypothesis: The Level of Pollination Specialization Within Each Syndrome Should Determine Its Predictability

The general pattern found here shows that within each syndrome, the predictive accuracy of the syndrome tends to be higher when the primary pollinator is alone (Syndrome-None, Fig. 11.2) than when one or more secondary pollinators are present (Syndrome-Alternative, Fig. 11.2). Therefore, results obtained here agree with our first hypothesis.

Interestingly, secondary pollinators were common regardless of the pollination syndrome (see Syndrome-Alternative sample sizes in Fig. 11.2) and may play an important role in the evolution of plant reproduction. However, with the exception of the fly syndrome, the presence of secondary pollinators did not imply the rejection of the pollination syndrome hypothesis, as pollinators predicted by the syndromes were the most efficient (i.e., effect sizes are positive for Syndrome-Alternative groups of plants). Thus, we argue that the concept of pollination syndromes does not necessarily imply the absence of secondary pollinators (Fig. 11.2). The interaction of plants with secondary pollinators might be expected to reduce the strength of selection exerted by primary pollinators, given that the relative efficiency of primary pollinators is decreased by the presence of secondary pollinators (Fig. 11.2). This does not imply a widespread generalization of pollination systems and the absence of pollination syndromes as proposed by Waser
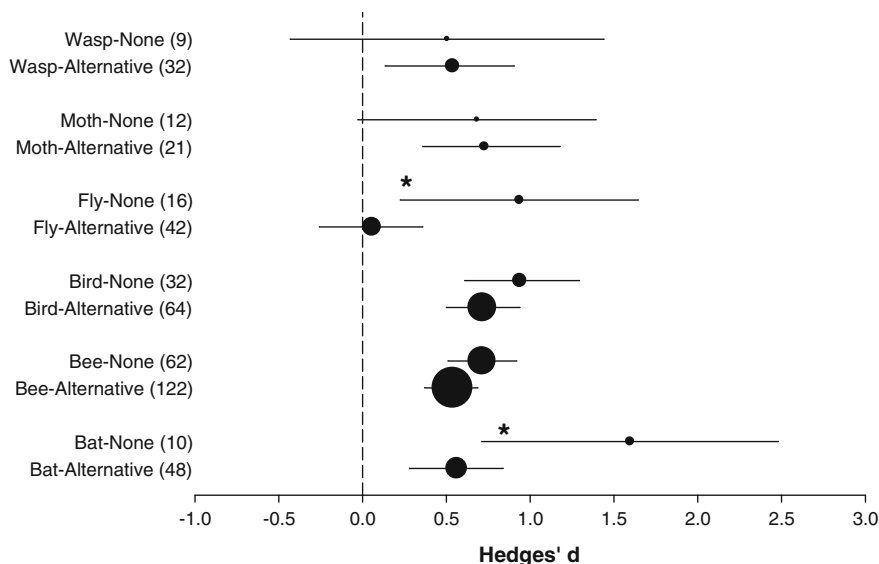
Fig. 11.2 Weighted-mean effect sizes and 95 % bias-corrected confidence intervals of the predictability of pollination syndromes on the most effective pollinators when each pollinator predicted by syndromes is alone (i.e., no other pollinator functional group was registered within the plant's pollinator assemblage) and when there are alternative pollinator functional groups within the plant's pollinator assemblage. Sample sizes for each category are shown in parentheses. The size of each dot represents the proportional 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. *Asterisks* indicate significance level at $p < 0.05$ associated with $Q_{between}$-values for each group comparison

et al. (1996). Instead, this study demonstrated that syndromes were correctly predicted even in the presence of secondary pollinators.

11.4 Second Hypothesis: Within Each Syndrome the Efficiency of Secondary Pollinators Varies Depending on Their Identity

We found great variation in the level of generalization of plant species among syndromes. Bat-, bird-, moth-, and wasp-syndrome flowers were pollinated by up to three functional groups of secondary pollinators while fly and bee flowers by five or six alternative functional groups of pollinators, respectively (Rosas-Guerrero et al. 2014). Our results show that within each syndrome, the relative efficiency of primary pollinators can be affected differentially by the identity of the secondary functional group of pollinators. In the case of bee-syndrome flowers, the efficiency of bees tends to be lower when birds are present (Bee–Bird), than when bees are

alone (Bee–NONE, Fig. 11.3). Such result implies that birds are rather efficient pollinators of bee-syndrome flowers. In contrast, for bee-syndrome flowers, the efficiency of bees is not affected when butterflies or flies are present as secondary pollinators (i.e., similar effect size between Bee–Butterfly or Bee–Fly and Bee–NONE, Fig. 11.3); thus, butterflies and flies would not be efficient pollinators in bee-syndrome flowers.

For bat-syndrome flowers, the presence of birds, bees, or moths as secondary pollinators (Bat–Bird or Bat–Moth) tends to reduce the efficiency of bats, as compared to bats alone (Bat–NONE, Fig. 11.3). Between these three groups, the relative efficiency of bats decreases more when moths or bees are the secondary pollinators (Fig. 11.3). For fly-syndrome flowers, the presence of beetles and bees as secondary pollinators tends to reduce the efficiency of flies, as compared to flies alone (Fig. 11.3). It should be noticed that the relative effect of a given secondary pollinator on the efficiency of a primary pollinator is not reciprocal. For example,
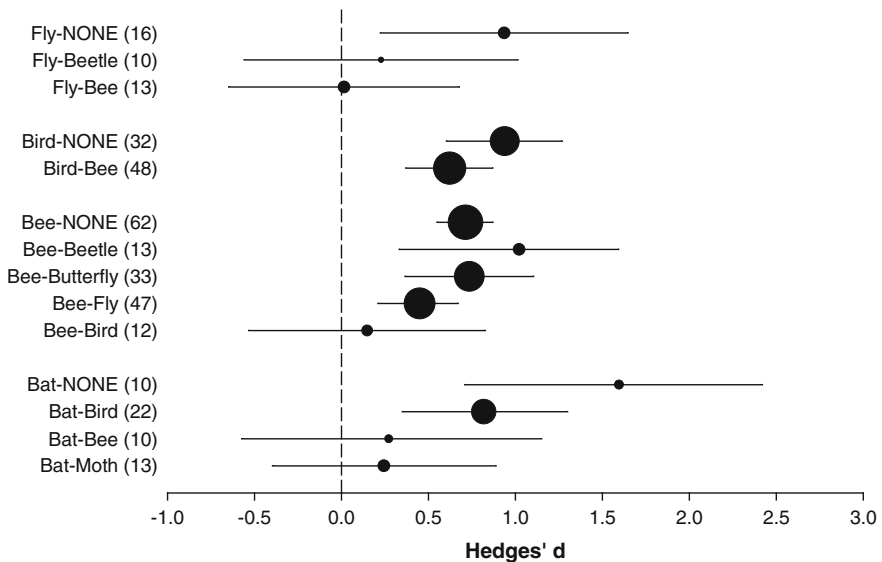

Fig. 11.3 Weighted-mean effect sizes and 95 % bias-corrected confidence intervals of the predictability of pollination syndromes on the most effective pollinators when each pollinator predicted by syndromes is alone (i.e., no other pollinator functional group was registered within the plant´s pollinator assemblage) and when another pollinator functional group is also present within the plant´s pollinator assemblage. Here, we only make comparisons when alternative pollinator functional groups were observed in 10 or more plant species. While differences in mean effect sizes are observed, they were not statistically significant following the omnibus $Q_{between}$ test among categories within each pollination syndrome. Sample sizes for each category are shown in parentheses. The size of each dot represents the proportional 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

for bee-syndrome flowers, the efficiency of birds (Bee–Bird in Fig. 11.3) is higher than the efficiency of bees on bird-syndrome flowers (Bird–Bee in Fig. 11.3).

Pollination networks showed that certain functional groups are more commonly found as secondary pollinators of particular syndromes (Rosas-Guerrero et al. 2014). The most frequent associations between primary and secondary pollinators were birds for bat-syndrome flowers, butterflies and flies for bee-syndrome flowers, bees for bird-syndrome flowers, and bees and beetles for fly-syndrome flowers (Fig. 11.3). Here, we show that this non-random association is related to the efficiency of the secondary pollinator; that is, the most frequent secondary group of pollinators of each syndrome is the one with the lowest impact on the relative efficiency of the primary pollinator. Under this situation, there would be no conflicting selection between primary and secondary pollinators and the primary pollinator would drive the evolution of floral traits. On the other hand, if secondary pollinators reduced the relative efficiency of the primary pollinators, they would have the potential to drive pollination syndrome transitions. For example, we found that birds are quite efficient secondary pollinators of bee-syndrome flowers, thus birds would have the potential to exert selection and drive floral transitions on bee-syndrome flowers; however, the opposite would not occur because bees are not efficient pollinators of bird-syndrome flowers. These differences in pollination efficiency may explain the asymmetry in evolutionary transitions showed in a recent review, where 43 transitions were registered from bee to bird, but only 13 transitions from bird to bee (van der Niet and Johnson 2012). Following the same reasoning, our data also show that bat-syndrome flowers would have more chances to evolve to moth- or bee-syndrome flowers than to bird-syndrome flowers. Similarly, bee-syndrome flowers would have a better chance to evolve to bird-syndrome flowers than to fly-, butterfly-, or beetle-syndrome flowers. Transitions from bat to other functional groups have been scantly registered in the literature (van der Niet and Johnson 2012), which may be due to the fact that the evolution of this pollinator group is relatively recent (see Table 1 in Rosas-Guerrero et al. 2014).

11.5 Third Hypothesis: Floral Symmetry Can Act as a Pollinator-Filtering Agent

Bilateral and radial flowers occurred in all pollination syndromes (i.e., bat, bee, bird, fly, moth, and wasp) and were equally frequent for bat, bird, and bee syndromes. Radial flowers were more common for fly, moth, and wasp syndromes. The predictive power of pollination syndromes did not differ between bilateral and radial flowers neither overall ($Q_{between}$ = 19.83; P = 0.098), nor within pollination syndromes ($Q_{between}$ ≤ 2.99; P ≥ 0.138). The traditional view is that the evolution of bilateral symmetry is associated with the increased levels of specialization (Wolfe and Krstolic 1999; Fenster et al. 2004). However, our results suggest that symmetry by itself is not directly related to levels of pollination specialization or to particular pollination syndromes. For example, in *Ipomoea* (Convolvulaceae), where flowers

are radial, there is a great variation in specialization and in pollination systems (Rosas-Guerrero et al. 2011). Similarly, in the radial flowers of *Aquilegia* (Ranunculaceae), the length of the nectar spur determines accessibility to effective pollinators and the level of pollination specialization (Whittall and Hodges 2007). In contrast, in the family Gesneriaceae, species with bilateral flowers have different specialized and generalized pollination systems, while radial symmetry occurs in species with specialized bee-pollination (Martén-Rodríguez et al. 2010). Further studies on groups of plants that include both types of floral symmetry should use a phylogenetic approach to assess the evolution of floral symmetry in relation to pollinator shifts. Since the genes that determine floral symmetry are known in various plant groups (e.g., *Antirrhinum*), experimental approaches using symmetry mutants could be useful in evaluating how changes in symmetry may affect the evolution of pollination systems.

11.6 Fourth Hypothesis: Pollinator-Dependent Species Should Experience More Consistent Selection on Floral Traits than Species Less Dependent on Pollinators

In general, pollinators expected by the syndrome are more efficient on pollinator-dependent plants (dioecious, monoecious, and self-incompatible hermaphrodite species) than on non-dependent species (self-compatible species) (Rosas-Guerrero et al. 2014). This pattern was statistically significant for the bat and bird syndromes only (Fig. 11.4). This result indicates that the fitness of plant species of these two syndromes is maintained by high outcrossing rates that, in turn, are apparently maintained by the effective pollination and long gene flow distances via pollen provided by bats and birds (e.g., Aldrich and Hamrick 1998; Quesada et al. 2004). On the other hand, for these groups, non-dependent species are less efficiently pollinated by the pollinator expected by the syndrome. Here, autogamy, either attained through autonomous self-pollination or effected by less mobile secondary pollinators, would have more chances to contribute to the reproduction of non-dependent than dependent plant species, and thus, we might expect more relaxed selection by primary pollinators on floral traits. For example, Lobo et al. (2005) found for the bat-pollinated tree *Ceiba pentandra* that high outcrossing rates predominate in regions with high pollinator visitation, while in environments with low pollinator visitation, trees changed to a mixed mating system with high levels of self-pollination.

Differences in efficiency among groups might be associated with differences in floral display, visitation rates, and pollinator behavior. It may be expected that bat- and bird-pollinated species allocate more resources per flower than bee-pollinated species (i.e., flowers are larger and have higher amounts of reward). At the same
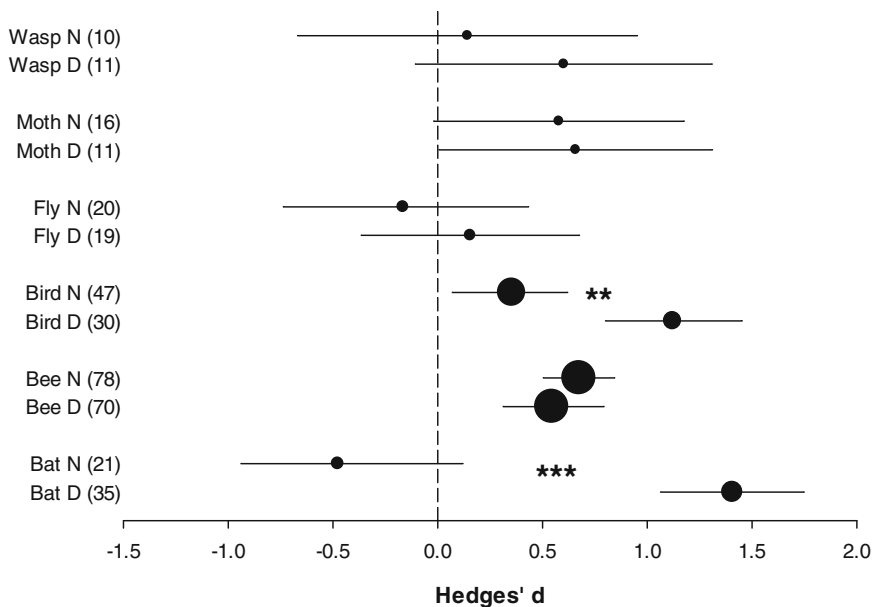
Fig. 11.4 Weighted-mean effect sizes and 95 % bias-corrected confidence intervals of the predictability of pollination syndromes on the most effective pollinators for plants with traits associated with higher predictability of pollination syndromes. Dependent (*D* self-incompatible, monoecious, and dioecious) and non-dependent (*N* self-compatible) species. Sample sizes for each category are shown in parentheses. The size of each dot represents the proportional 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. Asterisks indicate significance level at *p* < 0.05 associated with Qbetween-values for each group comparison

time, due to the smaller population sizes of birds and bats compared to bees, in general, visitation frequency of bat and bird flowers should be lower compared to bees which in turn might be related to lower fruit set (e.g., *Costus*, Kay and Schemske 2003; bee-pollinated Malvaceae, Spira et al. 1992, bat-pollinated Malvaceae, Quesada et al. 2004). Given the cost of producing large flowers and low pollinator visitation rates, a high efficiency per visit would be expected in pollinator-dependent plants pollinated by bats and birds. In non-dependent species, autonomous self-pollination as a reproductive assurance mechanism is expected to be more important. In contrast, bee-floral syndrome species should have larger floral displays and higher visitation rates, but since bees collect pollen to feed their brood, bee visits may be equally or less efficient than those of bats and birds (Thomson and Wilson 2008). Therefore, for bee-syndrome species, both dependent and non-dependent plants should have similar chances of getting pollinated and selection on floral traits may not differ between different breeding systems. Overall, our results suggest that pollinator-mediated selection on suites of floral traits may be stronger on outcrossing species pollinated by highly mobile organisms, in which fitness would be highly dependent on effective visits by pollinators.

11.7 Fifth Hypothesis: Predictability of Pollination Syndromes Differs Between Tropical and Extra-Tropical Plant Species

Floral syndromes predicted the most effective pollinators in species from tropical regions than in species from other regions, suggesting that interactions with effective pollinators generate stronger selection on floral traits in the tropics (Rosas-Guerrero et al. 2014). Some associations between pollination syndromes and geographical region in our dataset are worth mentioning. Plant species with bat syndrome were mainly from tropical regions, while species with fly and wasp syndromes were mostly found in extra-tropical regions (Figs. 11.1 and 11.5).

Bats, birds, and bees were significantly more effective pollinators of their predicted floral syndromes in plants from the tropics than in plants from temperate regions, but there were no differences for the wasp, moth, and fly syndromes (Fig. 11.5). Many species from the former pollinator groups have evolved specialized relations with their host plants in tropical regions. Interestingly, the areas with the highest number of chiropterophilous columnar cacti and of bat pollinator species in Mexico overlap (Valiente-Banuet et al. 1996). Additionally, specific evolutionary relationships have
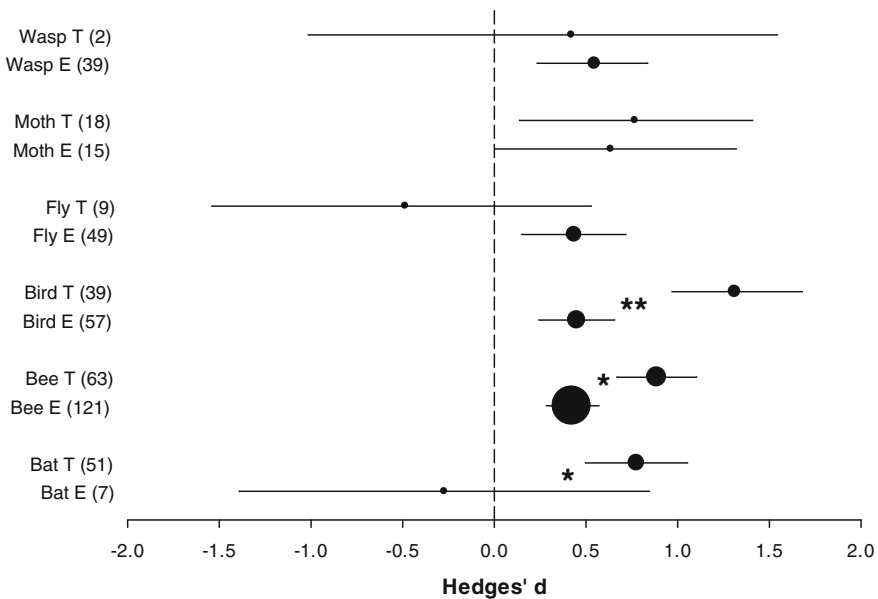

Fig. 11.5 Weighted-mean effect sizes and 95 % bias-corrected confidence intervals of the predictability of pollination syndromes on the most effective pollinators for plants belonging to tropical (*T*) and extra-tropical (*E*) regions. The size of each dot represents the proportional weight or contribution 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. *Asterisks* indicate significance level at $p < 0.05$ associated with $Q_{between}$-values for each group comparison

arisen between euglossine bee species and fragrance-producing orchid species (Ramírez et al. 2011), and oil- and resin-producing flowers and bees (e.g., *Dalechampia* spp. pollinated by *Eulaema* and *Eufriesea* bees, Armbruster 1993; Malpighiaceae pollinated by *Centris* bees, Sigrist and Sazima 2004).

The fact that floral syndromes best predicted the most effective pollinators in the tropics may be attributed to stronger biotic interactions and narrower niches (Mittelbach et al. 2007; Schemske et al. 2009). Selection to reduce niche overlap may be reflected in the non-overlapping flowering phenologies of various groups of tropical plants. For example, Bombacaceous trees at different tropical sites maintain similar flowering phenologies and sequential flowering at each site, which possibly maintains a steady supply of floral resources for pollinators promoting pollinator fidelity (Lobo et al. 2003; Rosas-Guerrero et al. 2014). These phenological patterns may allow selection on floral traits associated with effective and constant functional groups of pollinators (Janzen 1967).

Another possible explanation for the stronger association between floral syndromes and the most effective pollinators is that, in general, tropical plant taxa have had a longer evolutionary history than temperate taxa (Hawkins et al. 2011; Kerkhoff et al. 2014). For example, some temperate plant taxa (e.g., originally placed in families Apocynaceae, Apiaceae) are derived from plant lineages that originated in the tropics (e.g., Asclepiadaceae and Araliaceae, respectively; Judd et al. 1994). Therefore, tropical plant species may have had more time to experience selection by particular pollinators than their temperate counterparts.

Studies based on visitor assemblages that analyze specialization between geographical regions (e.g., Ollerton et al. 2009; Schleuning et al. 2012) are not directly comparable with our review, because they did not quantify the effectiveness of all floral visitors and frequent floral visitors are often poor pollinators (Fenster et al. 2004; King et al. 2013). Our approach allowed demonstrating that globally, pollinators expected by the syndromes are indeed the most efficient, among other pollinators. Our results significantly contrast with the findings of Ollerton et al. (2009) who found support for pollination syndromes for around 30 % of plants of six communities and stated that tropical communities did not exhibit greater predictability of pollination syndromes than temperate communities. Ollerton et al.'s conclusions are rather limited because they consider floral visitors of a subset of plant species from each community. Furthermore, their approach resulted in the evident mis-assignment of syndromes to many species of known floral syndromes, such as a fly syndrome to specialized resin-producing *Dalechampia*; and bee syndrome to *Heliconia* spp. The appropriateness of assignments can not be assessed due to the lack of taxonomic resolution of their dataset. Additionally, the lack of nocturnal pollinator observations in Ollerton et al.´s study would undoubtedly have caused disagreement between assigned moth or bat pollination syndromes and the observed floral visitors. While these authors argue to present a worldwide review of pollination syndromes, they only analyzed three tropical communities, mainly under disturbed conditions, with biased sampling effort against tropical communities that resulted in a large number of species without pollinator observations, and an extremely limited plant species taxonomic identification effort, which unfortunately precludes a real comparison between tropical

and temperate plant species. Last, Ollerton et al. (2009) did not include the major tropical biomes such as mature tropical rain or tropical dry forests and had an extremely limited sampling of important tropical life forms such as trees, epiphytes, and lianas. Our study is based on a representative sample of tropical and temperate natural communities, and therefore, we are confident in stating that pollinators expected by the syndrome are in fact better predicted in tropical than in temperate plant communities, indicating stronger selection on floral traits in the tropics.

11.8   Conclusions and Future Directions

In this study, we found that within each syndrome, there is greater predictive accuracy of the syndrome when only primary pollinators are involved than when secondary pollinators are present. However, the occurrence of secondary pollinators does not contradict the evolution of pollination syndromes, among other reasons, because the most frequent secondary pollinator was also the least efficient one. All pollination syndromes had species with 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 and Hodges 2007).

The only group of plants able to filter effectively secondary pollinators was the long-tongued fly-syndrome flowers (Rosas-Guerrero et al. 2014). Nevertheless, about 30 % of plant species were exclusively visited by the syndrome pollinator functional group. Exclusion of secondary pollinators would be favored by greater costs than benefits of secondary pollinators. In terms of the pollen presentation theory (Thomson 2003), the current lack of secondary pollinators in those species indicates that the marginal gain in fitness derived from secondary pollinator visitation is less than the costs to those plants in terms of lost mating opportunities and wasted rewards on visitors that do not contribute to the plant's fitness. However, the fitness landscape is bound to fluctuate with time and across environments. Many factors may influence the reliability of primary pollinators including climatic events and natural and anthropogenic disturbance (e.g., droughts, storms, hurricanes, pesticides) (Aguilar et al. 2006; Winfree et al. 2009; Goulson et al. 2015). An increase in the relative frequency of less vulnerable secondary pollinators could have evolutionary consequences for the plants (Thomson and Wilson 2008).

Widespread current human-induced disturbances often modify species distributions, abundance, composition, and biotic interactions. In mutualistic plant–pollinator relationships developed through evolutionary time, differential species-specific responses to human disturbances may alter original species matching by triggering changes at different levels, involving new temporal and spatial species distributions, and/or new physiological and morphological responses (Aizen and Vázquez 2006). Such new outcomes can modify the strength of interactions and promote novel plant–pollinator relationships (Aizen et al. 2008;

Tylianakis et al. 2008). Thus, under changes driven by human activities, we expect changes in pollinator-mediated selection on floral traits.

Incipient but consistent evidence indicates that human disturbances affect the composition of pollinator assemblages, their visitation rates to flowers, and/or their foraging behavior and efficiency (e.g., Aguilar et al. 2006; González-Varo et al. 2009; Parsche et al. 2011). For most flowering plants, such changes will have direct effects on their mating patterns (Aguilar et al. 2008), which may trigger the development of novel reproductive strategies to cope with new scenarios, which in turn may influence the evolution of floral traits. Plant species unable to exploit or to develop new interactions or alternative reproductive strategies will increase their local extinction probabilities (Biesmeijer et al. 2006; Anderson et al. 2011).

Furthermore, as a consequence of increased human mobility, habitat transformation, and global change, many species of plants and animals are increasing or shifting their distribution ranges, and some of them can become invasive in new habitats (Simberloff et al. 2013). Invasive plants may not only lose their natural enemies, but also some of their natural mutualists. This scenario may increase the importance of alternative pollinators, and depending on the relative rates of migration of the plants and their primary pollinators, it could lead to an evolutionary shift in primary pollinators.

A similar case is that of invasive pollinator species. For instance, as the Africanized bee expanded its range, it could have become an important secondary or even primary pollinator of many species. Apart from bee-syndrome plants, Africanized bees might easily exploit some bird-, fly-, and bat-syndrome plants (Fig. 11.3). Africanized bees have become as or more efficient than native pollinators of the herb *Kallstroemia grandiflora* (Zygophyllaceae), the prominent Amazonian tree *Dimizia excelsa* (Fabaceae), the South American tree *Tibouchina granolas* (Melastomataceae), and certain crops such as tomato (Osorio-Beristain et al. 1997; Dick 2001; Macias-Macias et al. 2009; Brizola-Bonacina et al. 2012).

A requisite for invasiveness of a plant species is its ability to use the resources in the novel environments to its favor in demographic terms. To become invasive, an animal-pollinated plant would have to be preadapted to the pollinator fauna of the novel environment and would be seen as rapidly integrated into that network (Lopezaraiza-Mikel et al. 2007). Further adaptation to a bee syndrome or floral specialization of invasive plants that would augment the efficiency of pollination by Africanized bees has not been documented yet, but cases in which invasive plant species are able to use the services of invasive pollinators have been documented (Beavon and Kelly 2012) and could be common. Neither of the above scenarios is exclusive of one another. Thus, one could hypothesize that the importance of secondary pollinators for a given plant (and even for plants of a given syndrome) is a function of the magnitude by which primary pollinators are differentially negatively affected by factors that fluctuate in time and across environments relative to secondary pollinators.

Here, we have found that the combinations of flower traits known as "floral syndromes" are significantly shaped by the most efficient pollinator functional group. However, most plant species are also visited by several animals with

different pollination efficiencies. Under changing environments sustained in time, the most efficient pollinator functional group may no longer prevail and its role may be taken up by another pollinator functional group. The increased relative contribution to effective pollination exerted by a different functional group can impose a potential venue to drive novel evolutionary changes in floral traits, eventually modifying floral syndromes in novel environments. Such possibility may be more feasible for plant species originally interacting with more than one functional group, that is, around 70 % of the plant species in our study, whereas plants interacting with mainly a single pollinator functional group (e.g., long-tongued fly syndrome) may sustain their syndrome by the presence of one or some species of the same functional group (redundant), and depending on its breeding system (more or less dependent on animal pollination), it will survive or perish in disturbed habitats. Here, we have presented for the first time, evidenced-based clues of the most probable venues or candidates of pollinator transitions for each pollination syndrome in currently changing environments.

Should disturbance-induced extinction probabilities differ among pollinator's functional groups, we may predict decreases in floral syndrome diversity. Certain ecological traits of animal pollinators such as their mobility capacity, niche breadth, life cycle requirements, or reproductive capacity may help to predict which functional types will be more likely to disappear (Alanen et al. 2011). For example, insect pollinators such as beetles, butterflies, and moths require different resources from multiple habitat types during their life cycle, and therefore, habitat disturbance may reduce populations of these animals, in some cases to the point of extinction (Alanen et al. 2011). Absent pollinator functional groups in novel environments will loosen their influence on their plant partners, which in turn may switch their "attention" to other functional groups. In contrast, more mobile or social functional groups such as birds, bats, and certain bees may be more resilient to habitat disturbance (Winfree et al. 2009; Phillips et al. 2010, but see Anderson et al. 2011) and potentially predominate as pollinators and agents of selection. However, a more realistic scenario should consider the likelihood of both, syndrome transitions and extinctions of functional groups of pollinators. Empirical evidence around these ideas is scant, but they certainly deserve research attention to achieve a better understanding of the potential future of floral evolution.

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