RESEARCH PAPER

Plant–pollinator interactions in a Mexican *Acacia* community

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Abstract Competition for pollination is thought to be an important factor structuring flowering in many plant communities, particularly among plant taxa with morphologically similar and easily accessible flowers. We examined the potential for heterospecific pollen transfer (HPT) in a community of four *Acacia* species in a highly seasonal tropical habitat in Mexico. Partitioning of pollen flow among sympatric species appears to be achieved, in part, through segregation of flowering in seasonal time, and interspecific differences in pollinator guilds. However, two coflowering species (*Acacia macracantha* and *Acacia angustissima*) shared multiple flower visitors, raising the possibility of HPT. Each of these coflowering species showed high intraspecific daily synchrony in pollen release, but dehisce at different times of day. Pollinators rapidly harvested available pollen from one species before abandoning it to visit the flowers of the second later in the day. The activity of shared pollinators, predominantly bees, is thus structured throughout the day, and potential for HPT reduced. Suggestive evidence in favour of a resource partitioning explanation for this pattern is provided by the fact that *A. macracantha* showed significantly greater intraspecific synchrony when coflowering with a potential competitor (*A. angustissima*) than when flowering alone. We discuss our results in light of previous work on coflowering acacia assemblages in Tanzania and Australia.

Keywords *Acacia* · *Acaciella* · Bees · Character displacement · Competition for pollination · Flower visiting insects · Mexico · Niche partitioning · Pollen dehiscence timing · Pollination ecology · Resource axis · *Vachellia*

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Introduction

Flowering plants compete for pollination in at least two ways. Where seed set is limited by pollen availability, plants can potentially compete for pollinator visits (Mosquin 1971; Bierzychudek 1981; Horvitz and Schemske 1990). In other cases, pollen quality (i.e., load purity) is the limiting factor (Rathcke 1983, 1988). If pollinators visit more than one flowering species in a short-time period, some pollen may be transferred between species (heterospecific pollen transfer, HPT). HPT can reduce fitness in two ways: through loss of pollen to heterospecific stigmas, and through physical blocking of limited stigmatic surface by heterospecific pollen (Waser 1978a, b; Waser and Fugate 1986; Fishbein and Venable 1996). Avoidance of HPT is thought to be more important than competition for pollinator visits in natural

systems (Waser 1983; Rathcke 1983, 1988), and minimizing costs associated with both mechanisms of competition is thought to be an important force structuring plant communities (Pleasants 1983; Waser 1983; Armbruster and Herzig 1984; Feinsinger 1987; Stone et al. 1998).

An expected evolutionary consequence of competition is partitioning of shared resources leading to reduction of negative interaction between coexisting species (Brown and Wilson 1956; Pianka 1973; Schoener 1983). Sympatric plants competing for pollination services can potentially diverge along several resource axes. They can escape competition by recruiting 'private' pollinators (Heinrich 1976; Inouye 1978; Pleasants 1983; Rathcke 1988; Stone et al. 1999a; Cook and Rasplus 2003; Fenster et al. 2004), or deposit pollen on different parts of a shared pollinator's body (Dressler 1968; Armbruster et al. 1994). Plants can also share pollinators through divergence of their flowering seasons (Mosquin 1971; Heithaus 1974; Poole and Rathcke 1979; Pleasants 1980; Kephart 1983; Rathcke 1983; Ashton et al. 1988; Stone et al. 1998). Sympatric plants are sometimes constrained to flower at the same point in seasonal time (coflower) through constraints resulting from seasonal availability of water or warmth (Janzen 1967; Hocking 1968; Reich and Borchert 1984; Rathcke 1988; Johnson 1992; Ollerton et al. 2003), or through limited divergence of contemporary species from ancestral flowering patterns (Kochmer and Handel 1986; Wright and Calderon 1995). Under such circumstances, plants can either evolve tolerance of competition (e.g., through increased floral longevity: Levin 1978; Motten 1986; Rathcke 1988; Ashman and Schoen 1994; Ashman 2000), or partition the activity of shared pollinators on finer, daily, timescales (Levin and Anderson 1970; Ollerton and Lack 1992). Because pollinators commonly track pollen resource availability in daily time (Frankie et al. 1983; Stone 1994, 1995; Stone et al. 1995, 1996, 1998, 1999a; Herrera 1997; Willmer and Stone 2004), and regularly remove pollen from their bodies (Gilbert 1981; Roubik 1989), the evolution of species-specific times of pollen release (dehiscence) has the potential to reduce competition for both pollinator visits and pollen purity (Armbruster and Herzig 1984; Armbruster 1985; Stone et al. 1996, 1998).

The importance of daily structuring in competition for pollination is unclear, and most analyses to date lack the necessary resolution to examine daily patterns. This is surprising, because whether plants whose flowering seasons overlap actually compete for pollination may depend crucially on whether such daily partitioning exists.

Daily partitioning of shared pollinators is expected to leave a characteristic signature of (1) intraspecific synchrony and (2) interspecific divergence in the timing of both pollen dehiscence and activity patterns of shared pollinators (Brown and Wilson 1956; Slatkin 1980; Stone

et al. 1996, 1998). Furthermore, resource partitioning by competitive displacement predicts daily peaks of pollen release to be significantly regularly spaced (overdispersed) across species (Poole and Rathcke 1979; Pleasants 1980; Cole 1981; Gleeson 1981; Waser 1983; Kochmer and Handel 1986; Minckley et al. 1994; Williams 1995). Tanzanian acacias provide an example of such daily patterning (Stone et al. 1996, 1998). However, although this pattern is consistent with ongoing competition for pollination, it could also represent the "ghost of competition past" (Connell 1980), or the ecological sorting of species (Grant 1972; Slatkin 1980) which differ in their timing of pollen release for other reasons (Armbruster 1985, 1986). The long evolutionary history of East African savannahs and the geographically stable structure of acacia communities (Ross 1981) both suggest that long-term evolutionary responses, rather than ecological sorting, are responsible for the patterns seen in Tanzania (Stone et al. 1998).

Resource partitioning through competitive displacement can potentially be demonstrated using manipulation experiments, in which one or more competing species are removed from an assemblage and observed responses are compared with predictions based on competitive release (Van Valen 1965; Rothstein 1973). However, many generations may be required before responses become detectable, rendering this powerful approach unsuitable for plants with long generation times. A second approach is to exploit natural variation in communities to approximate removal experiments (Huey and Pianka 1974; Fenchel 1975). Comparing conspecific patterns of resource exploitation in locations with and without putative competitors represents a longer-term equivalent to removal experiments. Hence, if coflowering acacia species do compete for shared pollinators we would expect competitor species to show greater intraspecific synchrony in pollen release when coflowering than when flowering alone (Stone et al. 1998). This is the approach we adopt here.

Three factors potentially predispose acacia species to daily partitioning of shared pollinators. First, multispecies acacia assemblages commonly coflower in highly seasonal tropical habitats (Ross 1981; Stone et al. 1998, 2003). Second, their scented and showy flowers are visited by a wide diversity of flower visitors, some of which are shared (Bernhardt 1987; Tybirk 1993; Stone et al. 1998, 2003). Third, the common, open 'pom–pom' structure of acacia flowers allows pollen transfer between coflowering species. Here we examine seasonal and daily patterns of flowering, and the composition and daily activity patterns of pollinator assemblages in a Mexican *Acacia* community at Chamela. We address the following specific questions:

1. When do the Chamela acacias flower in seasonal time, and when during the day do they release their pollen?

Table 1 Species composition at each study site (p = present)

Species	Site 1. El Super	Site 2. Playa el negrito	Site 3. Arroyo Chamela	Site 4. Arroyo Careyes	Site 5. Camino el piedro	Site 6. Disused airstrip
A. hindsii	p	p	p		p	p
A. macracantha	p	p	p	p		p
A. farnesiana	p	p		p	p	p
A. angustissima				p		

Are temporal patterns consistent among sites and among years?

2. Do coflowering acacias show patterns of daily pollen release consistent with character displacement?

3. Do species show higher-intraspecific synchrony in daily timing of pollen release when flowering together than when flowering alone?

4. Do coflowering acacia species share flower visitors likely to be significant pollen vectors, and hence possible agents of selection for divergence in the timing of daily pollen release?

5. Does the daily activity of shared pollinators track patterns of pollen release among coflowering acacias?

Materials and methods

Study area and species

This study was carried out between 1998 and 2000 near the *Estación de Biologia de Chamela*, IBUNAM, on the Pacific coast of Jalisco, México (19°29.91′ N, 105°02.67′ W). Rainfall (mean ± 1 SE = 798 ± 54 mm: Chamela biological station records 1977–2000) is strongly seasonal and concentrated between June and October. Most of the region's *ca.* 1,200 plant species flower during the rains (Bullock and Solis-Magallanes 1990). Our study focussed on a region of *ca.* 40 km^2 within which four acacia species (Acacia (Vachellia) farnesiana (L.) Willdenow, Acacia (Vachellia) hindsii (Bentham) and Acacia (Vachellia) macracantha (Humboldt & Bonpland ex. Willdenow), and Acacia (Acaciella) angustissima (Miller) Kuntze[1]) regularly form dominant multi-specific assemblages.

We established six study sites, each of which included at least two of the three most locally widespread species: *A. farnesiana*, *A. hindsii*, and *A. macracantha* (Table 1). Sites for *A. macracantha* were selected to allow comparison of pollen release and visitation patterns alone, and with, a putative competitor species *A. angustissima* (Table 1). Because *A. angustissima* was only found at one location (site 4) lack of replication necessarily renders our results of the with/without comparison for *A. macracantha* preliminary. Study sites were distributed along a 20 km stretch of coast, within 2 km of the shore (Fig. 1).

Seasonal flowering patterns

Leaves, flower buds, open flower heads, and pods were censussed on an 8-point ordinal scale (absent, very sparse, sparse, sparse/medium, medium, medium/abundant, abundant, and very abundant) for 1–25 tagged individual trees of all acacia species growing at each study site at 3-week intervals during the study period.
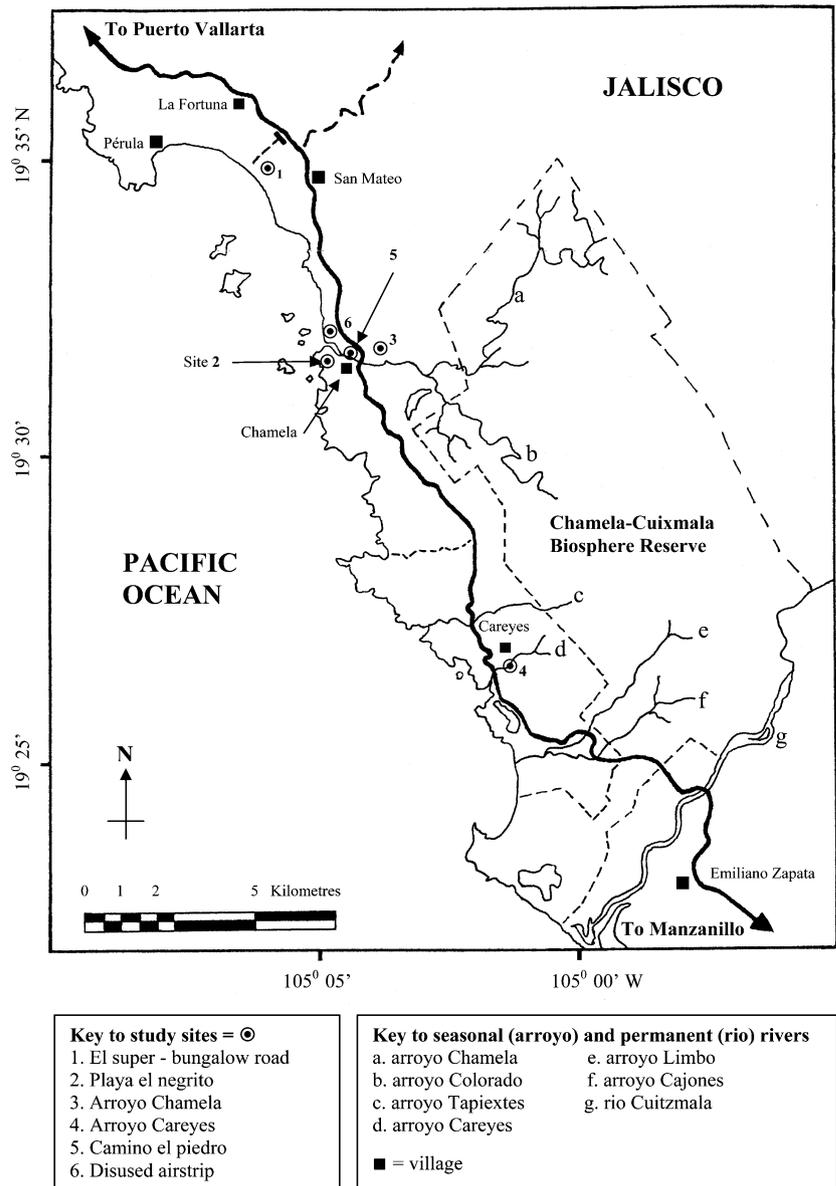
Flower head abundance, development and longevity

Acacia flowers are presented in spherical (capitate) or elongated (spicate) compound flower heads[2]. *A. macracantha* (capitate), *A. angustissima* (capitate) and *A. hindsii* (spicate) mass-flower on distinct reproductive branchlets (racemes), while *A. farnesiana* (capitate) flower heads arise singly (non-racemose) and at much lower density from bud cushions at the base of stipular spines. *A. macracantha*, *A. angustissima* and *A. hindsii* flowers are protandrous and complete both male and female reproductive phases within a single day (Raine 2001; Raine *et al*. 2002; Stone et al. 2003), persisting in a tattered post-reproductive state for one or more further days, after which unfertilised flower heads fall and fertilised ones develop seed pods. *A. macracantha* and *A. hindsii* flower heads open during the night and are fully open by dawn (0630–0700h), whereas *A. angustissima* flower heads begin opening around dawn and are not fully open until 1000–1200h. *A. farnesiana* flower heads are protogynous and last for several days, and

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[1] Recent evidence suggesting the genus *Acacia* is polyphyletic has lead to calls for a significant taxonomic revision (Maslin 2006). The names (*Vachellia* and *Acaciella*) given in parentheses indicate the genera to which these species would be assigned under the proposed revision (Maslin et al. 2003)

[2] Flower heads have often been termed 'inflorescences', although as defined by the Flora of Australia (vol. 11A, Mimosaceae, Acacia), the term 'inflorescence' more properly applies to groups of flower heads on a floral shoot. For clarity we use the term flower head throughout.

Fig. 1 Map of Chamela bay area showing study site locations

Key to study sites = ⊙
1. El super - bungalow road
2. Playa el negrito
3. Arroyo Chamela
4. Arroyo Careyes
5. Camino el piedro
6. Disused airstrip

Key to seasonal (arroyo) and permanent (rio) rivers
a. arroyo Chamela e. arroyo Limbo
b. arroyo Colorado f. arroyo Cajones
c. arroyo Tapiextes g. rio Cuitzmala
d. arroyo Careyes

■ = village

male and female reproductive phases probably occur on different days (Raine 2001; Stone et al. 2003).

Daily patterns of pollen availability

Acacias present pollen as a compound polyad with eight polyads per anther (Knox and Kenrick 1982; Chappill and Maslin 1995; Kenrick 2003). Pollen release (dehiscence) in each species was evaluated by examining the relative abundance of pollen available on the surface of flower heads sampled at intervals through the day using methods described in full by Stone et al. (1998) and Raine et al. (2002). We sampled four flower heads at random from each acacia tree at each sample time. Each flower head was rolled lightly across (the adhesive side of) a piece of clear adhesive tape and the progress of dehiscence scored using the ratio of polyads to anthers (P:A) collected on the tape. For each flower head, the P:A was recorded for six randomly chosen microscope fields and the mean calculated. For each acacia and time interval, the mean P:A ratio was calculated across the sampled flower heads. So that each tree contributed equally to calculated means, P:A ratios were constrained to vary between 0 and 1 for each tree and day by dividing them by the maximum value for that tree and day. When availability of flower heads allowed, data for *A. farnesiana* were collected using this standard protocol. However, due to low abundance of flower heads per tree we generated a site-specific population estimate for the mean P:A ratio by sampling a single flower head from 6 to 8 *A. farnesiana* trees at each time interval. Dehiscence was followed from dawn (0600–

0700h) until dusk (1700–1900h) at intervals of 60–90 min. In total we collected 150 tree-days of dehiscence data, with totals for each species in parentheses: *A. macracantha* (79), *A. angustissima* (29), *A. hindsii* (26), and *A. farnesiana* (16: Supplementary material–Appendix A).

Daily patterns of microclimate

The timing of anther dehiscence is highly sensitive to temperature and relative humidity (Buchmann 1983; Corbet et al. 1988; Stone et al. 1998). Because intraspecific variation in the timing of pollen release could potentially result from microclimatic differences across study sites, we recorded shade temperature and relative humidity using a Vaisala HM34 humidity and temperature meter for every tree studied at each sampling interval.

Patterns of flower visitation and visitor assemblages

Flower visitor behaviour was quantified in all three field seasons (Supplementary material-Appendix A) in the same way for each acacia species following Stone et al. (1996, 1998). A consistent set of selected flower heads was watched for a fixed observation period at regular intervals throughout the day, from before the onset of foraging until after it ceased (usually approximately 0730–1700h). In 1998 and 1999, focal flower heads were watched for a 10-min period every 80–120 min, allowing data collection from several individual trees per day. In 2000, focal flower heads on a single tree were watched for a 30-min period at hourly intervals from 0700 to 1700h, providing more detailed data for each observation day.

Visitation was quantified as the number of flower head visits made by each taxon (Horvitz and Schemske 1990; Stone et al. 1998), weighted equally regardless of visitor taxon, visit duration, or the number of flowers visited per flower head. Differences in forager activity patterns were analyzed using Kolmogorov–Smirnov tests (Sokal and Rohlf 1981; Stone et al. 1988). Similarities in floral visitation attributable to particular visitor taxa were quantified using proportional similarity (Schoener 1970; Kephart 1983; Horvitz and Schemske 1990; Stone et al. 1998) (PS), which ranges from 1 (maximum similarity) to 0 (no overlap).

Results

Seasonal flowering patterns

The Chamela acacias can be divided into two seasonal flowering groups: late dry season (*A. hindsii* and

A. farnesiana) and wet season (*A. angustissima* and *A. macracantha*: Fig. 2). Despite this general distinction, sympatric *Acacia* species frequently coflowered for extended periods. *Acacia macracantha* regularly coflowered with *A. hindsii* and *A. farnesiana* (Fig. 2a–c) and the longest coflowering (5 months) was between *A. macracantha* and *A. angustissima* (site 4; Fig. 2c, d). Seasonal flowering patterns were consistent across years at all study sites.
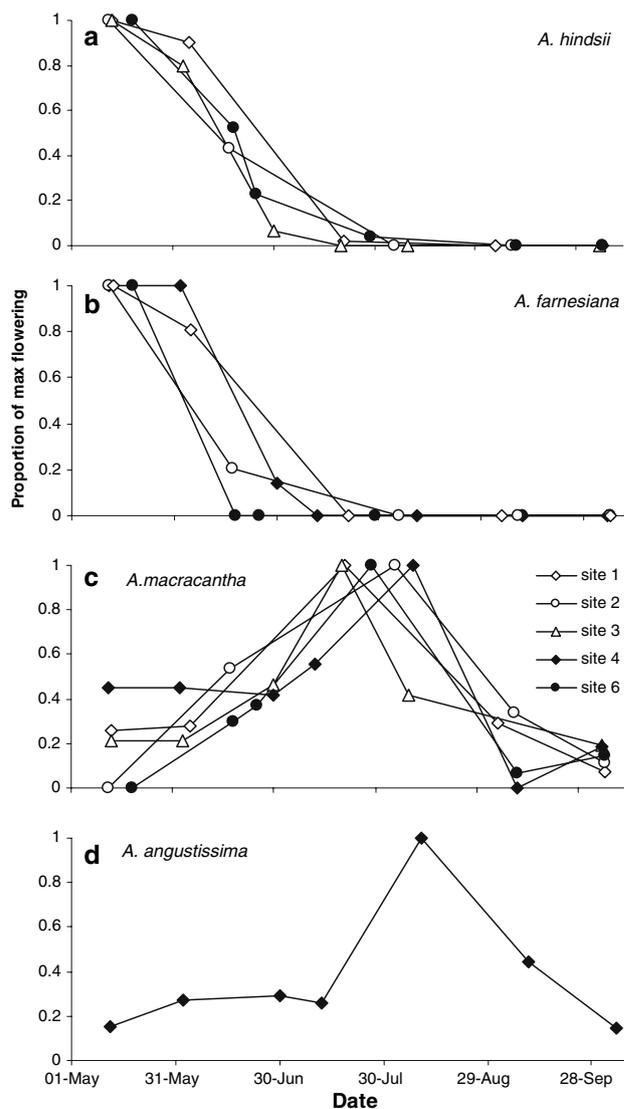

Fig. 2 Seasonal patterns of flowering abundance for (a) *A. hindsii*, (b) *A. farnesiana*, (c) *A. macracantha* and (d) *A. angustissima* in 1999. Each symbol type represents the population at a different study site. Flowering abundance at each site was constrained to vary between 0 and 1 by dividing them by the maximum seasonal abundance for that site. The wet season began on the 16 Jun 1999 – these were the first rains since 14 Oct 1998

Daily timing of pollen release

Acacia hindsii and *A. angustissima* dehisce in the early morning (around 0800h) and early afternoon (around 1200h), respectively, and show high-intraspecific synchrony among individuals (Fig. 3a, b). *A. macracantha* populations varied in their timing of pollen release: individuals coflowering with *A. angustissima* dehisced consistently earlier (around 0900h: Fig. 3c) and showed greater intraspecific synchrony than conspecifics flowering alone (Fig. 3d). The contrast in *A. macracantha* dehiscence synchrony between sites with (site 4) and without *A. angustissima* was significant for site 3 versus site 4 (*F*-test:

$F_{4, 4} = 7.92$, $p = 0.035$), and near significant for site 1 versus site 4 ($F_{3, 4} = 5.98$, $p = 0.058$), with no significant difference in synchrony between sites without *A. angustissima* (Site 1 vs. 3: $F_{4, 3} = 1.33$, $p = 0.424$). The similarity in dehiscence behaviour does not correlate simply with the spatial separation of sites, which would predict most similar behaviour at sites 1 and 3 (Fig. 1). Daily dehiscence patterns for individual trees were highly consistent across days and years for *A. hindsii*, *A. angustissima* and *A. macracantha* (Fig. 4), implying consistent temporal relationships among these species.

Daily peaks of pollen availability shown by *A. farnesiana* populations (six trees sampled per day) were less distinct than in the other three species and varied appreciably across consecutive days under similar microclimatic conditions (Fig. 5). Due to low flower head abundance per tree, it was impossible to assess intraspecific dehiscence synchrony in this species.
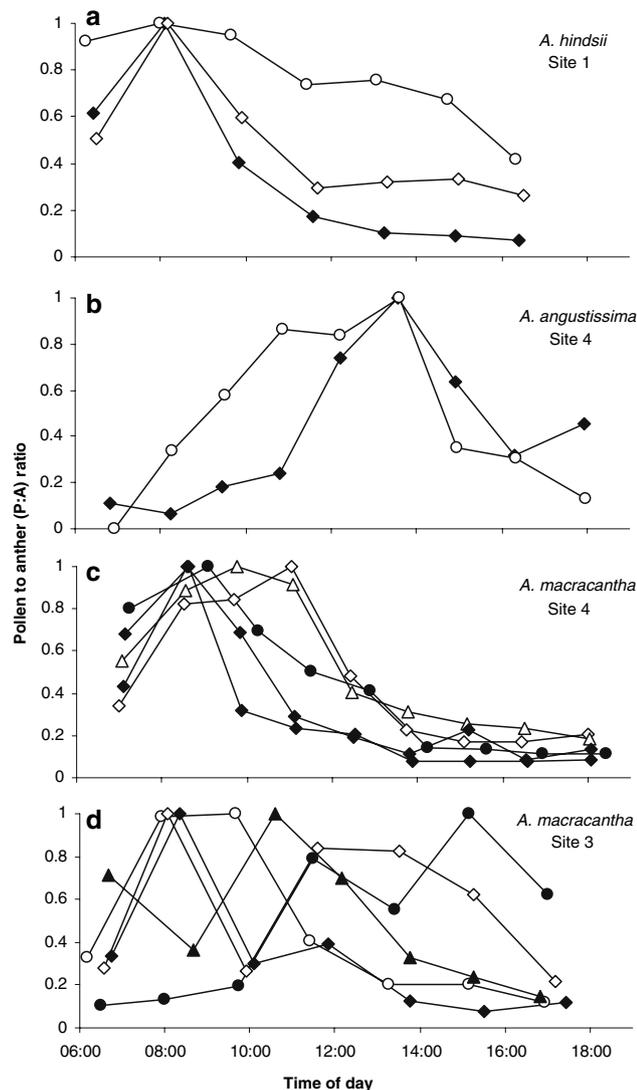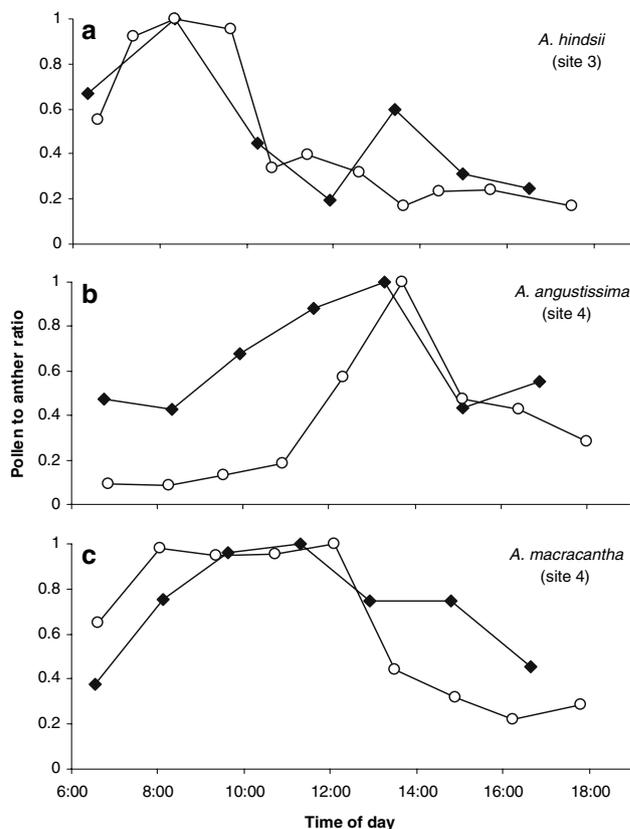

Fig. 3 Variation in daily patterns of pollen availability amongst conspecific individual trees sampled on the same day for: (a) *A. hindsii* (site 1), (b) *A. angustissima* (site 4), (c) *A. macracantha* (site 4) and (d) *A. macracantha* (site 3). Each symbol type represents data for an individual tree

Fig. 4 Variation in daily patterns of pollen availability for the same individual trees between consecutive flowering seasons. Data presented are the mean patterns of pollen availability for 1999 (*filled diamonds*) and 2000 (*open circles*) for the same individual trees for: (a) *A. hindsii*, (b) *A. angustissima* and (c) *A. macracantha*
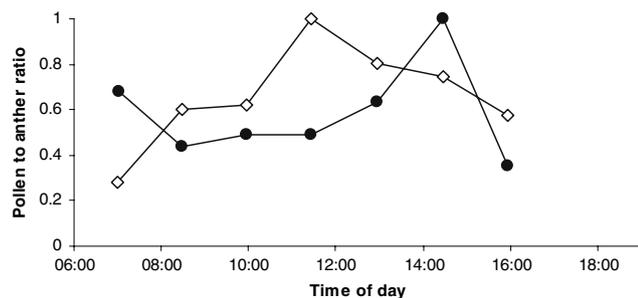
Fig. 5 Daily patterns of pollen availability for an *A. farnesiana* population on two consecutive days at site 6. Data presented show mean values of pollen availability (P:A ratios) calculated across six individual trees (1 flower head sampled per tree per sampling interval) sampled on 22 and 23 May 2000 (*open diamonds* and *filled circles*, respectively). This sampling regime was adopted due to low flower head densities on individual trees (see "Materials and methods" section)

The impact of relative humidity on daily dehiscence patterns

Variation in daily dehiscence profiles closely tracked between-day variation in relative humidity. Peak pollen availability at a given site occurred later on days when relative humidity was higher at the onset of dehiscence in *A. angustissima* (Fig. 6), *A. hindsii* (Fig. 7) and *A. macracantha* (Fig. 8). Coflowering *A. macracantha* and *A. angustissima* showed parallel responses to changes in ambient relative humidity, maintaining a constant separation of 3–4 h between their pollen availability peaks (Fig. 8). Lower intraspecific synchrony of dehiscence in *A. macracantha* flowering alone relative to the population coflowering with *A. angustissima* did not correlate with any measured microclimatic difference between sites.

Flower visitor assemblages of Chamela acacias

Bees dominated (68–93%) visitation to the mass-flowering species *A. macracantha*, *A. hindsii* and *A. angustissima* (Table 2), and all three shared many pollinator taxa (see Table 3 and Supplementary material—Appendices B–F for visitors recorded across sites and *Acacia* species). The major bee taxa were honeybees (*Apis mellifera* L.), native social bees (*Scaptotrigona hellwegeri* (Roubik) and *Trigona* spp.; Apidae), and solitary bees in the genera *Hylaeus* (Colletidae), *Augochloropsis* and *Lasioglossum* (Halictidae), *Ceratina* and *Xylocopa* (Anthophoridae) and *Megachile* (Megachilidae). Other solitary bee genera, including *Eulonchopria* (Colletidae), *Pseudoaugochloropsis* and *Halictus* (Halictidae), *Exomalopsis* (Anthophoridae), and *Anthodioctes* (Megachilidae) frequently visited at least
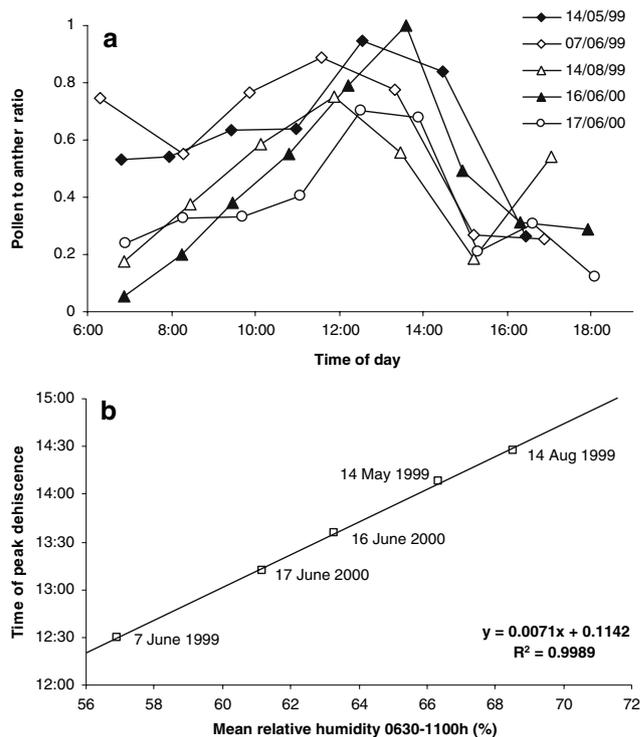

Fig. 6 (a) Intraspecific variation in daily patterns of pollen release over time for *A. angustissima* at site 4. Data points are means averaged across individuals on a single day at site 4. (b) Timing of maximum daily pollen availability as a function of mean relative humidity from 0630 to 1000h for *A. angustissima*. The fitted line is a least squares regression: $y = 0.0071x + 0.1142$, $r^2 = 0.9989$, $p < 0.0001$

two *Acacia* species. Bees (primarily *Lasioglossum* spp. and *Apis mellifera*) made a smaller proportion of visits to *A. farnesiana* (39%). *Acacia farnesiana* was visited predominantly by flies (41.2%: Table 2a), primarily pollen-feeding hoverflies (Syrphidae: 20%) in the genera *Allograpta* and *Eristalis* and bee flies (Bombyliidae: Table 2b). Beetles (primarily cantharids, chrysomelids, scarabids and bruchids) visited flower heads of all four *Acacia* species.

Flower visitor assemblages for each *Acacia* species varied among sites (Tables 4b, 5 and Supplementary material—Appendix F), and among days (Table 4a, 6a and Supplementary material—Appendices D, E), months (Table 6b and Supplementary material—Appendix D) and flowering seasons (Table 6c and Supplementary material—Appendices D, F) at a given site. Variation in flower visitor assemblages for each *Acacia* species was generally greater between sites than over time within sites (e.g., compare Table 4a and b for *A. hindsii*), implying patchiness in available visitor assemblages. For *A. angustissima*, *A. hindsii* and *A. macracantha* variation in visitation patterns within and across study sites was associated primarily with variation in the proportion of flower visits made by
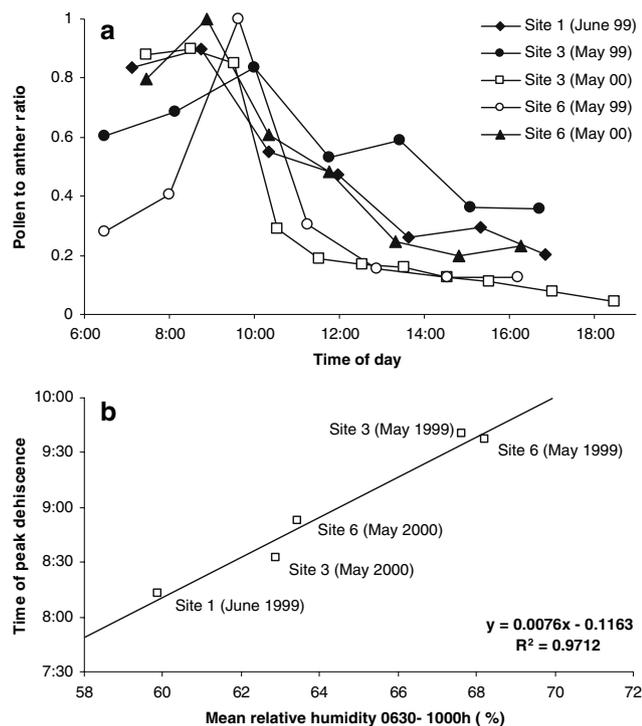
Fig. 7 (a) Intraspecific variation in daily patterns of pollen release over time between sites for *A. hindsii*. Data points are seasonal means for each site, i.e., means averaged across individual trees per day, then across days within a season. (b) Timing of maximum daily pollen availability as a function of mean relative humidity from 0630 to 1000h for *A. hindsii*. The fitted line is a least squares regression: $y = 0.0076x − 0.1163$, $r^2 = 0.971$, $p = 0.002$

Fig. 8 Timing of maximum daily pollen availability as a function of mean relative humidity from 0630 to 1000h for coflowering populations of *A. angustissima* (*filled circles*) and *A. macracantha* (*open diamonds*) at site 4. Data points represent the mean for two trees per species on a single day, with data for both species presented for the same four dates (7 June 1999, 14 Aug 1999, 16 June 2000 and 17 June 2000). Dotted lines indicate least squares regression lines for each species

different bee taxa. Social bees, notably *S. hellwegeri*, dominated flower visitation (especially to *A. hindsii* and *A. angustissima*) on particular days at some sites, and in their absence solitary bees became proportionally more abundant (Supplementary material—Appendices D–F). There were no consistent differences in flower visitor assemblages associated with *A. macracantha* when flowering alone when compared to the conspecific population coflowering with *A. angustissima* (Mann–Whitney $U = 10.5$, $p = 0.748$: Table 5).

Pollinator behaviour and the potential for heterospecific pollen transfer

Bees are probably the dominant pollen vectors for Chamela acacias. Medium-sized and large solitary bees, including *Megachile*, *Augochloropsis*, *Ceratina*, *Eulonchopria*, *Exomalopsis* and *Xylocopa* species, visited each individual flower head for a short-time and ranged over the entire surface. *Megachile* species showed characteristic somersaulting movements over each flower head for 1–2 s. These bees visited relatively few flower heads per
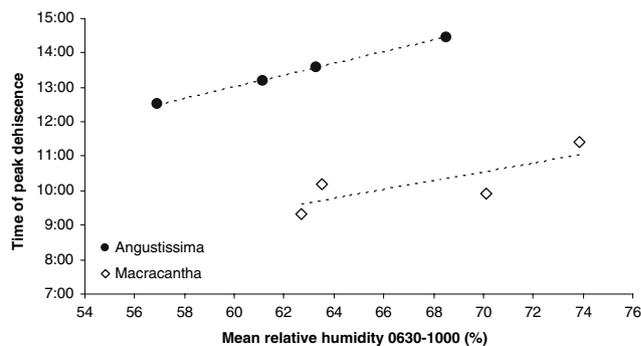
tree, and probably visited several trees during each foraging bout. In contrast, honeybees (*A. mellifera*) and other medium-sized social bees (particularly *S. hellwegeri*) foraged extensively within a single canopy, generally moving between flower heads that were close together.

These larger bees have the potential to mediate considerable HPT through shared pollinators in this community. Analysis of pollen loads showed that individual bees also moved between acacia species in a single foraging bout. Solitary bees from three genera (*Augochloropsis*, *Lasioglossum* and *Anthodioctes*) visiting *A. angustissima* flower heads (producing pale lemon yellow pollen) were observed to be carrying orange pollen loads shown by microscopic examination to comprise 16-grain polyads characteristic of *A. macracantha*. Honeybee and *Ceratina* individuals visiting *A. hindsii* flower heads at the end of the dry season were observed with yellow pollen loads originating from another coflowering mimosoid legume, *Mimosa quadrivalis* (Rose).

Smaller solitary bees (*Lasioglossum*, *Halictus* and *Hylaeus*) and social bees (e.g., *Trigona nigra* (Cresson)) spent long periods foraging on a single flower head (*ca.* 30–90 s), often leaving to hover alongside and comb pollen from their body before returning to forage on the same flower head. Thus, these chains of visits to a single flower head frequently lasted several minutes. Hoverflies (Syrphids) typically fed on a single flower head for more than 10 min, accumulating pollen on the underside of their bodies, and were seen to depart focal trees. Beetles often remained in a single flower head for several hours, or even the whole day, and most fed destructively on the flowers.

Table 2 Visitation by different insect taxa to flower heads of *Acacia* species

(a) Major flower visitor taxa

Species	Bees	Wasps	Beetles	Flies	Butterflies	Ants
A. macracantha	68.2 ± 11.4	3.6 ± 1.9	19.1 ± 6.8	8.5 ± 3.7	0.2 ± 0.2	0.4 ± 0.4
A. angustissima	93.1 ± 3.2	3.4 ± 1.4	1.5 ± 0.8	1.1 ± 0.6	0.1 ± 0.1	0.7 ± 0.7
A. hindsii	89.2 ± 3.7	2.9 ± 1.5	2.8 ± 1.3	4.0 ± 0.8	1.2 ± 1.2	0 ± 0
A. farnesiana	38.9 ± 26.4	2.2 ± 2.2	17.8 ± 13.5	41.2 ± 15.0	0 ± 0	0 ± 0

(b) Bee and fly taxa resolved to family

	Bee species							Other flower visiting taxa						
	Honey bees	Native Apids	Colletid bees	Anthophorid bees	Megachilid bees	Halictid bees	Other bees	Wasp sp.	Beetle sp.	Syrphid flies	Bombyliid flies	Other flies	Butterflies	Ants
A. macracantha	28.4 ± 11.7	5.7 ± 3.1	7.6 ± 1.2	5.6 ± 1.7	6.5 ± 5.2	10.9 ± 2.6	3.5 ± 3.3	3.6 ± 1.9	19.1 ± 6.8	3.1 ± 2.2	0.4 ± 0.4	5.1 ± 2.1	0.2 ± 0.2	0.4 ± 0.4
A. angustissima	1.1 ± 1.1	52.8 ± 26.5	3.6 ± 0.8	0.8 ± 0.8	30.8 ± 27.9	3.5 ± 1.7	0.3 ± 0.2	3.4 ± 1.4	1.5 ± 0.8	0.5 ± 0.3	0 ± 0	0.6 ± 0.4	0.1 ± 0.1	0.7 ± 0.7
A. hindsii	14.7 ± 7.0	16.8 ± 11.5	7.7 ± 5.6	21.3 ± 9.8	7.8 ± 5.3	19.5 ± 3.7	1.4 ± 0.8	2.9 ± 1.5	2.8 ± 1.3	0.1 ±0.03	1.8 ± 1.0	2.2 ± 1.3	1.2 ± 1.2	0 ± 0
A. farnesiana	21.8 ± 21.8	0 ± 0	0 ± 0	0 ± 0	0 ± 0	10.9 ± 10.9	6.3 ± 6.3	2.2 ± 2.2	17.8 ± 13.5	20.0 ± 11.3	4.4 ± 4.4	16.0 ± 8.2	0 ± 0	0 ± 0

Data presented are the mean percentage (±1 SE) of total visits contributed by a particular taxon (species means calculated across years within each study site, and subsequently averaged across study sites). The same data are presented at different levels of taxonomic resolution: (a) insects grouped into major visitor taxa, (b) the most numerous flower visitor taxa (bees and flies) broken down to family level

Table 3 Proportional similarities (PS) of flower visitation by pollinator taxa for all *Acacia* species (calculated from data in Table 2b)

	A. farnesiana	A. hindsii	A. angustissima
A. macracantha	0.65	0.61	0.28
A. angustissima	0.10	0.39	
A. hindsii	0.36		

PS values were calculated as follows: (1) the proportion of total flower visits attributable to each visitor taxon were calculated for the two *Acacia* groups to be compared; (2) the modulus of the difference in proportions was calculated for each visitor taxon; (3) PS = 1–0.5 (sum of the modulus values over all visitor taxa). PS values range from 1 (maximum similarity) to 0 (no overlap)

Table 4 Proportional similarities (PS) in levels of flower visitation by pollinator taxa for *A. hindsii* between (a) days at the same study site and (b) sites within the same year (calculated from data in Supplementary material—Appendix E)

(a) Variation between days at each site in 2000

Study site	PS	Dates compared
Site 3	0.38	12 vs. 27 May
Site 5	0.71	1 vs. 5 Jun
Site 6	0.80	22 vs. 23 May

(b) Variation between study sites in 2000

Study site	Site 5	Site 6
Site 3	0.41	0.27
Site 6	0.48	

Table 5 Proportional similarities (PS) in levels of flower visitation by pollinator taxa for *A. macracantha* compared between study sites (calculated from data in Supplementary material—Appendix F)

Study site	Site 6	**Site 4**	Site 3	Site 2
Site 1	0.60	**0.62**	0.62	0.51
Site 2	0.31	**0.46**	0.33	
Site 3	0.50	**0.47**		
Site 4	0.59			

Bold type indicates comparisons between sites where *A. macracantha* and *A. angustissima* coflower (site 4) with those where they flower apart (sites 1–3, 6)

Daily activity patterns of flower visitors

Daily patterns of flower visitation to each *Acacia* species were consistent across days and sites within a flowering season (Fig. 9). Flower visitation patterns closely tracked daily pollen release for all species at all sites (compare Fig. 9 with Fig. 3), peaking with or shortly after peak daily pollen availability. Social bees arrived in large numbers as pollen availability peaked and left as soon as the pollen

Table 6 Proportional similarities (PS) in levels of flower visitation by pollinator taxa for *A. angustissima* between (a) days, (b) months, and (c) seasons (calculated from data in Supplementary material—Appendix D)

(a) Variation between days (August–September 1998)

Date	24 Sep 98	27 Aug 98	26 Aug 98
25 Aug 98	0.75	0.75	0.80
26 Aug 98	0.80	0.80	
27 Aug 98	0.91		

(b) Variation between months (during 1999)

Date	14 Aug 99	13 Jul 99	7 Jun 99
14 May 99	0.79	0.05	0.98
7 Jun 99	0.79	0.03	
13 Jul 99	0.16		

(c) Variation between flowering seasons

Comparison	PS
Aug 98 vs. Aug 99	0.88
Jun 99 vs. Jun 00	0.01

standing crop began to fall (Fig. 10). In contrast, solitary bees often foraged from *Acacia* flower heads until later in the day (Fig. 10a).

Daily visitation patterns at *A. macracantha* differed consistently between sites, tracking patterns of pollen release. Visitation to *A. macracantha* (particularly by bees) began considerably earlier at site 4 (coflowering with *A. angustissima*) than at all other sites. Flower visitation to *A. macracantha* at site 4 also declined abruptly around noon (Fig. 9c) while at other sites it declined gradually during the afternoon (Fig. 9d). Visitation to coflowering *A. macracantha* and *A. angustissima* overlapped only briefly, with the abrupt changeover in pollinator activity between species most obvious in 1998 and 2000 (Fig. 11). This consistent difference in visitation patterns to coflowering *A. macracantha* and *A. angustissima* was statistically significant in all three flowering seasons 1998–2000 (Kolmogorov–Smirnov two sample test, all *p*-values <0.01: Table 7).

Discussion

Do Chamela acacias show a signature of competition for pollination?

Structuring of daily activity in response to resource availability has long been known for a wide range of pollinators, particularly for social and solitary bees whose resources are
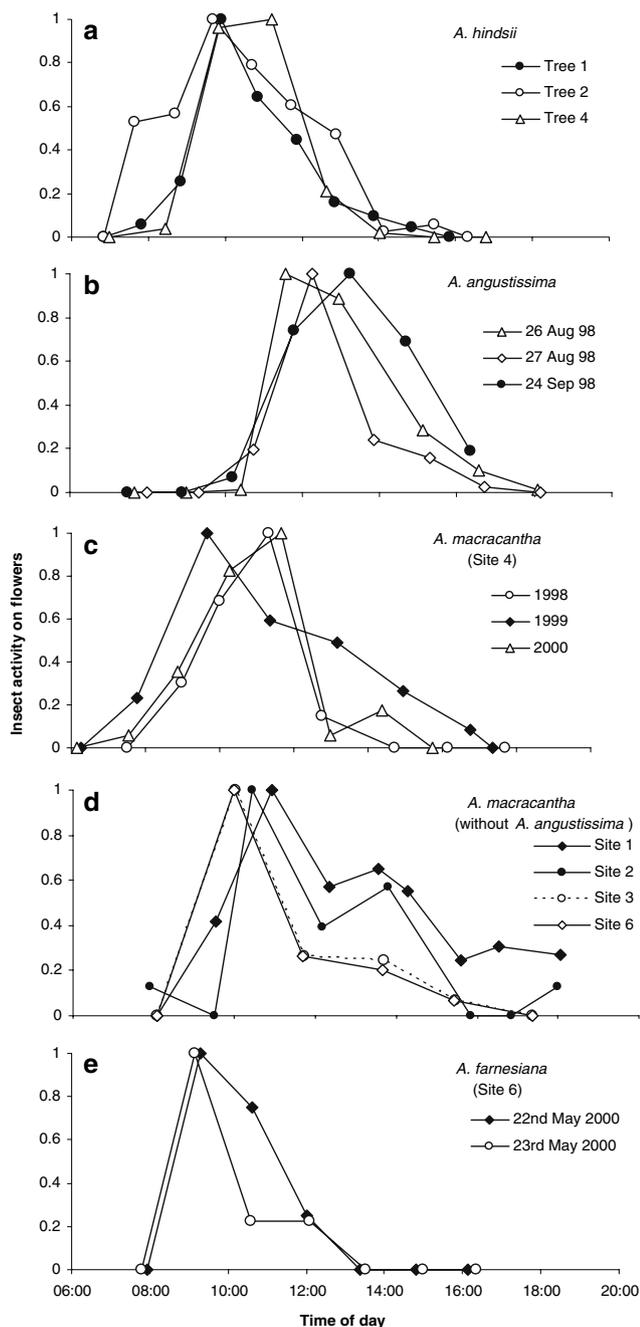
Fig. 9 Variation in the daily patterns of flower visitor activity by all insect taxa shown for (a) *A. hindsii* individuals across sites in 2000, (b) the *A. angustissima* population (at site 4) across dates in 1998, (c) the *A. macracantha* population at site 4 (coflowering with *A. angustissima*) across flowering seasons, (d) *A. macracantha* populations across sites (without *A. angustissima*) in 1998 and 1999 and (e) an *A. farnesiana* individual on two consecutive days at site 6. Data presented are mean relative activity levels of flower visitors

Fig. 10 Patterns of flower visitation in response to pollen availability for (a) honeybees (*A. mellifera*) and solitary bees visiting one *A. hindsii* individual (1 Jun 2000: site 5), and (b) social meliponine bees (*S. hellwegeri*) and solitary bees visiting two *A. angustissima* individuals (26 Aug 1998: site 4)

provided in discrete time windows (Butler and Finney 1942; Bennett and Bread 1985; Buchmann and Cane 1989; Stone 1994; Stone et al. 1999a; Raine et al. 2002, 2004; Willmer and Stone 2004). This sensitivity of foragers to
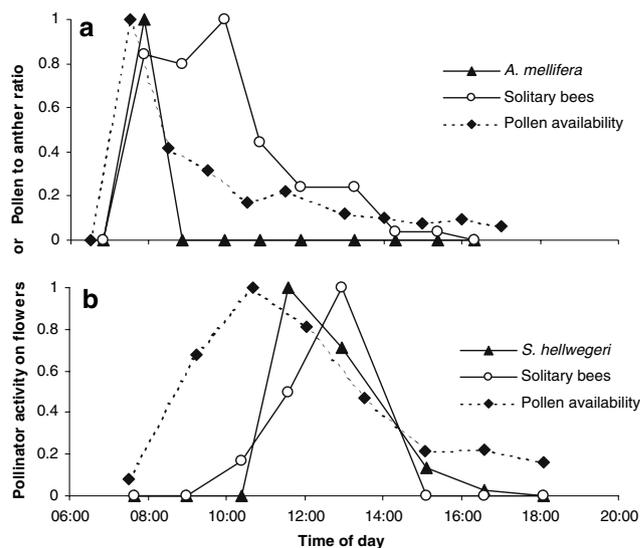
resources makes possible the community-wide structuring of plant–pollinator interactions through selection on plant floral behaviour. Daily partitioning of shared pollinators is just one possible outcome of such 'bottom-up' influences. Stone et al. (1996, 1998) proposed that flowering patterns in a Tanzanian acacia community supported a hypothesis of daily temporal partitioning of pollinators. The key findings of the Tanzania study were (i) seasonal coflowering and pollinator sharing (creating the potential for competition for pollination), (ii) daily intraspecific synchrony in dehiscence, and regular interspecific spacing of pollen dehiscence through the day (creating the potential for bottom-up structuring of pollinator behaviour), and (iii) pollinator tracking of pollen release (the predicted result). To what extent do patterns at Chamela mirror those found in Tanzania?

Although there is partial seasonal separation of flowering between dry (*A. hindsii* and *A. farnesiana*) and wet (*A. macracantha* and *A. angustissima*) season species pairs, Chamela acacias frequently coflower, as in Tanzania. The three mass-flowering *Acacia* species in this assemblage also often showed high intraspecific synchrony in daily pollen release. As in Tanzania, pollinators tracked pollen release very closely, showing the potential for bottom-up regulation of pollinator behaviour by selection on dehiscence times, and many flower visitor taxa (especially bees) are shared. Is there any evidence that pollinator sharing has influenced the floral behaviour of Chamela acacias?

A major difference between this study and the Tanzanian community is the lower species richness of
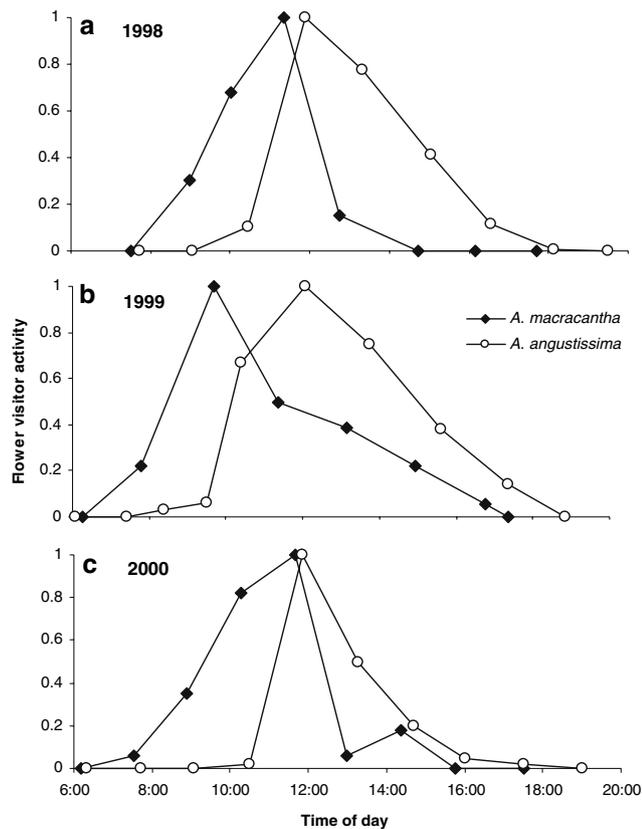
Fig. 11 Daily patterns of flower visitor activity for coflowering populations of *A. macracantha* and *A. angustissima* at site 4 in (a) 1998, (b) 1999, and (c) 2000. Data presented are the relative flower visitation profiles received by each species averaged across the following dates: (a) 26, 27 Aug 1998, (b) 14 May, 7 Jun, 13 Jul and 14 Aug 1999, and (c) 16 and 17 Jun 2000. The total number of flower head visits recorded per species per year are given in Table 7

coflowering acacias at Chamela. We thus cannot hope to detect signatures of resource partitioning by analysing the cross-species distribution of daily pollen release peaks, as applied by Stone et al. (1996, 1998). An intriguing result is the contrast in dehiscence behaviour between *A. macracantha* populations flowering alone, and the single population coflowering with *A. angustissima*. While intraspecific synchrony was universal for *A. hindsii* and *A. angustissima*, *A. macracantha* varied in its pollen

release behaviour between populations: intraspecific synchrony was appreciably higher when this species coflowered with *A. angustissima* than when they flowered apart. Timing of peak pollen availability in *A. macracantha* also varied with the presence/absence of coflowering *A. angustissima*. The pattern observed in *A. macracantha* is compatible with the predictions of resource partitioning and competitive release: high intraspecific synchrony could reflect stabilising selection in the presence of coflowering competitors, while low synchrony (in *A. macracantha* flowering alone) could represent competitive release. Our observation of movement by individual insect foragers between acacia trees within a single foraging bout shows the potential for HPT in this system. A similar contrast between coflowering (high intraspecific synchrony) and solitary flowering (low intraspecific variation) was observed in the Tanzanian acacia community studied by Stone et al. (1998).

However, in both studies, there is no replication and these results can only be considered preliminary. As the difference in dehiscence behaviour is confounded with differences in site, this pattern could also have resulted from past competition, ecological sorting, or chance effects (Grant 1972; Slatkin 1980; Armbruster 1985, 1986; Murray et al. 1987). Validation of the competitive hypothesis for differences in dehiscence behaviour requires replication of the observed contrast in other *A. macracantha* populations flowering with and without other acacias.

Contrasting floral behaviour in *Acacia farnesiana*

Acacia farnesiana shows much lower intraspecific synchrony of pollen release than the mass-flowering species, and its long-lived protogynous flower heads are more similar to Australian acacias in the phylogenetically distinct subgenus *Heterophyllum* (Stone et al. 2003). This could potentially reflect contrasting breeding strategies between species with long-lasting and short-lived flower heads (Stone et al. 2003). Increasing floral longevity may confer tolerance of competition for pollination (Levin 1978; Motten 1986; Rathcke 1988; Ashman and Schoen

Table 7 Results of Kolmogorov–Smirnov two sample tests of interspecific overlap in daily patterns of flower visitation for coflowering populations of *A. macracantha* and *A. angustissima* (site 4)

Year	Total flower visits		$D_{critical}$		Max. difference (D_{max})	p value
	A. macracantha	*A. angustissima*	$\alpha = 0.05$	$\alpha = 0.01$		
1998	15	434	0.357	0.427	0.431	<0.01
1999	43	191	0.230	0.275	0.480	<0.01
2000	42	82	0.258	0.309	0.488	<0.01

The null hypothesis (identity of the two distributions) can be rejected if D_{max} exceeds the $D_{critical}$ value at the appropriate significance level (α)

1994). Increased floral longevity could also facilitate the pollinating role of visitors (such as the smallest bees and many flies) whose very low rates of between-flower movement (Stone et al. 1999b) make them unsuitable as pollinators of short-lived flowers. The predominance of flies rather than bees in the visitor assemblages recorded for *A. farnesiana* is compatible with this hypothesis. *Acacia farnesiana* also showed consistently lower densities of flower heads than the other Chamela acacias. The paucity of bee visits to *A. farnesiana* might reflect the lower attractiveness of this acacia relative to others producing more showy floral displays (Proctor et al. 1996; Chittka and Raine 2006).

The potential role of relative humidity structuring multispecies plant–pollinator interactions

Our results show the significance of daily microclimate for patterns of pollen release in acacias, a further replication of patterns observed in the Tanzanian system. Drier days were predictably associated with earlier dehiscence peaks, particularly in *A. angustissima* and *A. hindsii*. Changes of relative humidity have been suggested as a causal mechanism triggering anther dehiscence in a wide variety of plant species through differential rates of tissue drying within the anther wall (Keijzer 1987; Bonner and Dickinson 1990). Parallel anther dehiscence responses with different threshold relative humidities shown by coflowering populations of *A. macracantha* and *A. angustissima* maintained a regular spacing between their respective peak times of pollen release over a wide range of humidity conditions (Fig. 8). If selection favoured the evolution of divergent dehiscence threshold humidities among coflowering species, the patterns we observe indicate that separation of pollen release in daily time (and hence pollinator activity) would be preserved over a wide range of ambient conditions. Heritable variation for other humidity-sensitive dehiscence mechanisms in plants is well established (Grant 1996; Bailey et al. 1997).

Flower visitor assemblages of Chamela acacias

Social bees played a dominant role in visiting the flowers of all three mass-flowering Chamela acacias, though their dominance varies spatially and temporally. The patterns of flower visitation by social bees (here predominantly *A. mellifera* and *S. hellwegeri*) suggest that these species visit mass-flowering *Acacia* trees when they are the most locally abundant pollen source, and that they are quickly abandoned if more profitable alternatives are discovered by the colony. Honeybees showed a similar pattern in

visitation to Tanzanian acacias (Stone et al. 1998). They are highly abundant in tropical ecosystems and information transfer amongst nest mates allows them to exploit multiple plant species in response to local variation in resource availability in space or time (Michener 1974; Roubik 1989; Dornhaus and Chittka 1999, 2004).

In contrast, solitary bees continued to visit mass-flowering acacias even when pollen availability was well below seasonal and daily maxima. This could reflect the reluctance of solitary bees to abandon waning resources due to uncertainty about locating better alternatives (Frankie et al. 1976; Strickler 1979; Ginsberg 1984), or their lower absolute pollen requirements in comparison to social colonies (Willmer and Stone 2004). Solitary bees may represent more reliable pollen vectors for mass-flowering *Acacia* species because they are predictably recruited if provided with minimal levels of floral reward. Some solitary species could be specialist pollen collectors from *Acacia* (or more generally mimosoid, including *Mimosa* and *Prosopis* at Chamela) species because of their predictable and relatively long flowering seasons. Strickler (1979) suggested such 'specialisation' might be characterised by fast flight between flower heads and specialist foraging behaviour (associated with reduced flower handling time), both shown by *Megachile* species visiting mass-flowering acacias in Mexico (this study) and Tanzania (Stone et al. 1998).

The continuation of visits by solitary bees after social bees have left may also enhance their contribution to seed set. In any protandrous species (including *A. angustissima*, *A. hindsii* and *A. macracantha*), the delay between anther dehiscence and stigma receptivity must balance the conflicting demands of avoiding self-pollination, whilst maximising the chances of receiving sufficient cross-pollen. In self-incompatible species, such as the three mass-flowering Chamela *Acacia* species, we expect stigma receptivity to occur long enough after dehiscence for stigmatic clogging by self-pollen to be rare. Most social bees arrived so soon after dehiscence that stigmas are unlikely to be receptive, meaning their visits probably dispersed pollen between flower heads within an individual canopy, rather than contributing to inter-tree dispersal and seed set. Later flower visits by large solitary bees, more coincident with female function, may well have contributed more to pollination than the frequency of their visits suggests (Strickler 1979; Motten et al. 1981; Minckley et al. 1994). Megachilid bees could be particularly effective vectors as they carry dry, unmodified pollen in a ventral abdominal scopa further enhancing potential pollen transfer (Thorp 1979, 2000).

Solitary bees showed considerable spatial variation in their patterns of visitation (see Supplementary material—Appendices C–F), which may reflect their dependence on

suitable nest sites and the limited foraging ranges of the smallest species (e.g., *Lasioglossum*). This observed spatial and temporal variation suggests that there are unlikely to be any tightly coevolved species-specific acacia–pollinator relationships, but that pollination is conducted by a diffuse, somewhat interchangeable, species guild. This observation is supported by the relative rarity of truly specialist pollinators in tropical environments (Roubik 1989, 1992). For the mass-flowering species, this guild is dominated by solitary bees, while *A. farnesiana* relies heavily on syrphid flies. The fact that syrphids are relatively specialised pollen feeders, show high levels of floral constancy (Goulson and Wright 1998) and innately prefer yellow flowers (Parmenter 1958; Kay 1976; Lunau and Maier 1995) makes them potentially good *Acacia* pollinators. They might be especially suited to pollinating sparsely flowering *A. farnesiana*, whose rewards may not meet the metabolic requirements of many bees. The beetles observed visiting acacia flowers are unlikely to be useful pollen vectors. They move between flowers too rarely, and most were destructive florivores or pollen feeders (Jolivet 1995, Proctor et al. 1996).

Potential impacts of shared pollinators

Many visitor taxa were shared across the three mass-flowering species, although their relative abundance varied across days and sites. Such variation suggests that the intensity of any acacia interactions mediated by shared pollinators probably also fluctuates between sites and seasons. The effectiveness of shared bee species as pollen vectors depends on multiple factors, including size, metabolic requirements (Strickler 1979), and floral constancy (Waser 1986; Raine and Chittka 2005, 2007a). The smallest bees are expected to be relatively poor pollinators because they fly relatively short distances from their nest and make extended visits to individual flower heads, often spending an entire foraging bout within a single *Acacia* canopy (Bernhardt et al. 1984). Larger solitary bees range over the entire surface of flower heads, contact large numbers of individual florets during short flower visits, visit fewer flower heads per canopy than smaller species, and probably fly further between visited trees. The fidelity (constancy) of shared pollinators is clearly linked to the potential for HPT (Waser 1986; Chittka et al. 1999, 2004; Raine et al. 2006). The morphological uniformity of acacia flowers means that although appropriate handling methods may need to be learned, these can then be applied to all acacias (Laverty 1980, 1994; Raine and Chittka 2007b). We might thus expect pollinators to move between coflowering *Acacia* species, with associated risk of HPT, unless other factors promote fidelity. Daily partitioning of pollen availability amongst coflowering species could potentially reduce such movement because available pollen is concentrated on a single species at a given time, promoting temporary floral constancy.

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