RESEARCH PAPER

Pollination ecology of *Disterigma stereophyllum* (Ericaceae) in south-western Colombia

L. Navarro[1], P. Guitián[2] & G. Ayensa[1]

1 Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Vigo, Vigo, Spain
2 Departamento de Botánica, Facultad de Farmacia, Universidad de Santiago de Compostela, Santiago de Compostela, Spain

ABSTRACT

Several authors have recently expressed doubts that the 'pollination syndromes' as usually expressed are an adequate description of correlated suites of floral characters, or that they adequately describe evolutionary or ecological associations of plants with pollinators. *Disterigma stereophyllum* is a neotropical Ericaceae with floral characteristics intermediate between the 'entomophilous' syndrome and the 'ornithophilous' syndrome: the corolla is short, white and urceolate, but flowers produce large amounts of dilute nectar. We studied the pollination ecology of this species in south-western Colombia, and found it to be pollinated almost exclusively by hummingbirds at our study site. Two hummingbird species were responsible for about 75 of visits. Despite the fact that nectar standing crop remained more or less constant throughout the day, visit frequencies were highest in the morning and declined throughout the day. Pollinator efficiency, measured as the number of pollen grains deposited on a virgin stigma by each visitor after one visit, did not differ among the species of hummingbirds, but was lower for a nectar-robbing bird, *Diglossa albilatera*. This species does not contact the surface of the stigma during nectar robbing, but can produce some self-pollination indirectly because it shakes branches vigorously while piercing the flower. These findings indicate a need for further studies of neotropical Ericaceae in order to elucidate whether floral visitors of species like *D. stereophyllum* fluctuate through time or space, and whether floral characteristics reflect a compromise between such different visitors, or a transitional stage between pollination syndromes, or some other possibility.

INTRODUCTION

In the understorey of neotropical forests, hummingbird pollination is as frequent as that by medium to large bees (Bawa 1990). Although species of Ericaceae are prominent in tropical montane forests throughout the world, surprisingly little is known about their biology and ecology (Luteyn 1989). There have been relatively few studies of the breeding systems and pollination biology of neotropical Ericaceae (Melampy 1987; Murray *et al.* 1987; Murcia & Feinsinger 1996; Navarro 1999, 2001; Busby 2000; Kraemer 2001; Navarro *et al.* 2007). Within this family, many species show floral traits apparently adapted to hummingbird pollination (*i.e.* brightly coloured, long tubular flowers with inferior ovaries and abundant dilute nectar).

Several studies of Ericaceae in Colombian montane forest have shown that species of this type are indeed mainly pollinated by hummingbirds (Snow & Snow 1980; Navarro 1999; Busby 2000). Other neotropical ericads show floral traits apparently adapted to bee pollination (*i.e.* shorter, urceolate, white or light-coloured corollas) but, in spite of the commonness of such 'bee pollination syndrome' species, their pollination has received little attention (although see Snow & Snow 1980; Busby 2000).

Within the genus *Disterigma* there are species that appear to conform to the bee pollination syndrome, hummingbird pollination syndrome, or both. However, floral characteristics do not always correspond well to the observed pollinator spectrum. For example, *Disterigma alaternoides* has small, white flowers that produce small

amounts of concentrated nectar, suggesting mellitophily (bee pollination), but other floral traits such as rigid anthers attached to the outside of a nectariferous disk forming a tunnel leading to the nectar, inferior ovaries and scheduling of pollen delivery, suggest ornithophily (Snow & Snow 1980; see Thomson *et al.* 2000 for traits assigned to these pollination syndromes). In spite of these mixed characteristics, the species is reported to be entirely bee-pollinated in the Colombian Andes (Snow & Snow 1980). This example exemplifies the fact that whereas pollination syndromes (*sensu* Faegri & van der Pijl 1979) apply to some specific cases (*e.g.* Hargreaves *et al.* 2004; Wilson *et al.* 2006), many other studies of single species have failed to match the putative syndrome with predicted major pollinators (Ollerton *et al.* 2003; Zhang *et al.* 2005; Valdivia & Niemeyer 2006).

In the present study, we investigated the pollination ecology of the neotropical species *Disterigma stereophyllum* with the aim of assessing whether floral traits match its usual pollinator fauna. *D. stereophyllum* inhabits neotropical montane forest, with a distribution restricted to southern Colombia and northern Ecuador, and exhibits a mix of floral characteristics that suggests adaptation for pollination by both hummingbirds and bees (Navarro *et al.* 2007). Traits suggesting adaptation for hummingbirds include copious amounts of dilute nectar and the manner of pollen presentation, whereas the short, white, and urceolate corolla, together with its erect orientation suggest bee visitation.

STUDY AREA

The study was carried out in the La Planada Nature Reserve, near the village of Ricaurte (Nariño Department, Colombia) (1°10′ N, 77°58′ W) during March–April 1998. The reserve is located on the western flank of the Andes and comprises 3200 ha of montane wet forest (bmh-PM in the classification of Holdridge 1996), at altitudes ranging from 1200 to 2100 m above sea level. Mean annual precipitation is 4375 mm and temperature ranges between 12 and 23 °C. More information on the study area can be found in Orejuela (1987) and Restrepo & Gómez (1998).

PLANT NATURAL HISTORY

Disterigma stereophyllum (A. C. Sm.) Luteyn (Ericaceae) is an epiphyte. In the study area it typically occurs in fringe communities around mature forest. It has several flowering peaks over the year. Flowers are hermaphrodite, with a 9-mm long fleshy, white urceolate corolla with small purple lobes. Each flower has on average 362 ovules (ranging among 252–501). Flowers are protandrous and open for 4 days. The style is slightly exerted and extends beyond the anthers (Fig. 1). On average, flowers produce 48 μl of nectar per day, with a low-sugar concentration ($21.2 \pm 6.6\%$ w/w), and, except for pollen, this species did not present any other
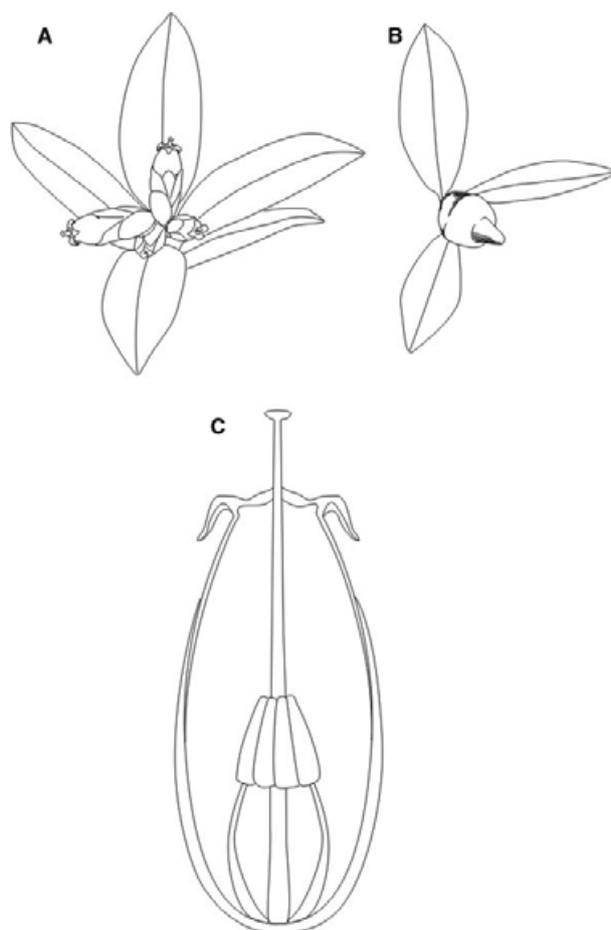

Fig. 1. Flowers (A) and fruits (B) of *Disterigma stereophyllum*, and a detailed cross-section of a flower (C).

floral reward. The species is cryptically self-incompatible (Navarro *et al.* 2007). The fruit, a translucent white berry when mature, is eaten by frugivorous birds (the golden tanager *Tangara arthus* and the orange-bellied euphonia *Euphonia xanthogaster*; L. Navarro, unpublished results). Voucher specimens of *D. stereophyllum* from the study site are deposited at the herbarium of the Universidad de Pasto (Nariño Department, Colombia).

METHODS

Standing crop of nectar

On three different days, we measured the amount of nectar available to visitors in the same areas in which we did pollinator censuses (see below). Just before each pollinator census, at 6:30, 8:30, 10:30, 12:30, 14:30 and 16:30 hours, we selected 10 flowers at random and extracted nectar with micropipettes. Sugar concentration in nectar was measured with a pocket refractometer. All measurements were made during dry weather.

Floral visitation

We censused flower visitors in two standard adjacent patches of plants of no more than 20 m² area, each of which could be easily observed from a distance of about 4 m. All plants were at a height of <3 m. Both areas formed part of fringe communities around mature forest. The number of flowers ranged between 120 and 150 per patch during the censuses. We tallied visits during the month of March in a series of 60-min censuses at different times of the day, totalling 66 h, with equal effort at different times of day. For each visit, we recorded the species of visitor and the number of flowers probed. We also recorded type of visit (nectar extraction or primary nectar robbery if the visitor made a hole in the corolla tube; Inouye 1983). All visitors were identified with the aid of both field guides (Hilty & Brown 1986) and collections deposited at La Planada Nature Reserve.

Pollinator efficiency on pollen deposition

The day before each census, we bagged a number of virgin flowers on two or three plants. During each census, these flowers were unbagged, and, after a single visit, each pistil was collected to count the number of pollen grains deposited on the stigma by the visitor in question.

Nectar robbing

We examined a total of 1106 flowers from more than 70 plants across the flowering season, recording whether or not each flower had been robbed. Field determination of whether a flower has been robbed is straightforward, as the robber leaves a clearly visible incision in the corolla.

Data analysis

We used analysis of variance to compare nectar standing crops (volume and concentration) over time, the number of flowers visited by each visitor on arrival, and the number of pollen grains found on the stigma after each visit. All proportional data were arcsine-square root transformed before ANOVA. Number of pollen grains was transformed by square root (x + 0.5). All analyses were carried out with the statistical package Systat (1997). In the text, mean values are given with their standard errors.

RESULTS

Nectar properties

Nectar standing crop showed apparent alternation between observation periods (Fig. 2a), but analysis of variance did not reveal any significant among-period variation ($F_{5,54} = 1.9$; $P = 0.1019$). Sugar concentration of nectar varied significantly over the day ($F_{5,42} = 4.3$; $P = 0.0030$): *a posteriori* Tukey tests showed that concentration was significantly lower in the early morning than
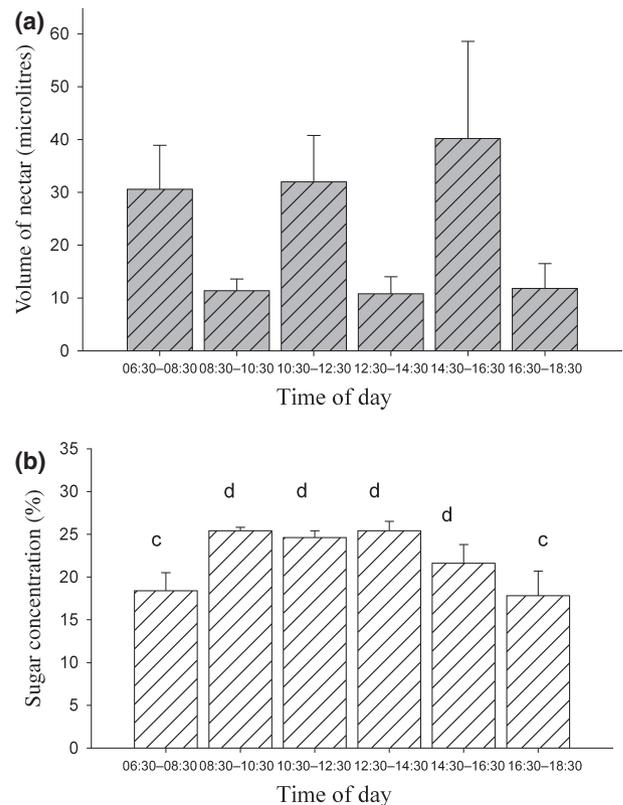
Fig. 2. Diurnal variation in nectar (a) volume and (b) concentration available to visitors of *Disterigma stereophyllum*. The bars represent mean values with standard errors (n = 10 different flowers per observation session). In (b) bars with the same letter do not differ significantly (multiple comparisons test).

at midday, and lower in the late afternoon than at midday (Fig. 2b).

Floral visitation

Disterigma stereophyllum was one of the most abundant nectar sources for nectarivorous birds at La Planada during the study period (L. Navarro, unpublished results). Flowers of *D. stereophyllum* were visited by a diverse guild of visitors (Table 1). Of the 4178 recorded visits to individual flowers in both patches, 93.9% were 'legitimate' nectar extraction visits, while the remaining 6.1% were visits by primary nectar robbers (in all cases the white-sided flower-piercer *Diglossa albilatera*). We observed no secondary nectar-robbing visits. Thus, the ratio of legitimate visits to nectar-robbing visits was 15.4:1.

The most frequent legitimate visitor was the booted racket-tail (*Ocreatus underwoodii*), accounting for 49.5% of total visits, followed by the blue-tailed emerald (*Chlorostilbon mellisugus*), accounting for 24.8% of visits. Both of these hummingbird species have territorial behaviour, defending patches from visits by other hummingbirds. There was significant variation among pollinators in the
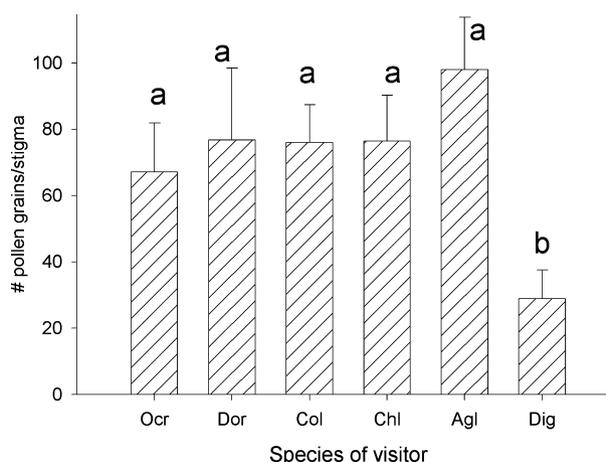
Table 1. Visitors to *Disterigma stereophyllum* in the study area. Number of floral visits for each of the two foraging modes and mean number (±SD) of flowers visited on each arrival.

species	type of visit	no. of visits (%)	no. of flowers visited
Aves			
Trochilidae			
Ocreatus underwoodii	P	2067 (49.5)	2.2 ± 3.7
Doryfera ludoviciae	P	70 (1.6)	11.7 ± 13.2
Colibri thalassinus	P	197 (4.7)	1.7 ± 2.0
Adelomyia melangenys	P	45 (1.1)	1.2 ± 0.4
Coeligena torquata	P	94 (2.4)	1.2 ± 0.6
Chlorostilbon mellisugus	P	1038 (24.8)	1.8 ± 2.1
Aglaiocercus coelestis	P	380 (9.1)	1.9 ± 3.6
Thraupidae			
Diglossa albilatera	R	256 (6.1)	2.6 ± 1.9
Diptera			
Diptera sp.	P	2 (0.05)	2.0 ± 0.0
Hymenoptera			
Bombus sp.	P	29 (0.7)	14.5 ± 14.9
Total		4178	

P = nectar extraction + pollination; R = nectar robber making holes in corolla tubes. Numbers in brackets show the percentage of total visits.

Fig. 4. Number of pollen grains (mean ± SE) of *Disterigma stereophyllum* placed on the stigmas after a single visit by its main pollinators (Ocr = *Ocreatus underwoodii* (n = 11); Dor = *Doryfera ludoviciae* (n = 8); Col = *Colibri thalassinus* (n = 8); Chl = *Chlorostilbon mellisugus* (n = 10); Agl = *Aglaiocercus coelestis* (n = 9); Dig = *Diglossa albilatera* (n = 8). Bars with the same letter do not differ significantly (multiple comparisons test).

number of flowers visited per legitimate visit ($F_{9,2042}$ = 11.7, P < 0.0001). Tukey tests indicated that this variation was due to the high number of flowers visited per visit by the green-fronted lancebill (*Doryfera ludoviciae*) and bumblebees (*Bombus* sp.).

During nectar robbing, robbers did not contact the surface of the stigma, although they tended to vigorously shake branches. *D. albilatera* pierced the corolla tube near the base with its lower mandible, while holding the flower with its upper mandible, leaving a highly visible slit in the tube. Usually, the robbery did not cause damage to the reproductive organs and none of the robbed flowers

examined (n = 250) had a damaged style. However, when the robber forcefully shook the flower, this caused some release of pollen from the poricide anthers, most of which fell to the ground but some adhered to stigmas within the pierced flowers. Our examination of flowers showed that 11.5% of them had been robbed at some point (n = 1106 flowers).

The number of visits varied over the day (Fig. 3). About half of all visits in the two patches occurred between 8:30 and 10:30 (mean 46.7 flowers per hour in the observed patches). Visit frequency then declined to 18.1 flowers per hour after 16:30. Visit frequency by all three main pollinators decreased towards the end of the
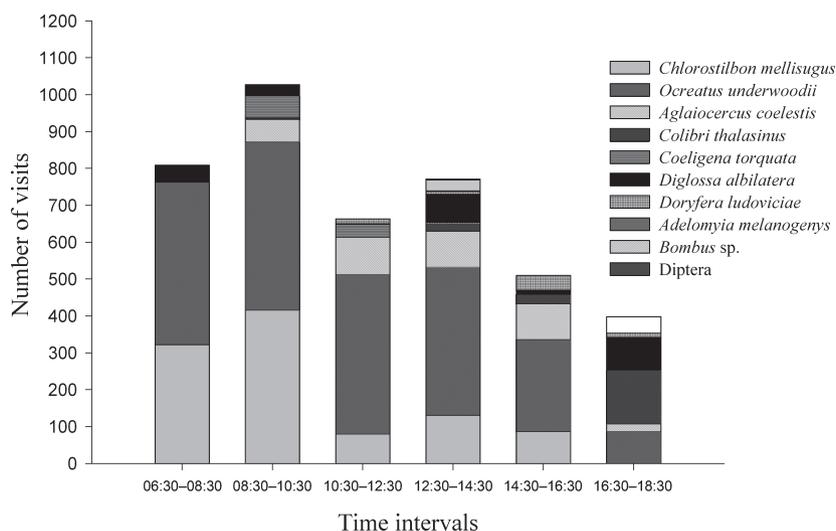
Fig. 3. Diurnal variation in relative frequency of visitors to flowers of *Disterigma stereophyllum*.

day, although only *C. mellisugus* showed zero activity during this last period.

Pollinator efficiency on pollen deposition

All pollen grains found on stigmas were conspecific (when the study was carried out, *D. stereophyllum* was the only species of this genus in flower, and its pollen is distinct from that of other ericads in the area). There were significant differences in the number of pollen grains found on the stigma after each visit ($F_{5,31} = 3.546$, $P = 0.0120$). Tukey tests showed that the differences were mainly due to the lower number of pollen grains found after *D. albilatera* visits (Fig. 4).

DISCUSSION

During our study, the flowers of *D. stereophyllum* were mainly visited by two territorial hummingbirds and a few 'trapliner' hummingbirds, with the two territorial species responsible for *ca.* 75% of visits. These pollinators show activity peaks early in the day, with activity subsequently declining. Diurnal patterns of this type have been observed in other tropical hummingbirds (Tiebout 1992), and have been attributed to the decline in nectar standing crop often observed towards the end of the day in hummingbird-pollinated flowers (Stiles 1975; Stiles & Wolf 1979). In the present study, we did not detect any significant decline in nectar availability towards the end of the day, but did observe a decline in nectar concentration. Castellanos *et al.* (2002) suggest that this floral mechanism could aid maintenance of pollinator visitation rates, providing a more constant reward (in terms of volume of nectar) to the pollinators. Regardless of this, the diurnal activity patterns observed here are very similar to those reported previously for other hummingbird-pollinated plants in the area, (Navarro 1999).

In spite of the lack of morphological fit with the flowers, all the species of hummingbird visiting *D. stereophyllum* show a good capacity to deposit pollen grains onto the stigma. Mayfield *et al.* (2001) showed that the 'unexpected' visitors for a syndrome can be as efficient during each visit, as the 'right' pollinator, or more so. Only *D. albilatera*, that behaves as a nectar robber (*sensu* Inouye 1983), showed reduced capacity to deposit pollen. In fact, this species did not contact the stigma during nectar robbing as some other nectar robbers do (Navarro 2000), but its shaking of the flower did cause some self-pollen to reach the stigma.

Disterigma stereophyllum apparently has a bee-pollination syndrome in its flower colour, size, shape and erect disposition. But it also shows certain floral characteristics that match those expected for the ornithophilous floral syndrome (Thomson *et al.* 2000) and that Luteyn & Sylva (1999) have suggested as adaptations to ornithophily in neotropical Ericaceae. These characteristics include style length equal to corolla length, rigid anthers arranged on the external face of the nectariferous disc, and abundant nectar with sucrose content of about 20% (Navarro *et al.*

2007). This dilute nectar places the species within the range classically reported for hummingbird-pollinated plants (Pyke & Waser 1981).

Luteyn (1989) suggests that the neotropical Ericaceae are switching from entomophily (the ancestral state) to ornithophily, with a superior ovary being replaced by an inferior ovary. In the genus *Bejaria*, generally considered to be one of the most primitive extant genera of the Ericaceae (Abbott 1936; Camp 1941; Copeland 1943), *B. aestuans* for example shows white or pink corollas with distinct extended petals, and is normally insect-pollinated, while *B. resinosa* has imbricate petals that produce a red tubular corolla and is hummingbird pollinated (Melampy 1987; Luteyn 1989; see however Kraemer 2001). Similar evolution of floral characteristics has been reported in other families with neotropical members, such as the Scrophulariaceae (Kampny 1995). Studies on *Disterigma* have indicated that most species of this genus produce small quantities of highly concentrated nectar and are visited by bees (Snow & Snow 1980; Luteyn & Sylva 1999; but see Bleiweiss & Olalla 1983). As pointed out above, this is not the case for *D. stereophyllum*, which produces large amounts of relatively dilute nectar, in accordance with a strong predominance of hummingbird visits in our study area (Table 1). In fact, *D. stereophyllum* shows what has been called a 'mixed pollination system', a combination of floral characters that are consistent with pollination by both insects and birds (Navarro *et al.* 2007). Similar patterns have been reported for *Alepis flavida*, a Loranthaceae from New Zealand (Ladley *et al.* 1997) and for *Penstemon pseudoespectabilis* (Scrophulariaceae), which attracts frequent hummingbird visits, but which retains the capacity for self-pollination and may be also pollinated by bees (Lange & Scott 1999). Wilson *et al.* (2006) suggest that 'despecialised' stages might occur in the transition from the bee to the hummingbird pollination syndrome in *Penstemon*. But, in our case, unfortunately, it is still not possible to infer any evolutionary pathway because the phylogeny of the genus is still incomplete (but see Powell & Kron 2003; Pedraza 2006).

In conclusion, the results of this study suggest that *D. stereophyllum* is basically pollinated by hummingbirds, despite the fact that its floral morphology does not fully match the hummingbird floral syndrome. We should stress, however, that pollinators of the species could vary through its geographic range, and could vary through time; it is always somewhat risky to draw overall conclusions from a single study. But taking our results at face value, *D. stereophyllum* seems to be another of the growing list of species for which there is no clear relationship between the usual pollinator spectrum and floral traits. More detailed elucidation of this question will require further ecological studies of this and related species. To this end, also, more studies are necessary to resolve the group phylogeny and to evaluate if there has been an evolution toward hummingbird pollination from entomophilous ancestors, as suggested by Luteyn (1989) for neotropical ericaceae and as shown in other neotropical genera (*e.g. Costus*, Kay *et al.* 2005).

REFERENCES

Abbott C.L. (1936) The phylogeny of the Ericales. *Trillia*, **9**, 62–69.

Bawa K.S. (1990) Plant–pollinator interactions in tropical rain forest. *Annual Review of Ecology and Systematics*, **21**, 399–422.

Bleiweiss R., Olalla M. (1983) Notes on the ecology of the Black-breasted Puffleg on Volcain Pichincha, Ecuador. *The Willson Bulletin*, **95**, 656–661.

Busby W.H. (2000) Hummingbird pollination of epiphytic Ericaceae in the cloud forest canopy. In: Nadkarni N.M., Wheelwright N.T. (Eds), *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, Oxford: pp. 267–268.

Camp W.H. (1941) Studies in the Ericales. A discussion of the genus *Befaria* in North America. *Bulletin of the Torrey Botanical Club*, **68**, 100–111.

Castellanos M., Wilson P., Thomson J. (2002) Dynamic nectar replenishment in flowers of *Penstemon* (Scrophulariaceae). *American Journal of Botany*, **89**, 111–118.

Copeland H.F. (1943) A study, anatomical and taxonomic, of the genera of Rhododendroideae. *American Midland Naturalist*, **30**, 533–625.

Faegri K., van der Pijl L. (1979) *The Principles of Pollination Ecology*, 3rd edition. Pergamon, Oxford.

Hargreaves A.L., Johnson S.D., Nol E. (2004) Do floral syndromes predict specialization in plant pollination systems? An experimental test in an ''ornithophilous'' African *Protea*. *Oecologia*, **140**, 295–301.

Hilty S.L., Brown W.L. (1986) *A Guide to the Birds of Colombia*. Princeton University Press, New Jersey, USA.

Holdridge L. (1996) *Ecología Basada en Zonas de Vida*. 4ª Reimpresión. Ed. IICA/CIRA, San José.

Inouye D.W. (1983) The ecology of nectar robbing. In: Bentley B., Elias T.S. (Eds), *The Biology of Nectaries*. Columbia University Press, New York: pp. 153–174.

Kampny C.M. (1995) Pollination and flower diversity in Scrophulariaceae. *Botanical Review*, **61**, 350–366.

Kay M.K., Reeves P.A., Olmstead R.G., Schemske D.W. (2005) Rapid speciation and the evolution of hummingbird pollination in neotropical *Costus* subgenus *Costus* (Costaceae): evidence from nrDNA ITS and ETS sequences. *American Journal of Botany*, **92**, 1899–1910.

Kraemer M. (2001) On the pollination of *Bejaria resinosa* Mutis ex Linné f. (Ericaceae), an ornithophilous Andean páramo shrub. *Flora*, **196**, 59–62.

Ladley J.J., Kelly D., Robertson A.W. (1997) Explosive flowering, nectar production, breeding systems, and pollinators of New Zealand mistletoes (Loranthaceae). *New Zealand Journal of Botany*, **35**, 345–360.

Lange R.S., Scott P.E. (1999) Hummingbird and bee pollination of *Penstemon pseudospectabilis*. *Journal of the Torrey Botanical Society*, **162**, 99–106.

Luteyn J.L. (1989) Speciation and diversity of Ericaceae in neotropical montane vegetation. In: Holm-Nielsen L.B., Nielsen I.C., Balslev H. (Eds), *Tropical Forest: Botanical Dynamics, Speciation and Diversity*. Academic Press, London: pp. 297–310.

Luteyn J.L., Sylva D.S. (1999) 'Murri' (Antioquia Department, Colombia): hotspot for neotropical blueberries (Ericaceae: Vaccinieae). *Brittonia*, **51**, 280–302.

Mayfield M.M., Waser N.M., Price M.V. (2001) Exploring the 'most effective pollinator principle' with complex flowers: bumblebees and *Ipomopsis aggregata*. *Annals of Botany*, **88**, 591–596.

Melampy M.N. (1987) Flowering phenology, pollen flow and fruit production in the Andean shrub *Befaria resinosa*. *Oecologia*, **73**, 293–300.

Murcia C., Feinsinger P. (1996) Interspecific pollen loss by hummingbirds visiting flower mixtures: effects of floral architecture. *Ecology*, **77**, 550–560.

Murray K.G., Feinsinger P., Busby W.H., Linhart Y.B., Beach J.H., Kinsman S. (1987) Evaluations of character displacement among plants in two tropical pollination guilds. *Ecology*, **68**, 1283–1293.

Navarro L. (1999) Pollination ecology and effect of nectar removal in *Macleania bullata* (Ericaceae). *Biotropica*, **31**, 618–625.

Navarro L. (2000) Pollination ecology of *Anthyllis vulneraria* subsp. *vulgaris* (Fabaceae): nectar robbers as pollinators. *American Journal of Botany*, **87**, 980–985.

Navarro L. (2001) Reproductive biology and effect of nectar robbing on fruit production in *Macleania bullata* (Ericaceae). *Plant Ecology*, **152**, 59–65.

Navarro L., Ayensa G., Guitián P. (2007) Adaptation of floral traits and mating system to pollinator unpredictability: the case of *Disterigma stereophyllum* (Ericaceae) in Southwestern Colombia. *Plant Systematics and Evolution*, **266**, 165–174.

Ollerton J., Johnson S.D., Cranmer L., Kellie S. (2003) The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Annals of Botany*, **92**, 807–834.

Orejuela J.E. (1987) La reserva natural La Planada y la biogeografia andina. *Humboldtia*, **1**, 117–148.

Pedraza P. (2006) *Phylogenetic Studies of Disterigma, an Andean Blueberry. The Evolution of Ericales: Recent Insights Using Both Morphology and Molecules. Symposium of the American Society of Botany*. California State University, Botanical Society of America.

Powell E.A., Kron K.A. (2003) Molecular systematics of the northern Andean blueberries (Vaccinieae, Vaccinioideae, Ericaceae). *International Journal of Plant Sciences*, **164**, 987–995.

Pyke G.H., Waser N.M. (1981) The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica*, **13**, 260–270.

Restrepo C., Gómez N. (1998) Responses of understorey birds to anthropogenic edges in a neotropical montane forest. *Ecological Application*, **81**, 170–183.

Snow D.W., Snow B.K. (1980) Relationships between hummingbirds and flowers in the Andes of Colombia. *Bulletin of the British Museum of Natural History*, **38**, 105–139.

Stiles F.G. (1975) Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology*, **56**, 285–301.

Stiles F.G., Wolf L.L. (1979) *Ecology and Evolution of lek Mating Behavior in the Long-Tailed Hermit Hummingbird*. American Ornithologists' Union, Washington, DC.

Systat (1997) *Statistics, Version 7*. Systat, Evanston, IL.

Thomson J.D., Wilson P., Valenzuela M., Malzone M. (2000) Pollen presentation and pollination syndromes, with special reference to *Penstemon*. *Plant Species Biology*, **15**, 11–29.

Tiebout H.M. (1992) Comparative energetic of divergent foraging modes: a doubly labelled water experiment on hummingbird competition. *Animal Behaviour*, **44**, 895–906.

Valdivia C.E., Niemeyer H.M. (2006) Do floral syndromes predict specialization in plant pollination systems? Assessment of diurnal and nocturnal pollination of *Escallonia myrtoidea New Zealand Journal of Botany*, **44**, 135–141.

Wilson P., Castellanos M.C., Wolfe A.D., Thomson J.D. (2006) Shifts between bee and bird pollination in *Penstemon*. In: Waser N.M., Ollerton J. (Eds), *Plant–Pollinator Interactions: from Specialization to Generalization*. University of Chicago Press, Chicago, IL, 47–68.

Zhang L., Barrett S.C.H., Gao J.-Y., Chen J., Cole W.W., Liu Y., Bai Z.-L., Li Q.-J. (2005) Predicting mating patterns from pollination syndromes: the case of 'sapromyophily' in *Tacca chantrieri* (Taccaceae). *American Journal of Botany*, **92**, 517–524.