

Relationship between floral traits and floral visitors in two coexisting *Tecoma* species (Bignoniaceae)

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Abstract In this paper, we studied the floral biology of *Tecoma fulva* ssp. *garrocha* and *T. stans* in Vaqueros (Salta, Argentina), where both species coexist. We tested the idea that floral traits are associated with the pollinator types that visit them. According to our results, *T. fulva* ssp. *garrocha* presented traits common to bird flowers and were visited by two species of Trochilidae (*Colibri serrirostris* and *Chlorostilbon lucidus*). In addition, *T. stans* exhibited traits common to hymenoptera flowers and were visited principally by *Apis mellifera* and *Bombus atratus*. This study showed that floral traits are predictive of animal visitors.

Keywords Bees · Bignoniaceae · Hummingbirds · Floral traits · Pollination syndromes · *Tecoma*

Introduction

A common idea in pollination biology is that plant–pollinator interactions are specialized. Therefore, we should find strong relationships between floral traits and pollinators (Faegri and van der Pijl 1971). Comparative biology has provided evidence of the convergent evolution of floral traits (Alcantara and Lohmann 2010; Fenster et al. 2004; Goldblatt et al. 2004; Johnson et al. 1998; Pérez et al. 2006). These studies have linked floral traits to specific

pollinator types, supporting the idea that floral phenotypes are the result of convergent selection pressures exerted by a given pollinator. However, many studies have shown that a taxonomically diverse assemblage of pollinators can visit and pollinate the same plant species (Eckhart 1992; Gómez and Zamora 1999; Gómez 2002; Herrera 1996; Ortega-Baes et al. 2011; Waser et al. 1996). Those visitors can vary in abundance, flight distance, and pollen load (Waser et al. 1996), thus their effectiveness as pollinators can vary spatially and temporally, favoring generalized interactions (Gómez 2002; Herrera 1996; Ollerton et al. 2007). Ollerton et al. (2007) discussed the different ways in which a flower can be a generalist, distinguishing between functional and ecological generalization. At community level, some studies have reported significant relationships (partial or total) between pollinators and floral traits (Dicks et al. 2002; Hingston and McQuillan 2000; Lázaro et al. 2008), whereas others have shown nonsignificant relationships (Hegland and Totland 2005; Herrera 1988; Ollerton et al. 2009).

Fenster et al. (2004) have suggested that the relationship between floral traits and pollinators can be better understood if the latter are studied as functional groups, because they exert similar selective pressures and they share common preferences and behaviors. Consequently, the effectiveness of pollination for each functional group varies according to the different floral phenotypes (Castellanos et al. 2004; Fenster et al. 2004; Wilson et al. 2004). Wilson et al. (2004) evaluated the relationship between floral phenotypes and functional groups in *Penstemon* species. These authors recognized two floral phenotypes, “hymenoptera flowers” and “bird flowers.” In their study, the former were yellow or violet, presented with nectar guides, landing platforms, horizontal positioning, and large staminodes and were pollinated by bees. Bird flowers could only be differentiated by corolla color.

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In this context, we have studied the floral biology of two coexisting *Tecoma* species, *Tecoma fulva* ssp. *garrocha* (Hieron.) J.R.I. Wood and *Tecoma stans* (L.) Juss. ex Kunth. The former species has tubular red-orange flowers that resemble bird flowers, whereas *T. stans* has yellow flowers that resemble hymenoptera flowers (*sensu* Wilson et al. 2004). These floral phenotypes would correspond with Martinella and Anemopaegma, two floral types that were described by Gentry (1974) for Bignoniaceae and which were associated with hummingbirds and bees, respectively (Gentry 1974). We believe that coexisting related species with different floral types enable the assessment of floral traits that may be predictive of pollinator types. If floral traits facilitate or restrict the visit of some animals, then plant species with different floral types would be visited by only a part of the local community of potential pollinators, which would differ among species. Specifically, we answer the following questions: (1) How phenotypically different are *T. fulva* ssp. *garrocha* and *T. stans* flowers? (2) Do the floral traits of *T. fulva* ssp. *garrocha* actually correspond with bird flowers and those of *T. stans* with hymenoptera flowers according to Wilson et al. (2004)? and (3) Do floral visitors correspond with these floral phenotypes?

Materials and methods

Study area

The study was conducted in Vaqueros (Salta, Argentina; 24°51'59"S; 65°21'57"W). The climate in this region is subtropical with mean annual rainfall of 652 mm (Bianchi and Yañez 1992). Mean temperature in January (summer) and July (winter) is 21.9°C and 10.5°C, respectively (Bianchi 1996). In the study area, vegetation corresponds to transition vegetation between the Yungas and Chaco phytogeographic regions, with species of the *Acacia*, *Cestrum*, *Oenothera*, *Zinnia*, *Macroptilium*, *Baccharis*, *Echinopsis*, and *Gymnocalycium* genera. In this area, *Tecoma fulva* ssp. *garrocha* blossoms from September to December, whereas *Tecoma stans* does so from November to December.

Floral traits and floral visitors

In Fig. 1, the floral phenotypes of the two species studied are shown. The following floral traits: corolla length, corolla diameter, stamen length, stigma length, and sugar concentration, were recorded for 15 flowers (in 15 individuals, one flower per individual) of each species. Stamen length corresponds with the measurement of the longer stamens, taken from the base of the corolla (i.e., total stamen length). We registered sugar concentration with a

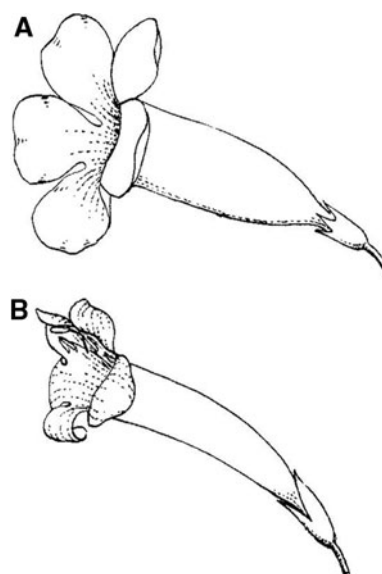


Fig. 1 Floral phenotypes of studied *Tecoma* species: (a) *Tecoma stans* and (b) *Tecoma fulva* ssp. *garrocha*. The *Tecoma stans* flower presents a corolla with vestibular form, non-reflected corolla lower lips, and the stamens included in the corolla, whereas the *Tecoma fulva* ssp. *garrocha* flower has a corolla with tubular form, reflected corolla lower lips, and exerted stamens

handheld Brix refractometer as a measure of nectar dilution grade. We classified flowers according to: corolla phenotype (tubular, vestibular; Wilson et al. 2004), corolla lower lip reflection (coded on 1–4 scale; Wilson et al. 2004), position of anthers with relation to corolla lips (exerted or included), and color (coded on 1–4 scale; Wilson et al. 2004). Corolla lower lip reflection ranged from completely extended (value 1) to completely retracted (value 4; Wilson et al. 2004). Color ranged from yellow (value 1; associated with hymenoptera pollination) to red (value 4; associated with bird pollination).

Floral visitors were recorded by focal observations. For both species, they were conducted on three flowers every 2 h for 30-min periods from 08:00 to 18:00 h, during three nonconsecutive days in November. Observations were carried out the same days for both species. Previous to the visits sampling, insects visiting nonfocal flowers were collected by hand using a net and identified in the laboratory. Birds were identified through binoculars with the aid of a field guide (Narosky and Izurieta 2003).

Statistical analyses

We carried out multivariate analysis of variance (MANOVA) to analyze whether floral phenotypes differ between species. This analysis was performed with the following floral traits: corolla length, corolla diameter, stamen length, stigma length, and sugar concentration. In addition, we performed a *t* test for each floral trait to evaluate if there

were differences between the two floral phenotypes. Floral visitors of *Tecoma* species were compared using a chi-square homogeneity test. Statistical analyses were conducted using the statistical program InfoStat (2009).

Results

Floral traits

Tecoma stans had a corolla length of 40.62 ± 4.30 mm. Corolla diameter was 13.21 ± 1.59 mm. In this species, flowers were monoclones and had four stamens and one staminode. Stamen length was 20.93 ± 3.26 mm, and stigma length was 30.73 ± 3.45 mm. Sugar concentration was 30.63 ± 2.14 (grade Brix). *T. stans* had yellow (score 1 on the scale) flowers with vestibular phenotypes and no reflections of the corolla lower lips (score 1 on the scale). The stamens were included in the corolla (Fig. 1a).

Tecoma fulva ssp. *garrocha* had a corolla length of 52.39 ± 2.12 mm, and corolla diameter was 7.13 ± 0.87 mm. Flowers were monoclones and presented four stamens and one staminode. Stamen length was 49.43 ± 2.44 mm, and stigma length was 51.06 ± 2.44 mm. Sugar concentration was 27.88 ± 2.69 (grade Brix). This species had red-orange (score 3 on the scale) flowers with tubular phenotypes and reflections of the corolla lower lips (score 4 on the scale). As corolla lower lips were retracted, the stamens were considered exerted (Fig. 1b).

According to MANOVA, the two floral phenotypes were significantly different ($F = 133.97$, $gl = 4$, $P < 0.0001$). We registered significant differences for each variable (stamen length: $t = 2.34$, $P < 0.0001$; stigma length: $t = 16.54$, $P < 0.0001$; corolla diameter: $t = -16.25$, $P < 0.0001$; corolla length: $t = 8.52$, $P < 0.0001$; sugar concentration: $t = -3.08$, $P = 0.0046$).

Floral visitors

The flowers of *T. fulva* ssp. *garrocha* were visited by two hummingbirds (*Colibri serrirostris* and *Chlorostilbon lucidus*) and two bees (*Bombus atratus* and *Apis mellifera*). *Tecoma stans* flowers were visited by three hymenopteran species (*Apis mellifera*, *Bombus atratus*, and *Xylocopa* sp.) and one hummingbird (*Chlorostilbon lucidus*). Visit proportion of floral visitors differed between *Tecoma* species ($\chi^2 = 147.519$, $P < 0.0001$). For *T. fulva* ssp. *garrocha* the highest visit proportion (0.6) corresponded to *C. serrirostris*, followed by *C. lucidus* with 0.24. They visited the flowers from sunrise. *Apis mellifera* was an infrequent visitor (visit proportion: 0.16; Table 1). *Bombus atratus* behaved as a nectar thief, lacerating the corolla. For *T. stans*, the highest visit proportion (0.81) corresponded to *A. mellifera*. In this

Table 1 Visit proportion (VP) of animal visitors to *Tecoma fulva* ssp. *garrocha* and *Tecoma stans* flowers at Vaqueros (Salta, Argentina)

Floral visitor	<i>Tecoma fulva</i> ssp. <i>garrocha</i>	<i>Tecoma stans</i>
<i>Apis mellifera</i>	0.16 (0.16 \pm 0.01)	0.81 (0.71 \pm 0.24)
<i>Bombus atratus</i>	0	0.14 (0.19 \pm 0.13)
<i>Chlorostilbon lucidus</i>	0.24 (0.23 \pm 0.06)	0.03 (0.07 \pm 0.11)
<i>Colibri serrirostris</i>	0.60 (0.61 \pm 0.05)	0
<i>Xylocopa</i> sp.	0	0.03 (0.03 \pm 0.02)

VP was calculated from the number of visits registered for each animal species, in 3 days. Mean \pm standard deviation (SD) proportion of visits per day is expressed in parentheses

species, we observed *C. lucidus* visiting the flowers at sunrise; however, their visit proportion was low (0.03; Table 1).

Discussion

According to our results, the flowers of the two species were differentiated by quantitative and qualitative traits. *Tecoma fulva* ssp. *garrocha* was characterized by red-orange flowers with long narrow corolla with lower lip reflections. In addition, *Tecoma stans* showed yellow flowers and vestibular corolla with extended lower lips. The features of *Tecoma fulva* ssp. *garrocha* have been described as typical of bird flowers, whereas the features of *Tecoma stans* were typical of hymenopteran flowers (Thomson et al. 2000; Wilson et al. 2004). It has been reported that corolla color is the most important feature enabling differentiation of bird flowers from bee flowers (Thomson et al. 2000; Wilson et al. 2004). We also registered that this trait is important, although other morphological characteristics allowed us to differentiate between the two flowers as well. Furthermore, we observed differences in sugar concentration between species. *Tecoma fulva* ssp. *garrocha* had more dilute nectar than *T. stans*, as has been reported for other plant species with bird flowers (Fenster et al. 2006; Nicolson and Fleming 2003; Pyke and Waser 1981; Stiles and Freeman 1993).

The results show that floral traits are predictive of main floral visitors (or functional groups *sensu* Fenster et al. 2004); however, they also indicate that other floral visitors, distinct from those expected, can visit flowers. Although we have not evaluated the ability of floral visitors to remove pollen from anthers and deposit it on stigmas, a positive relationship between visit rate and pollinator service has already been indicated (Price et al. 2005). *Tecoma fulva* ssp. *garrocha* flowers were mainly visited by hummingbirds (*Colibri serrirostris* and *Chlorostilbon lucidus*) and occasionally by *Apis mellifera* and *Bombus atratus*.

We observed the exotic bee foraging only pollen from anthers and the bumblebee damaging the corolla tube to steal nectar. The visit of pollen-collector bees to bird flowers may be because the anthers are exerted and present pollen more generously (Thompson et al. 2000; Wilson et al. 2004). The behavior of *Bombus* as a nectar thief is a common phenomenon related to the impossibility of having access to nectar in narrow tubular corollas. Nectar thieves affect pollinator behavior and reduce the female fitness of the plants (Irwin and Brody 1998; Irwin et al. 2001; Urcelay et al. 2006). In addition, *T. stans* flowers were mainly visited by bees (*Apis mellifera*, *Bombus atratus*, and *Xylocopa* sp.) and occasionally by hummingbirds. We did not evaluate the effectiveness of the floral visitors, and thus future studies should aim to answer whether pollen-collector bees are effective pollinators of *T. fulva* ssp. *garrocha* flowers and whether hummingbirds can effectively pollinate *T. stans* flowers. Mayfield et al. (2001) have reported that bird flowers of *Ipomopsis aggregata*, a hummingbird-pollinated species, can also be effectively pollinated by long-tongued bumblebees. Besides, it has been indicated that hummingbirds remove pollen from the anthers of bee flowers efficiently, though the amount of pollen that they deposit is lower than that deposited by bees (Wilson et al. 2006).

Thomson et al. (2000) have discussed *Penstemon* specialization to bee and bird pollination in the context of pollen presentation theory. They suggested that the most effective pollinators are those that deposit more of the pollen than they remove. Due to their high rate of visits, bees remove more pollen than they deposit; therefore, bee-pollinated plants should dose the pollen to minimize pollen wastage. On the other hand, bird-pollinated plants should present anthers that open quickly and widely, because birds behave as low-removal high-deposition visitors. Since in these plants pollen is exposed for removal by hummingbirds as well as by pollen-collector bees, there should be other plant traits reducing losses to pollen collectors. In this sense, Thomson et al. (2000) have predicted that ornithophilous *Penstemon* species would produce nectar and present pollen early in the day, when only hummingbirds are active in the flowers. This could be expected in *Tecoma fulva* ssp. *garrocha*, since hummingbirds also visited the flowers earlier than bees.

In the studied system, *Apis mellifera* was the most frequent visitor to *T. stans* flowers and the only bee registered collecting pollen from *T. fulva* ssp. *garrocha* flowers. We do not know the effects of honeybees on the sexual reproduction of these species. Some studies have indicated that this bee can be as effective a pollinator as native bees. However, other studies have shown that honeybee activity affects sexual reproduction of native

plants, altering their population structure (Aizen and Feinsinger 1994; Freitas and Paxton 1998; Goulson 2003; Gross and Mackay 1998).

Our results confirm the previous idea that studied species correspond with Martinella and Anemopaegma floral types, two of the ten floral types proposed by Gentry (1974) for Bignoniaceae. Alcantara and Lohmann (2010) reported that pollination systems in the Bignoniaceae tribe (Bignoniaceae) have evolved from the Anemopaegma floral type, with several shifts in floral morphology leading to both generalized and specialized pollination systems. These authors have indicated that certain floral traits have had high evolutionary lability in this lineage. They have also proposed that the functional relationships between flowers and pollinators played a significant role in the morphological diversification of the Bignoniaceae tribe, and that bird flowers (Martinella floral types) represent evolutionary dead-ends in this tribe. If these patterns in floral evolution are common to the lineage in which *Tecoma* is included, then bird flowers would have evolved from bee flowers. Integrated studies on the reproductive biology of the *Tecoma* genus (or more adequately for the Tecomaeae tribe) are necessary to understand the evolution of pollination systems in this lineage. These studies should evaluate not only floral morphology but also the way in which this morphology corresponds with the animals that effectively pollinate the flowers. *Tecoma* is a relatively small genus with approximately 14 species distributed in the Neotropics, from the Southwestern USA to Andean South America (Olmstead et al. 2009; Wood 2008). The remaining *Tecoma* species have yellow or red-orange flowers with morphological traits resembling those registered for *T. stans* and *T. fulva* ssp. *garrocha*, respectively (Wood 2008). We hypothesize that the *Tecoma* species with yellow flowers would correspond to bee flowers, while those with red-orange flowers would correspond to bird flowers. A noteworthy observation is that the *Tecoma* species can hybridize, and this may be due to the behavior of pollinators (Wood 2008). We did not find hybrids in our study site; however, this could occur if the occasional visitors were effective pollinators, i.e., bees pollinate *T. fulva* ssp. *garrocha* flowers, and hummingbirds pollinate *T. stans* flowers. Further studies on the reproductive biology of hybrids and their parents should be carried out to discern the extent of specialization or generalization of the pollination systems in the *Tecoma* genus.

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References

- Aizen MA, Feinsinger P (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75:330–351
- Alcantara S, Lohmann LG (2010) Evolution of floral morphology and pollination system in Bignoniaceae (Bignoniaceae). *Am J Bot* 97:782–796
- Bianchi AR (1996) Temperaturas medias estimadas para la región noroeste de Argentina. INTA, Salta, Argentina
- Bianchi AR, Yañez CE (1992) Las precipitaciones en el noroeste argentino. INTA, Salta, Argentina
- Castellanos MC, Wilson P, Thomson JD (2004) Anti-bee and pro-bird changes during the evolution of hummingbird pollination in *Penstemon* flowers. *J Evol Biol* 17:876–885
- Dicks LV, Corbet SA, Pywell RF (2002) Compartmentalization in plant–insect flower visitor webs. *J Anim Ecol* 71:32–43
- Eckhart V (1992) Spatio-temporal variation in abundance and variation in foraging behavior of the pollinators of gynodioecious *Phacelia linearis* (Hydrophyllaceae). *Oikos* 64:573–586
- Faegri K, van der Pijl L (1971) The principles of pollination ecology. Pergamon, USA
- Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and floral specialization. *Ann Rev Ecol Syst* 35:375–403
- Fenster CB, Cheely G, Dudash MR, Reynolds RJ (2006) Nectar reward and advertisement in hummingbird-pollinated *Silene virginica* (Cariophyllaceae). *Am J Bot* 93:1080–1087
- Freitas BM, Paxton RJ (1998) A comparison of two pollinators: the introduced honey bee *Apis mellifera* and an indigenous bee *Centris tarsata* on cashew *Anacardium occidentale* in its native range of NE Brazil. *J Appl Ecol* 35:109–121
- Gentry AH (1974) Coevolutionary patterns in Central American Bignoniaceae. *Ann Mo Bot Gard* 61:259–728
- Goldblatt P, Nänni I, Berhardt P, Manning JC (2004) Floral biology of *Hesperantha* (Iridiaceae: Crocoideae): how minor shifts in floral presentation change the pollination system. *Ann Mo Bot Gard* 91:186–206
- Gómez JM (2002) Generalización en la interacciones entre plantas y polinizadores. *Rev Chil Hist Nat* 75:105–116
- Gómez JM, Zamora R (1999) Generalization vs. Specialization in the pollination system of *Hormathophylla spinosa* (Cruciferae). *Ecology* 80:796–805
- Goulson D (2003) Effects of introduced bees on native ecosystems. *Annu Rev Ecol Syst* 34:1–26
- Gross CL, Mackay D (1998) Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biol Conserv* 86:169–178
- Hegland SJ, Totland Ø (2005) Relationships between species' floral traits and pollinator visitation in a temperate grassland. *Oecology* 145:586–594
- Herrera J (1988) Pollination relationships in southern Spanish Mediterranean shrublands. *J Ecol* 76:274–287
- Herrera CM (1996) Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In: Lloyd DG, Barrett SCH (eds) *Floral biology: studies on floral evolution in animal-pollinated plants*, 1st edn. Chapman & Hall, New York, pp 140–190
- Hingston AB, McQuillan PB (2000) Are pollination syndromes useful predictors of floral visitors in Tasmania? *Austral Ecol* 25:600–609
- InfoStat (2009) InfoStat versión 2007. Grupo InfoStat. FCA, Universidad Nacional de Córdoba, Argentina
- Irwin RE, Brody AK (1998) Nectar robbing in *Ipomopsis aggregata*: effects on pollinator behaviour and plant fitness. *Oecology* 116:519–527
- Irwin RE, Brody AK, Waser NM (2001) The impact of floral larceny on individuals, populations, and communities. *Oecology* 129:161–168
- Johnson SD, Linder PH, Steiner KE (1998) Phylogeny and radiation of pollination systems in *Disa* (Orchidaceae). *Am J Bot* 85:402–411
- Lázaro A, Hegland S, Totland Ø (2008) The relationships between floral traits and specificity of pollination systems in three Scandinavian plant communities. *Oecology* 157:249–257
- Mayfield MM, Waser NM, Price MV (2001) Exploring the most effective pollinator principle with complex flowers: bumblebees and *Ipomopsis aggregata*. *Ann Bot* 88:591–596
- Narosky T, Izurieta D (2003) Guía para la identificación de las aves de Argentina y Uruguay. Vázquez-Mazzini, Argentina
- Nicolson SW, Fleming PA (2003) Nectar as food for birds: the physiological consequences of drinking dilute sugar solutions. *Plant Syst Evol* 238:139–153
- Ollerton J, Killick A, Lamborn E, Stella Watts, Whiston M (2007) Multiple meanings and modes: on the many ways to be a generalist flower. *Taxon* 56:717–720
- Ollerton J, Alarcón R, Waser NM, Price MV, Watts S, Cranmer L, Hingston A, Peter CI, Rotenberry J (2009) A global test of the pollination syndrome hypothesis. *Ann Bot* 103:1471–1480
- Olmstead RG, Zjhra ML, Lohmann LG, Grose SO, Eckert AJ (2009) A molecular phylogeny and classification of Bignoniaceae. *Am J Bot* 96:1731–1743
- Ortega-Baes P, Saravia M, Suhring S, Godínez-Alvarez H, Zamar M (2011) Reproductive biology of *Echinopsis terscheckii* (Cactaceae): the role of nocturnal and diurnal pollinators. *Plant Biol* 13:33–40
- Pérez P, Arroyo MTK, Medel R, Hershkovitz MA (2006) Ancestral reconstruction of flower morphology and pollination systems in *Schizanthus* (Solanaceae). *Am J Bot* 93:1029–1038
- Price MV, Waser NM, Irwin RE, Campbell DR, Brody AK (2005) Temporal and spatial variation in pollination of a montane herb: a seven-year study. *Ecology* 86:2106–2116
- Pyke GH, Waser NM (1981) The production of dilute nectar by hummingbird and honeyeater flowers. *Biotropica* 13:260–270
- Stiles GF, Freeman CE (1993) Patterns in floral nectar characteristics of some bird-visited plant species from Costa Rica. *Biotropica* 25:191–205
- Thomson JD, Wilson P, Valenzuela M (2000) Pollen presentation and pollination syndromes, with special reference to *Penstemon*. *Plant Species Biol* 15:11–29
- Urcelay C, Morales CL, Chalcoff VR (2006) Relationship between corolla length and floral larceny in the South American hummingbird pollinated *Campsidium valdivianum*. *Ann Bot Fenn* 43:205–211
- Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060
- Wilson P, Castellanos MC, Houge JN, Thomson JD, Armbruster SW (2004) A multivariate search for pollination syndromes among penstemons. *Oikos* 104:346–361
- Wilson P, Castellanos MC, Wolfe AP, Thomson JD (2006) Shifts between bee and bird pollination in Penstemons. In: Waser NM, Ollerton J (eds) *Plant-pollinator interactions: from specialization to generalization*, 1st edn. The University of Chicago Press, Chicago, pp 47–69
- Wood JRI (2008) A revision of *Tecoma* Juss (Bignoniaceae) in Bolivia. *Bot J Linn Soc* 156:143–172