

**Pollinator assemblages of *Colletia spinosissima*
(Rhamnaceae):
composition, behavior, and specificity
(with 4 tables & 1 figure)**

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Abstract. The flowers of *C. spinosissima* Gmel. at three sites in Argentina during the 1998-2000 flowering seasons received visits of both day- and night flying insects which fed on nectar and/or pollen. The seventy-three visitor species include Diptera (39.7%), Hymenoptera (23.3%) and Lepidoptera (28.8%).

Across sites, the share of Hymenoptera and Lepidoptera in the visitor assemblage increased in the sequence Carretero, San Isidro, Los Aromos. Natural fruit set increased correspondingly, which may be related to the distinctly larger and more specific pollen loads carried by these groups.

The proportion of specialized visitors is the highest so far recorded within the tribe Colletieae. The moderately specialized, Lepidoptera-biased pollination syndrome of *C. spinosissima* is viewed as an intermediate step in a trend to pollination specialization taking place within Colletia.

Key words: *Colletia spinosissima*, pollinator assemblages, pollination specificity, Rhamnaceae

Pollinator service is crucial to reproduction of self-incompatible entomophiles. Within the Rhamnaceae, all species of Colletieae studied to date are self-incompatible (7, 3, 13, 12, 10).

We thank the owners of San Isidro, Carretero, and El Molino sites for permission to carry out field work. L Galetto and C Torres offered us logistic support during our work at Los Aromos. M Devoto helped us with the work at this site. ML Maldonado, JC Mariluis and A Roig-Alsina provided insect identifications. N Bartoloni assisted us with statistical analysis. Helpful comments by NH Montaldo and R Pozner contributed to improve this paper.

Financial support: Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (CONICET) PIP 4027-96 and the Universidad de Buenos Aires UBACYT TG-28. This work was done during a postdoctoral scholarship granted by the CONICET to AM Basilio. D Medan is a member of CONICET, Argentina

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Received 13.VII.2001; accepted 07.VIII.2001

In the present study we report on the composition and specificity of the pollinator assemblage of *C. spinosissima* Gmel., by comparing data from three populations distributed in two regions of Argentina. We investigate the constancy of the assemblage's composition among sites and along the blooming period within a site, and about the specificity of the different visitor groups as pollinators of *C. spinosissima*. We also inquire the variability of the assemblage's composition in the genus *Colletia*, comparing our data with those available for the related species *Colletia paradoxa*.

MATERIAL & METHODS

Study sites. Field work was done between July 1998 and February 2000 at three sites located in the provinces of Buenos Aires and Córdoba (Table 1). Both Buenos Aires sites are included in the MAB-UNESCO Biosphere Preserve "Parque Costero del Sur" in which agricultural work and cattle raising are routinely done (4). The Córdoba

Table 1.- Description and localization of field sites

Site	San Isidro	Carretero	Los Aromos
Province	Buenos Aires	Buenos Aires	Córdoba
Coordinates	35°S 57°30'W	35°20'S 57°20'W	31°44'10"S 64°26'34"W
Elevation (m a.s.l.)	2-5	2-5	620
N° of one day - period of field work)	12 (August 1998-February 2000)	15 (February 1999-February 2000)	2 September 1999-November 1999)
Longer stay of field work	One week during the 1998 flowering peak	4 days during the 1999 flowering peak	4 days during the 1999 flowering peak
Description of site	Mixed shrubland-grassland in open areas of the "talar" forest on sandy, calcareous soil	Mixed shrubland-grassland in open areas of the "talar" forest on sandy, calcareous soil	Riparian scrub on rocky soil
Size of the population of <i>Colletia spinosissima</i>	> 300 individuals	>1000 individuals	9 individuals
Herbarium vouchers	BAA 24166 to 24173	BAA 24362 and 24363	BAA 24306

site (Los Aromos) is located in a suburban area on the right bank of the Anisacate river.

Plant species. *C. spinosissima* is a spiny, virtually leafless shrub broadly distributed from Ecuador to the NE of Buenos Aires province in Argentina (15). Flowers (up to 55 presented in compact short-shoots) (16) are perfect, actinomorphic, 5-merous, with a white, pink, yellowish or greenish floral tube up to 7 mm long. Five deltoid sepals 1.5-3 mm long are located at the rim of the floral tube. The 5 stamens alternate with the sepals, with the anthers located at the level of the floral tube mouth. A nectariferous disc is near the bottom of the floral tube. The tri-carpellate gynoecium is composed by a semi-inferior, 3-ovulate ovary, style, and a terminal, trilobular stigma located at the level of the anthers.

Procedures. Insect behavior was studied by direct observation and by recording visits to 0.25 m² of flowering plant surface in 10 min censuses. A total of 26 censuses were made and direct observations on insect visitation for over ca. 65 h day and night. Representative individuals were caught for identification and for examining pollen loads. All collected material is deposited at our departament. Pollen was extracted from insects by rubbing on them a small piece of glycerin jelly, or by washing them in absolute ethanol and mounting the evaporated sediment in glycerin jelly.

The proportion of *Colletia* pollen in the pollen loads was determined to compute the Pollination Probability Index (PPI) = $PCP \times PBP$, where PCP = mean proportion of conspecific pollen grains in a pollen load of each insect, and PBP = the proportion of insect carrying that conspecific pollen captured on the flowers of the focal species (14). This index reflects floral constancy of each pollinator species at population level. The PPI varies from 0 (when no individual visitor carries the specific pollen) to 1 (when all visitors carry pure loads of the specific pollen), but does not inform about of quality of the pollen loads.

Data on reproductive system and maternal success of the focal species were published elsewhere (11). Information relevant to the present work is referred to in the discussion.

RESULTS

Composition of assemblages. All sites taken together, seventy-three insect species from 19 families in four orders visited the flowers of *C. spinosissima*. These included Diptera (39.7%), Lepidoptera (28.8%), Hymenoptera (23.3%) and Coleoptera (8.2%). The composition of the visitor assemblage varied among populations (Table 2). Taken

Table 2.— Composition of visitor assemblages to *Colletia spinosissima* flowers in three study sites (SI= San Isidro, C= Carretero, LA= Los Aromos). At the leftmost column the species which also visit *Colletia paradoxa* [according to D'Ambrogio & Medan (1993)] are pointed out. Species' occurrence at all three sites and *C. paradoxa* highlighted in boldface.

Visitor species	Family	Order	Field work sites			<i>Colletia paradoxa</i>
			SI	C	LA	
<i>Astylus cf. quadrilineatus</i>	Melyridae	Coleoptera	x	x		
<i>Astylus rubricosta</i>	Melyridae	Coleoptera			x	
Unidentified cantharid beetle sp. 1	Cantharidae	Coleoptera				x
Unidentified cantharid beetle sp. 2	Cantharidae	Coleoptera	x			
Unidentified coccinelid beetle sp. 1	Coccinelidae	Coleoptera	x			
Unidentified meloid beetle sp. 1	Meloideae	Coleoptera				x
Unidentified bionid fly sp. 1	Bibionidae	Diptera	x			
<i>Calliphora nigribasis</i>	Calliphoridae	Diptera	x	x		
<i>Sarconesia chlorogaster</i>	Calliphoridae	Diptera	x	x		
Unidentified calliphorid fly sp. 1	Calliphoridae	Diptera	x			
Unidentified muscid fly sp. 1	Muscidae	Diptera	x	x		
Unidentified muscid flies spp. 2-4			x			
<i>Oxysarcodexia culminata</i>	Sarcophagidae	Diptera	x	x		
Unidentified Stratiomyiid fly sp. 1	Stratiomyiidae	Diptera	x			
<i>Allograpta exotica</i>	Syrphidae	Diptera		x	x	x
<i>Allograpta</i> sp. 2	Syrphidae	Diptera		x	x	
<i>Argentinomyia</i> sp.	Syrphidae	Diptera		x		
<i>Copestylum spinigerum</i>	Syrphidae	Diptera			x	
<i>Eristalis tenax</i>	Syrphidae	Diptera	x			x
<i>Eristalis</i> sp.	Syrphidae	Diptera			x	
<i>Sphiximorpha barbipes</i>	Syrphidae	Diptera			x	
<i>Ocyrtamus</i> sp.	Syrphidae	Diptera			x	
<i>Palpada distinguenda</i>	Syrphidae	Diptera	x	x		x
<i>Palpada rufiventris</i>	Syrphidae	Diptera	x	x		
<i>Carposcalis saltana</i>	Syrphidae	Diptera		x		
<i>Platycheirus</i> sp. 2	Syrphidae	Diptera		x	x	
<i>cf. Syrphus</i> sp.	Syrphidae	Diptera		x		
<i>Toxomerus</i> sp.	Syrphidae	Diptera	x	x		
Unidentified syrphid fly sp. 1	Syrphidae	Diptera		x		
Unidentified syrphid fly sp. 2	Syrphidae	Diptera			x	
Unidentified tachinid fly sp. 1	Tachinidae	Diptera	x			
Unidentified therevid fly sp. 1	Therevidae	Diptera			x	
Unidentified muscoid fly sp. 1		Diptera	x			
<i>Apis mellifera</i>	Apidae	Hymenoptera	x	x	x	x
<i>Bombus bellicosus</i>	Apidae	Hymenoptera	x	x	x	
<i>Bombus</i> sp.	Apidae	Hymenoptera	x			

Table 2.— Continuation

Visitor species	Family	Order	Field work sites			<i>Colletia paradoxa</i>
			SI	C	LA	
Unidentified braconid wasp sp. 1	Braconidae	Hymenoptera	x			
<i>Augochlora amphitrita</i>	Halictidae	Hymenoptera	x			
<i>Augochlora phaeonoe</i>	Halictidae	Hymenoptera	x			
<i>Augochloropsis tupacamaru</i>	Halictidae	Hymenoptera	x			
<i>Augochloropsis</i> sp.1	Halictidae	Hymenoptera	x	x	x	
<i>Dialictus</i> sp.	Halictidae	Hymenoptera	x			
<i>Pseudagapostemon</i> sp.	Halictidae	Hymenoptera	x			
Unidentified halictid bees spp. 1-3	Halictidae	Hymenoptera			x	
<i>Brachygastra lecheguana</i>	Vespidae	Hymenoptera	x	x		
<i>Mischocyttarus</i> sp.	Vespidae	Hymenoptera		x	x	
<i>Polybia scutellaris</i>	Vespidae	Hymenoptera	x	x		
<i>Polybia</i> sp.	Vespidae	Hymenoptera			x	
<i>Phyloros rubriceps</i>	Ctenuchidae	Lepidoptera	x			x
<i>Cyanopepla jucunda</i>	Ctenuchidae	Lepidoptera		x		
<i>Eurota</i> sp.	Euchromiidae	Lepidoptera			x	
Unidentified geometrid moths spp. 1-2	Geometridae	Lepidoptera			x	
<i>Hylephila phyleus</i>	Hesperiidae	Lepidoptera	x	x	x	x
<i>Cnoides</i> sp.	Hesperiidae	Lepidoptera			x	
<i>Peridroma saucia</i>	Noctuidae	Lepidoptera			x	
<i>Plusia bonaerensis</i>	Noctuidae	Lepidoptera			x	
<i>Rachiplusia nu</i>	Noctuidae	Lepidoptera			x	
Unidentified noctuid moth sp. 1	Noctuidae	Lepidoptera			x	
<i>Agraulis vanillae</i>	Nymphalidae	Lepidoptera	x	x	x	x
<i>Euptoieta claudia</i>	Nymphalidae	Lepidoptera			x	
<i>Hypanartia bella</i>	Nymphalidae	Lepidoptera			x	
<i>Pampasatyris</i> cf. <i>periphias</i>	Nymphalidae	Lepidoptera			x	
<i>Ortilia ithra</i>	Nymphalidae	Lepidoptera	x		x	x
<i>Vanessa carye</i>	Nymphalidae	Lepidoptera	x	x	x	
<i>Vanessa braziliensis</i>	Nymphalidae	Lepidoptera	x	x	x	
<i>Tatochila vanvolxemii</i>	Pieridae	Lepidoptera	x	x		x
<i>Tatochila autodice</i>	Pieridae	Lepidoptera	x	x	x	x
<i>Atteva punctella</i>	Yponomeutidae	Lepidoptera			x	
Unidentified small moths spp. 1-2		Lepidoptera			x	
Total = 72	19	4	39	28	39	10

together, the Buenos Aires sites supported an assemblage of 46 species, of which 43.5% were present at both San Isidro and Carretero. The Córdoba assemblage (39 species) had only 11 species in common with one or both Buenos Aires sites. In terms of number of species, the

relative importance of the four insect orders did not significantly differ among sites ($\text{Chi}^2= 11.8$, $p > 0.05$). However, when taken together the more specialized pollinator groups Hymenoptera + Lepidoptera were better represented than Diptera + Coleoptera at Los Aromos (27/12 species), than they were at Carretero (13/15), and the difference approached significance ($\text{Chi}^2= 3.52$, $\text{df}=1$, $p= 0.06$). At Carretero only 26 insect species were observed visiting *C. spinosissima* flowers (Table 2). Again, Diptera made up a large part. At the Buenos Aires sites the composition of the visiting assemblage varied within the blooming period (Fig. 1). Diptera was the only group constantly present across the period, with Syrphidae prevailing over muscoid families. In San Isidro *Apis mellifera* was conspicuously present during the first half of the flowering period, while other Hymenoptera (mainly the wasps *Polybia scutellaris* and *Brachygastra lecheguana*) became frequent by the end of bloom (Fig. 1). The proportions of the visitors' taxa varied less at Carretero than at San Isidro, because Hymenoptera (especially honeybees) visited the focal species during the whole period and at significantly higher rates Carretero (Fig. 1), than at San Isidro (Chi^2 tests, $p < 0.01$ at all four blooming stages).

At Los Aromos population 39 insect species were observed visiting *C. spinosissima* flowers (Table 2). In number of species, Lepidoptera (including butterflies and moths) dominated the visitors' assemblage. Although Lepidoptera ranked third in terms of species diversity within

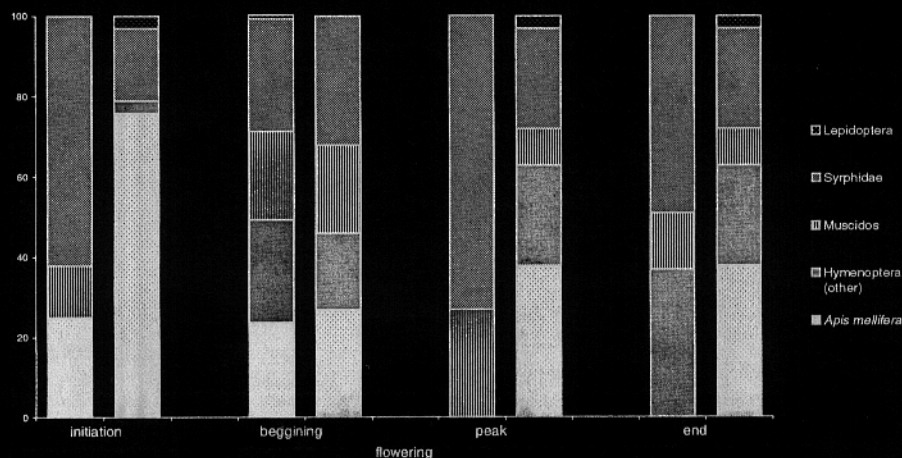


Figure 1.- Relative composition of visitor assemblages to *Colletia spinosissima* at four stages of the blooming period during the 1998 reproductive season (San Isidro, left column of each pair) and the 1999 reproductive season (Carretero, right column of each pair). For each site, censuses included in each blooming stage were averaged. Based on a total of 26 censuses.

the whole assemblage, it contributed the largest group of taxa present in all three sites (five species including Nymphalid, Hesperiid and Pierid butterflies). In fact, apart from Lepidoptera only the domestic bee, a *Bombus* sp. and an halictid bee were common to all sites.

Visitor behavior and specificity. Most Hymenoptera and Diptera visitors landed on a branch and then visited flowers successively before flying to another inflorescence or another plant, thus being able to effect both geitonogamous- and cross-pollination.

Lepidoptera carried out brief visits in sequences of 2-3 flowers on the same plant, and flew among plants more often than the other floral visitors. As a group, Lepidoptera carried the largest pollen loads (147.9 grains on average, Table 3), which were often pure *C. spinosissima* pollen (Table 4), resulting in the highest PPI. Pollen was more abundant on mouthparts of moths than on proboscides of butterflies (Table 3). The large amounts of specific pollen in the loads, together with apparent high fidelity to *C. spinosissima*, points to moths as the chief putative pollinator group in Los Aromos, the only site where moths visited the focal species.

Individuals of Hymenoptera carried the second-largest pollen loads (excluding corbicular loads) with an average of 118 pollen grains per load and with a high proportion of *C. spinosissima* grains (Table 3). Among Hymenoptera, the most frequent visitor was *Apis mellifera*, that only visited recently-opened (and even unopened) flowers (when nectar was not present) to gather pollen. Honeybees remained for a long time on a given plant, and made within-plant sequences of over 20 visits, thus removing all available pollen within 1-2 h after anthesis. Pollen loads of honeybees contained an average of 170.8 grains of *C. spinosissima* (Table 3), and the Pollination Probability Index (PPI) was 0.9. *Polybia scutellaris* visited plants frequently and often walked around flowers accidentally contacting anthers and stigmas. Average individuals of this vespid wasp carried 32 grains of *C. spinosissima* (Table 4) and the PPI was 1.0.

Table 3.— Size, and richness in *Colletia spinosissima* pollen, of pollen loads carried by the main groups of insect visitors.

Data from San Isidro, Carretero and Los Aromos were pooled.

Visitor group	Diptera	Hymenoptera	Lepidoptera
Mean number of pollen grains in the load	26.7	118.7	147.9
Percent of <i>Colletia</i> grains in the load	75.2	93.3	93.3
Number of sampled individuals	21	11	18
Number of insect species in the sample	9	5	8

Table 4.— Size and composition of pollen loads (corbicular pollen excluded) carried by the main insect visitors to *Colletia spinosissima* flowers. PPI was calculated as $PPI = (1) \times (2)$. C= Carretero, LA= Los Aromos, SI= San Isidro.

Insect species	Mean number of pollen grains per load	Proportion of <i>Colletia</i> grains in the load (1)	Proportion of visitors carrying <i>Colletia</i> grains (2)	Pollination probability index (PPI)	Mean number of <i>Colletia</i> grains in the load	Number of non- <i>Colletia</i> pollen species in the loads	Number of loads examined	Sampled sites
Muscoid flies	10.6	0.9	1.0	0.9	9.5	2	5	C,SI
<i>Allograpta</i> -type flies	43.3	0.7	1.0	0.7	30.3	3	7	C,LA,SI
<i>Palpada</i> sp.	25.0	0.5	1.0	0.5	12.5	5	6	C,LA,SI
<i>Apis mellifera</i>	181.0	0.9	1.0	0.9	162.9	5	7	C,LA,SI
<i>Vanessa</i> spp.	54.5	0.9	1.0	0.9	49.0	2	8	C,LA,SI
<i>Rachiptusia</i> nu	676.7	1.0	1.0	1.0	676.7	0	3	LA
<i>Polybia scutellaris</i>	32.0	1.0	1.0	1.0	32.0	0	2	SI
<i>Copestylum</i> sp.	117.5	0.6	1.0	0.6	70.5	8	2	LA
<i>Peridroma saucia</i>	62.5	1.0	1.0	1.0	62.5	0	2	LA
<i>Ortilia ithra</i>	11.5	1.0	1.0	1.0	11.5	0	2	LA

Small-sized Syrphidae (e.g., *Allograpta* spp., *Platycheirus* spp., *Toxomerus* spp.) performed sequences of up to 7 flowers on a branch. Besides collecting pollen they were seen licking the stigma. Pollen loads of *Allograpta*-type flies included on average about 29 *C. spinosissima* grains, but other pollen species were often present (e.g. *Jodina rhombifolia*, *Eucalyptus* sp., Fabaceae), lowering the PPI to 0.7. Larger-sized Syrphidae of the genus *Palpada* showed territorial behavior, flying around a given branch and chasing all other approaching insects except honeybees. *Palpada* individuals were seen sucking nectar from flowers, and carried on average 12 *C. spinosissima* pollen grains (Table 4), mixed with other pollen types (e.g. *Brassica* sp., *Glandularia* sp., *Eucalyptus* sp., Apiaceae), so lowering the PPI (0.5). *Copestylum* individuals carried on average 65 *C. spinosissima* grains, mixed with up to 8 other pollen species (e.g. *Brassica* sp., *Schinus* sp., *Eucalyptus* sp., Asteraceae-Cardueae, *Acacia* spp., Lamiaceae, and Fabaceae) resulting in a PPI of 0.6.

Muscoid flies (including Muscidae, Calliphoridae, Tachinidae and Sarcophagidae) visited flowers occasionally and spent a lot of time sunbathing on branches. They carried small amounts of pollen (the group average was 9.7 grains; Table 4) but since it was mostly *C. spinosissima* pollen, the PPI reached 0.9.

Coleoptera and Thysanoptera (the latter of common occurrence in flowers of all plants examined) were probably not involved in between-plants pollen transport, since individuals of these groups apparently consumed pollen only, and tended to linger in the same flower for long periods.

DISCUSSION

The proportion of relatively specialized groups in the visitor's assemblage (Lepidoptera plus Hymenoptera = 52.1%) is the highest so far recorded within the Colletieae (8, 3, 12, 10). This agrees with expectations, because the flower tube of *C. spinosissima* is the second deepest in the tribe (9), and this should exclude short-tongued visitor types such as most Diptera and Coleoptera.

Nectar-searching insects are probably responsible for most successful pollen transfers. Nectar is secreted at the bottom of the flower tube; thus, contact of mouthparts and heads of such visitors with anthers and stigmas is expected to occur frequently. Exclusive pollen-feeders are also potential pollinators, but these are expected to be less efficient: while pollen is easily accessible, pollen availability is often limited by its early removal by honey bees. Moreover, small pollen feeders like the minor Syrphidae may simply not contact the stigma. Successful transfer requires interplant flights, since *C. spinosissima* is strongly self-incompatible (11).

The *C. spinosissima* pollinator assemblage (72 insect species) is three times as diverse as that of the related species *Colletia paradoxa* [25 species (3)], a difference that should not, however, be overemphasized in view of the stronger sampling effort made in the present study. In a qualitative comparison, the *C. spinosissima* assemblage is noteworthy for its richness in Hymenoptera (the exotic, domestic bee being the sole representative of this order among the visitors of *C. paradoxa*). Only 13.7% of the *C. spinosissima* visitors were shared by *C. paradoxa* (Table 2) but, interestingly, this fraction included three out of the five butterfly species that occurred at all three *C. spinosissima* sites. Such fidelity suggests that Lepidoptera may play an important role in *Colletia* pollination. This is supported by the distinctly larger and specific pollen loads of *C. spinosissima* carried by Lepidoptera, and by the tendency of butterflies and moths to perform interplant flights. We propose to characterize the pollination

syndrome of *C. spinosissima* as moderately specialized and Lepidoptera-biased.

The other visitor groups seem to contribute less to pollination. Because of their foraging habit, *Apis mellifera* bees were mostly pollen robbers, and since they visited numerous flowers on the same plant, they probably caused much geitonogamous pollination and even clogging of the stigmas with incompatible pollen. The harsh flower handling exhibited by honeybees at *C. spinosissima* was also observed in *C. paradoxa* (3), and was already mentioned (1). In spite of the large pollen loads they carried and their high PPI values, their effectiveness might well be restricted to the pollination of the first flowers visited when first visiting a plant.

Syrphidae (mainly *Allograpta*-type spp. a *Palpada* sp.) performed short sequences of visits but showed the lowest PPI values due to the many pollen species carried in addition to *C. spinosissima*. *Palpada* flies showed territorial behavior, probably causing much geitonogamy. In spite of this, species of *Palpada* were likely important pollinators in the Buenos Aires sites, where Lepidoptera were relatively scarce.

Visitor assemblages of *C. spinosissima* changed in space and with time. The added proportions of Hymenoptera and Lepidoptera increased from Carretero (42.3%) to San Isidro (51.3%) and to Los Aromos (69.2%). Interestingly, size of stigmatic loads and natural fruit set increased in the same sequence (average stigmatic load: 34.9, 71.9, and 376.5 pollen grains per stigma; average fruit set: 0.4%, 10.9%, and 28.8%, respectively (11), indicating that, among populations, differences in the composition of the pollinator assemblage may be related to variations in fecundity. Differences in the integration of visitor guilds have been shown to cause changes in reproductive success of some plants (2, 5, 6). Since *C. spinosissima* is self-incompatible (11), it becomes crucial that a fraction of the available pollen be removed by efficient, 'long-distance' pollinators. Thus, the removal of most pollen by pollen-collecting honeybees would so severely deplete the exportable fraction that, wherever *Apis mellifera* is abundant, effective pollination would become a rare event.

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