Plant Syst Evol (2017) 303:51–59
DOI 10.1007/s00606-016-1351-1

ORIGINAL ARTICLE

Bamboo flowers visited by insects: do insects play a role in the pollination of bamboo flowers?

Eduardo Ruiz-Sanchez[1] · Luis C. Peredo[2] · Jezabel B. Santacruz[2] · Ricardo Ayala-Barajas[3]

Received: 24 March 2016 / Accepted: 5 September 2016 / Published online: 16 September 2016

Abstract Relatively little is known about pollination and other aspects of the reproductive biology of bamboos, but wind pollination is assumed to be the rule, at least in woody bamboos. Documenting the reproductive biology of woody bamboos is a complex task due to the long periods of time between flowering cycles, which range from 3 to 120 years. Insects visiting *Guadua paniculata* and *G. inermis* flowers were collected in the field. Scanning electron micrographs were taken of the visiting insects. Four species of bees, three from tribe Meliponini (*Geotrigona acapulconis*, *Plebeia frontalis* and *Trigona fulviventris*) and one from tribe Apini (*Apis mellifera*), along with a syrphid fly (*Toxomerus teligera*) were found visiting bamboo flowers. Some species of Hemiptera were also found feeding on the flowers, such as *Neortholomus jamaicensis* (Lygaeidae), or preying on the flower visitors (*Apiomerus pictipes* (Reduviidae)). Insects visiting bamboo inflorescences may facilitate the release of pollen grains into the air, promoting outcrossing and genetic flow among the individuals of the flowering bamboo populations.

Keywords Ancestral character estimation · Bamboos pollination · Bees · Fly · *Guadua* · Meliponini

Introduction

The Poaceae or grass family comprises 12 subfamilies, 771 genera and more than 12,074 described species (Soreng et al. 2015). One of those subfamilies is Bambusoideae (bamboos) with 1481 described species in 119 genera (BPG 2012; Clark et al. 2015). The bamboos are classified into three monophyletic tribes: Arundinarieae, Bambuseae (the woody bamboos), and Olyreae (the herbaceous bamboos) (Sungkaew et al. 2009; Kelchner and BPG 2013; Wysocki et al. 2015; Zhang et al. 2016). Arundinarieae species are distributed in Africa, Asia, and North America. Most of the Bambuseae species are distributed in the tropics and are divided into Paleotropical and Neotropical woody bamboo lineages. Almost all of the Olyreae species are distributed in the Americas (Kelchner and BPG 2013).

The flowers of grasses are very small and packaged somewhat differently than in most groups of flowering plants (Clark and Pohl 1996; Kellogg 2015). Grass flowers consist of a gynoecium, androecium, lodicules, palea, and a lemma with the exception of *Anomochloa* Brongn., and *Streptochaeta* Schard. ex Nees (Kellogg 2015). The flowers of grasses are arranged on a short axis (rachilla) and follow a distichous pattern forming the spikelet (Kellogg 2015). The flowers of bamboos follow this same pattern of small flowers, pendant position of anthers, and the lack of nectar, all of which are characters of the wind pollination syndrome (Judziewicz et al. 1999; Kellogg 2015). However,

Handling editor: Livia Wanntorp.

In memory of Luis Cervantes Peredo, a great colleague and friend.

✉ Eduardo Ruiz-Sanchez
ruizsanchez.eduardo@gmail.com

[1] Escuela Nacional de Estudios Superiores Unidad Morelia (UNAM), Antigua Carretera a Pátzcuaro 8701, Col. Ex Hacienda de San José de la Huerta, 58190 Morelia, Michoacán, Mexico

[2] Biodiversidad y Sistemática, Instituto de Ecología A.C., Carretera Antigua a Coatepec 351, 91070 Xalapa, Veracruz, Mexico

[3] Estacion de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Apartado Postal 21, 48980 San Patricio, Jalisco, Mexico

there are studies that have demonstrated insect pollination is possible, at least in *Eremochloa ophiuroides* (Munro) Hack., and *Paspalum dilatatum* Poir., grass species (Adams et al. 1981; Jones 2011).

Woody bamboo flowers are always bisexual, while unisexual flowers are found in the herbaceous bamboos (Judziewicz et al. 1999). The woody bamboos possess two types of reproductive structures, conventional spikelets, and pseudospikelets. Each of these can have one or more flowers; however, the pseudospikelets are more complex in structure and development due to the presence of gemmiparous bracts. These bracts can develop buds in their axils and rebranch to produce successive orders of pseudospikelets (Judziewicz et al. 1999; Kellogg 2015). In several bamboo genera, such as *Dendrocalamus* Nees, *Ochlandra* Thwaites, etc., the flowers are dichogamous and mostly protogynous (i.e. the stigma is exserted first followed by the stamens) (Venkatesh 1984; Nadgauda et al. 1993; Koshy and Harikumar 2001; Koshy et al. 2001). But in some *Bambusa* Schreb., species and *Merostachys riedeliana* Rupr. ex Döll both sexes mature together (homogamous) (Koshy et al. 2001; Guilherme and Ressel 2001), though protandrous (i.e. the stamens are exserted first followed by the stigma) flowers have been observed in *Melocanna baccifera* (Roxb.) Kurz and *Aulonemia aristulata* (Döll) McClure (Ramanayake and Weerawarde 2003; Grombone-Guartini et al. 2011). Woody bamboos typically exhibit gregarious flowering cycles, followed by the death of the parental plants (monocarpy) (Judziewicz et al. 1999).

Soderstrom and Calderón (1971) documented insect visits to the flowers of some herbaceous bamboo species. Nadgauda et al. (1993) did a floral biology study with *Dendrocalamus strictus* (Roxb.) Nees, a Paleotropical woody bamboo species, and tested for insect pollination in this species, but found no evidence of it. The insects fed on the pollen but were not pollen vectors. Grombone-Guartini et al. (2011) studied the floral biology of *A. aristulata*, a Neotropical woody bamboo species, with results similar to those of Nadgauda et al. (1993); i.e., the plant is wind pollinated and the insects only feed on the pollen grains.

Documenting the reproductive biology of woody bamboos is a complex task because of the long periods of time between flowering cycles. There are reports in the literature of flowering cycles that last 3–120 years (Janzen 1976; Guerreiro 2014; Veller et al. 2015). Franklin (2004) described four spatiotemporal patterns of flowering in addition to the gregarious monocarpy detected among semelparous bamboos: (1) a small percentage of clumps flower the year (or two) before and after the main flowering event, (2) gregarious flowering occurs in patches in successive years, (3) variation in periodicity among populations leads to diffuse temporality within species, and (4) sporadic flowering may imply a random or other nongregarious pattern of flowering (Troup 1921; Janzen 1976; Franklin 2004). However, there are documented cases (Table 1) of insects visiting flowers in woody and herbaceous bamboos in all three tribes (Soderstrom and Calderón 1971; Nadgauda et al. 1993; Guilherme and Ressel 2001; Koshy et al. 2001; Koshy and Harikumar 2001; Huang et al. 2002; Grombone-Guartini et al. 2011). Although they are not specific pollinators of bamboo, these insects are known to visit other species in the grass family.

In this paper, we report insects visiting the flowers of *Guadua paniculata* Munro and *G. inermis* Rupr. ex E.Fourn. Finally, based on the literature we wanted to know what role is played by the insects that visit bamboo flowers.

Materials and methods

Field work sampling

A flowering population of *G. paniculata* was found in the state of Oaxaca, Mexico, in the locality near Pochutla, Km 215 Oaxaca-Pochutla, at 15°51′46″N, 96°28′29″W, 316 m a.s.l. (voucher *E. Ruiz-Sanchez* and *L. Cervantes 447*, IEB). Specimens were collected on June 1, 2013, between 1200 and 1500 h. We observed several bee species, along with other insects, foraging for pollen during these hours. Only part of the bamboo population was flowering, and both insects and flowers were collected from a small patch of approximately 5 square meters. For *Guadua inermis,* we made observations of bees visiting flowers for two consecutive days (July 8–9, 2015) between 1200 and 1600 h. We observed only a couple of bees foraging for pollen during these hours. A small population was found where only one clump of bamboo was flowering, the rest was sterile. The locality was close to Aguilera, Veracruz, on the highway from Acayucán to Matías Romero at 17°52′2.3″N, 94°58′22.9″W, 7 m a.s.l. (voucher *E. Ruiz-Sanchez* and *A. Ortíz 530*, IEB). The bamboo specimens were deposited in the herbarium (IEB) and insect specimens in the Colección Entomológica (IEXA) of the Instituto de Ecología, A.C. Xalapa, Veracruz, Mexico, and in the Colección Entomológica Estación Chamela, Instituto de Biología, UNAM, Jalisco, Mexico (IBUNAM).

Scanning electron microscopy (SEM)

The SEM images were taken of bee and fly specimens with a JEOL JSM-5600LV Scanning Electron Microscope. The SEM samples were glued to aluminum stubs and coated with gold–palladium (1:1). These images of bee and fly specimens are necessary to better see the part of the insect's body on which the pollen grains are being carried.

Table 1 Bamboo species and the insect visitors recorded on their flowers

Woody bamboo species		Insect visitor			References
Species	Tribe: subtribe	Order	Family/subfamily/tribe	Species	
Actinocladum verticillatum (Nees.) McClure	Bambuseae: Arthrostylidiinae	Hymenoptera	Apidae: Meliponini	*Trigona* sp.	Filgueiras and Pereira (1988)
Aulonemia aristulata (Döll) McClure	Bambuseae: Arthrostylidiinae	Diptera	Syrphidae		Grombone-Guartini et al. (2011)
Bambusa bambos (L.) Voss	Bambuseae: Bambusinae	Hymenoptera	Apidae: Apini	*Apis cerana* F.	Koshy et al. (2001)
			Halictidae	*Halictus* sp.	
Bambusa chunii L.C.Chia & H.L.Fung		Hymenoptera	Apidae: Apinae	*Apis* sp.	Benton and Weatherhead (1995)
Bambusa flexuosa Munro		Hymenoptera	Apidae: Apini	*Apis* sp.	Benton and Weatherhead (1995)
Bambusa vulgaris Schrad. ex J.C.Wendl		Hymenoptera	Apidae: Meliponini	*Trigona biroi* Friese	Koshy et al. (2001) and Koshy and Hairkumar (2000)
			Halictidae	*Halictus* sp.	
Bambusa sp		Hymenoptera	Apidae: Apini	*Apis cerana* F.	Koshy et al. (2001)
			Halictidae	*Halictus* sp.	
Dendrocalamus strictus (Roxb.) Nees.		Hymenoptera	Apidae: Apini	*Apis mellifera* L.	Nadgauda et al. (1993)
			Apidae: Xylocopinae: Allodapini	*Allodape marginata* Smith	
Dendrocalamus copelandii (Gamble ex Brandis) N.H.Xia & Stapleton		Hymenoptera	Apidae: Apini	*Apis* aff. *mellifera* L.	Observation made by Khun Dieter in Kanchanaburi Thailand (Personal communication)
Guadua inermis Rupr. ex E.Fourn*	Bambuseae: Guaduinae	Hymenoptera	Apidae: Meliponini		This study
Guadua paniculata Munro*		Hymenoptera	Apidae: Apini	*Apis mellifera* L.	This study
			Apidae: Meliponini	*Geotrigona acapulconis* (Strand), *Plebeia frontalis* Friese, *Trigona fulviventris* Guerin	
		Diptera	Syrphidae	*Toxomerus teliger* (Fluke)	
Merostachys riedeliana Rupr. ex Döll	Bambuseae: Arthrostylidiinae	Hymenoptera	Apidae: Apini	*Apis mellifera* L.	Guilherme and Ressel (2001)
			Apidae: Meliponini	*Trigona spinipes* (F.)	
Ochlandra ebracteata Raizada & Chatterji	Bambuseae: Melocanninae	Hymenoptera	Apidae: Apini	*Apis cerana* F.	Koshy et al. (2001)
			Apidae: Xylocopinae: Ceratinini	*Ceratina heiroglyphica* Smith	
			Apidae: Xylocopinae: Allodapini	*Braunsapis mixta* Smith	
			Halictidae	*Halictus* sp.	
		Diptera	Calliphoridae		

Table 1 continued

Woody bamboo species		Insect visitor			References
Species	Tribe: subtribe	Order	Family/subfamily/tribe	Species	
Ochlandra scriptoria (Dennst.) C.E.C.Fisch.		Hymenoptera	Apidae: Apini	*Apis cerana* F.	Koshy et al. (2001), Koshy and Harikumar (2001)
Ochlandra travancorica (Bedd.) Benth. ex Gamble		Hymenoptera	Apidae: Apini	*Apis cerana* F.	Koshy et al. (2001) and Venkatesh (1984)
				Apis dorsata fabricius	
				Apis mellifera L.	
			Apidae: Meliponini	*Trigona biroi* Friese	
			Apidae: Xylocopinae: Allodapini	*Allodape marginata* Smith	
				Braunsapis picitarsis Cameron	
			Halictidae	*Halictus proteus* Vachal	
				Halictus sp.	
Phyllostachys nidularia Munro	Arundinarieae	Hymenoptera	Apidae: Apini	*Apis cerana* F.	Huang et al. (2002)
Schizostachyum zollingeri Steud.	Bambuseae: Melocaninae	Hymenoptera	Apidae: Apini	*Apis* sp.	Wong (1995)
			Apidae: Meliponini	*Trigona* sp	

Herbaceous bamboo species		Insect visitor			References
Species	Tribe	Order	Family	Species	
Olyra glaberrima Raddi	Olyreae: Olyrinae	Hymenoptera	Apidae: Meliponini	*Trigona amalthea* Olivier	Soderstrom and Calderón (1971)
Olyra obliquifolia Steud.		Coleoptera	Chrysomelidae	*Cyrsylus* sp.	
			Curculionidae: Cryptorhynchinae	*Cryptorhynchus* sp.	
		Diptera	Lauxaniidae	*Allominettia* sp., *Poecilominettia* sp.	
			Syrphidae	*Mesograpta Croesus* Hull	
		Hymenoptera	Apidae: Meliponini	*Partamona cupira* Smith, *T. fulviventris* Guérin, *T. pallida* Latr.	
Pariana campestris Aubl.	Olyreae: Parianinae	Coleoptera	Staphylinidae		
		Diptera	Chloropidae	*Ectecephala nitidifrons* Duda	
			Micropezidae	*Taeniaptera annulata* Fabricius	
		Hymenoptera	Formicidae	*Crematogaster* sp., *Ectatomma* sp, *Gigantiops destructor* (Fabricius)	
Pariana stenolemma Tutin		Coleoptera	Curculionidae: Baridinae: Limnobarini	*Valdenus laevis* Casey	
		Diptera	Cecidomyiidae: Clinodiplosini	*Chauliodontomyia agregia* Gagné, *C. parianae* Gagné	

Table 1 continued

Herbaceous bamboo species		Insect visitor			References
Species	Tribe	Order	Family	Species	
Pariana vulgaris Tutin		Coleoptera	Chrysomelidae	*Cyrsylus* sp., *Platymorpha* sp.	
			Curculionidae: Baridinae: Limnobarini	*Valdenus laevis* Casey	
			Curculionidae: Baridinae: Centrinini	*Parasaldius* sp.	
			Staphylinidae		
		Diptera	Cecidomyiidae: Clinodiplosini	*Chauliodontomyia. parianae* Gagné	
			Chironomidae: Orthocladiinae		
			Phoridae: Metopininae: Metopinini	*Pericyclocera gramminicola* Borgmeier, *P. parianae* Borgmeier	
			Rhicardiidae	*Richardia* sp.	
		Hymenoptera	Apidae: Meliponini	*Trigona cilipes* Fabricius	
				Partamona cupira Smith, *T. fulviventris* Guérin, *T. pallida* Latr.	
			Cynipidae: Eucoilinae		

* Insects recorded visiting bamboo flowers in this study

We also used a Leica Camera DFC290HD adapted to a dissecting microscope (Leica Microscope M50) to obtain images of the insect specimens.

Results

Insects visiting *Guadua paniculata* and *G. inermis* flowers

Four bee species were observed visiting the flowers of *G. paniculata* (Table 1; Fig. 1). Three were from tribe Meliponini (family Apidae): *Geotrigona acapulconis* (Strand, 1919), *Plebeia frontalis* (Friese, 1911), and *Trigona fulviventris* Guérin-Méneville, 1844; one from tribe Apini,

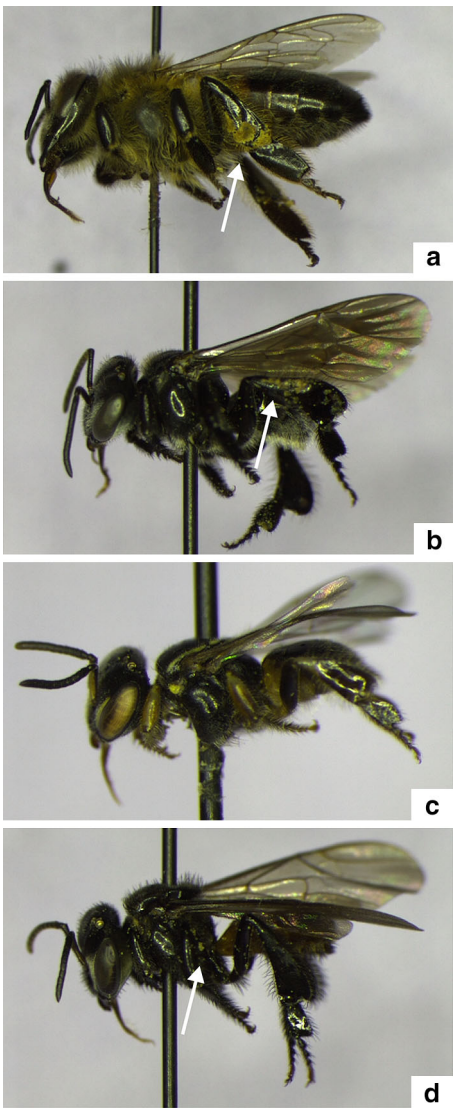

Fig. 1 Bee species included in this study. **a** *Apis mellifera*, **b** *Geotrigona acapulconis*, **c** *Plebeia frontalis*, and **d** *Trigona fulviventris*. *White arrows* indicate attached pollen grains (Photos by Luis Cervantes)

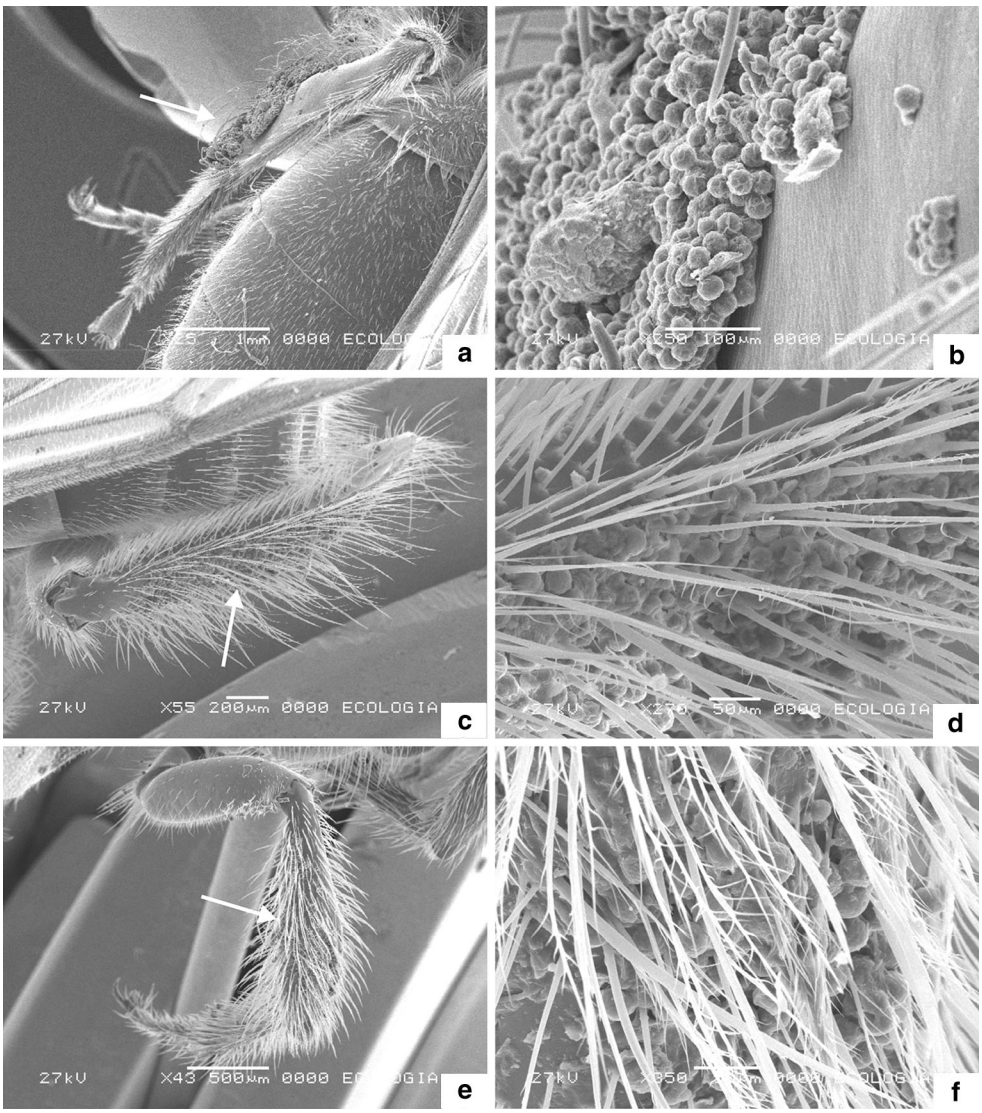

Fig. 2 SEM bee images. **a** Leg of *Apis mellifera* with pollen grains. **b** Close-up of *A. mellifera*'s leg showing pollen grains. **c** Leg of *Geotrigona acapulconis* with pollen grains. **d** Close-up of leg of *G. acapulconis* showing pollen grains. *White arrows* indicate attached pollen grains. **e** Leg of *Trigona fulviventris* with pollen grains. **f** Close-up of *T. fulviventris*'s legs showing pollen grains (Images taken by Tiburcio Laez)

Apis mellifera Linnaeus, 1758; there was also a syrphid fly, *Toxomerus teligera* (Fluke, 1953). Meliponini bees and *A. mellifera* were also observed visiting the flowers of *Guadua inermis* (Table 1; Fig. 1). Pollen was detected on the legs or bodies of bees, but not on flies. The bees of these species have specialized hairs on their legs for carrying pollen, as shown in Fig. 2. Some Hemiptera were also found feeding on the flowers, the Lygaeidae *Neortholomus jamaicensis* (Dallas, 1852), or preying on the flower visitors, the Reduviidae *Apiomerus pictipes* Herrich-Schaeffer, 1846 (Fig. 3).

We observed that the flowers of *G. paniculata* and *G. inermis* are dichogamous, with male and female organs exposed at different times and for different lengths of time and protandrous, i.e. the stamens exsert first.

Discussion

Insects visiting *Guadua* flowers

Santana-Michel (1992) reported several populations of *G. paniculata* flowering in the Sierra de Manantlán mountain range, Jalisco, Mexico. He mentioned that this species has flowering cycles of 25–26 years and flowered continuously from 1989 to 1991, but he did not report insects visiting the flowers in these *Guadua* populations. The beginning of the bloom in a population of *G. paniculata* in Oaxaca was recorded in 2009, with the last bloom event recorded in 2013 and the first record of insects visiting the flowers of this bamboo species. Our records and those of Santana-Michel

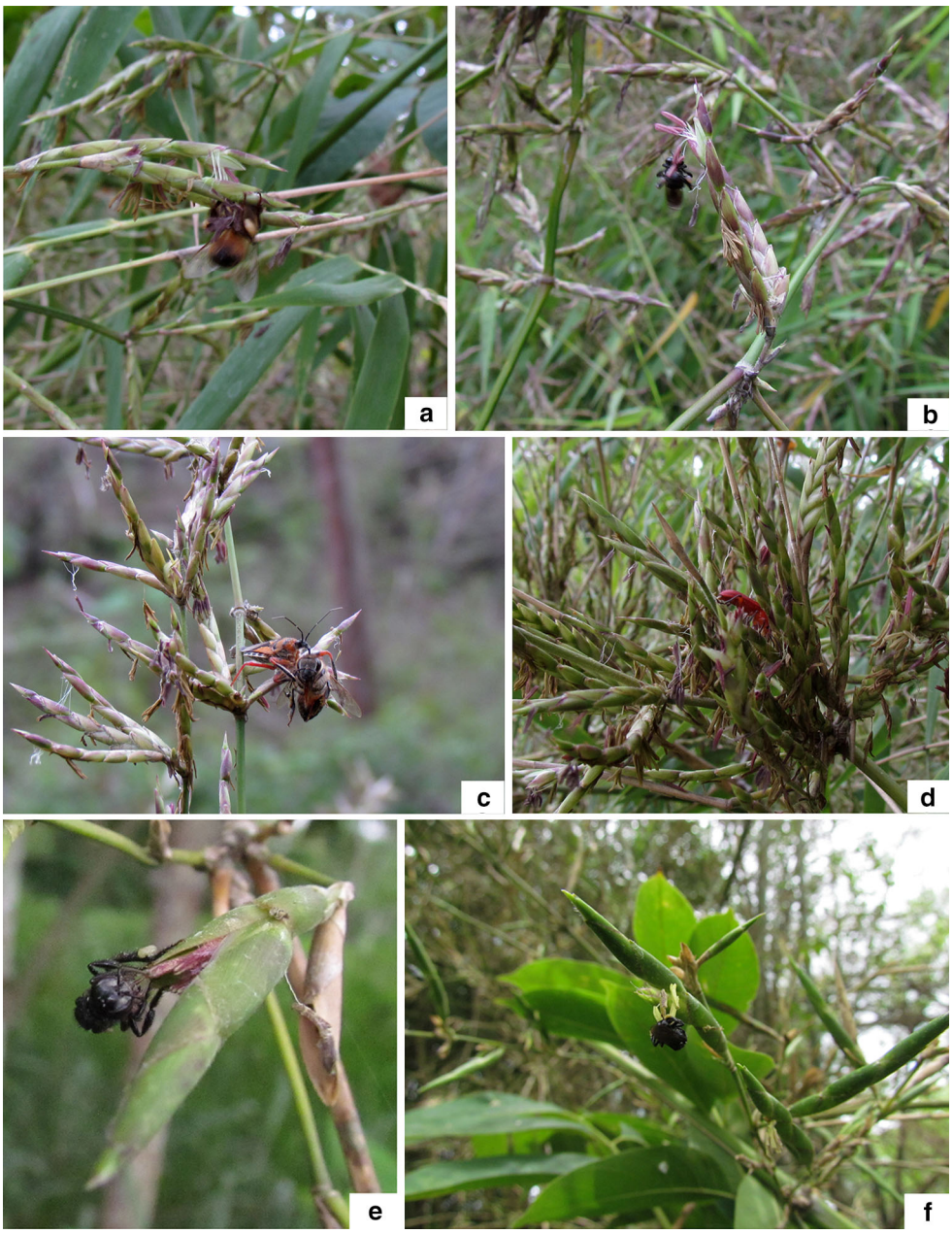

Fig. 3 Insect visitors to *Guadua paniculata* flowers. **a** *Apis mellifera*, **b** Meliponini bee removing pollen grains. **c** *Apiomerus pictipes*, preying on an *A. mellifera* bee, and **d** *Neortholomus jamaicensis* feeding on *G. paniculata* flowers. **e**, **f** Meliponini bee visiting *Guadua inermis* flowers (Photos by E. Ruiz-Sanchez)

(1992) coincide with Franklin's second pattern of spatiotemporal flowering events (Franklin 2004); i.e., gregarious flowering that occurs in patches in successive years. During fieldwork in the summer of 2015, four different populations of *G. inermis* were collected in the state of Veracruz, where one clump with flowers was observed in one of those populations. Two populations of *G. inermis* had mature flowers, one starting to grow pseudospikelets and only one with flowers in anthesis. This flowering behavior coincides with Franklin's fourth pattern of sporadic flowering and could imply a random pattern or other nongregarious pattern of flowering (Franklin 2004). We observed both species of *Guadua* have dichogamous and protandrous flowers. Ramanayake and Weerawarde (2003) mention that protandrous flowers are uncommon in bamboos.

Four species of bees from four genera and one fly species were recorded foraging for pollen on *G. paniculata* and *G. inermis*, and species of the genera *Geotrigona* and *Plebeia* were recorded for first time foraging for bamboo pollen (Figs. 1, 2). The bee species are generalists and typically forage for pollen on many different plant species. The genus *Geotrigona* is widely distributed throughout the Neotropics, occurring from Mexico to Argentina. It has 22 species and is related to the *Trigona* and *Tetragona* genera (Gonzalez and Engel 2012). *Geotrigona acapulconis* is only known from Mexico (Ayala 1999). The genus *Plebeia*

is the second largest genus of stingless bees in the Neotropics, with 39 species (Camargo and Pedro 2007; Melo and Costa 2009); this genus is likely to be more diverse when fully revised. *Plebeia* has 11 known species in Mexico (Ayala 1999). *Trigona fulviventris* is the most widespread Neotropical stingless bee species and occurs from northern Mexico to southern Brazil. Its highly plastic behavior confers flexibility on this species, which opportunistically obtains a variety of resources, such as fungi, dead animals, feces, and many types of pollen and nectar (Hernández et al. 2007). *Apis mellifera*, the honeybee, is the most widely distributed bee species in the world.

Species of the genus *Toxomerus* are the most abundant in the New World. In North America, the most common and widespread species is *Toxomerus marginatus* (Say, 1823). In the Neotropics, *Toxomerus dispar* (Fabricius, 1794) is the most common and widespread species, but in some areas, species such as *T. pulchellus* (Macquart, 1846) are more abundant. The common and widespread species *T. politus* (Say, 1823) is found in close association with corn (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.), with adults and presumably the larvae feeding on the pollen of these plants (Nunes-Silva et al. 2010). All other species for which data are available are predaceous as larvae, feeding on aphids (Heiss 1938). The larvae of *T. apegiensis* (Harbach, 1974) feed on the pollen of *Olyra obliquifolia* Steudel, an herbaceous bamboo (Reemer and Rotheray 2009). *Toxomerus apegiensis* and *T. politus*, which feed on the pollen of corn (*Zea mays*), are the only known phytophages within the otherwise predatory genus *Toxomerus* (Reemer and Rotheray 2009). The species *Toxomerus teliger* (Fluke, 1953) is distributed from the southern United States to Brazil (Metz and Thompson 2001).

Additionally, we found *A. pictipes* Herrich-Schaeffer, the assassin bug, on flowers preying on bees. In the genus *Apiomerus* (Hemiptera: Reduviidae), also known as bee killers, there are more than a hundred described species distributed from the northern USA to Argentina. *Apiomerus pictipes* is distributed from Mexico to Venezuela and Colombia (Berniker et al. 2011). *Neortholomus* is a Neotropical genus of Hemiptera (Lygaeidae) with nine recognized species (Hamilton 1983); *N. jamaicensis* has a wide distribution from California to Brazil and the Caribbean islands and feeds on different plant species (Hamilton 1983).

Insects visiting bamboo flowers have been recorded on species of herbaceous (Olyreae), woody tropical (Bambuseae) and woody temperate (Arundinarieae) bamboos (Table 1). Soderstrom and Calderón (1971) first documented insect visits to the flowers of five herbaceous bamboo species (Table 1). They stated that the insects visiting the flowers of these species transfer pollen among flowers rather than the wind doing so, because these herbaceous bamboos live in the forest understory where the wind is a limiting factor for pollination. Koshy et al. (2001) recorded the visit of bees on six Paleotropical woody bamboos species (Table 1). They mention that the bees never touch the stigmas in *Ochlandra* species, *Bambusa bambos* (L.) Voss, *B. vulgaris* Schrad. ex J.C. Wendl., or *Bambusa* sp., but if the flowers are widely open, pollen transfer could occur. Huang et al. (2002) observed bees visiting the flowers of *Phyllostachys nidularia* Munro, a temperate woody bamboo. They mention that the bees fed on pollen grains and that the anthers released huge amounts of pollen, so the bees play an indirect role in pollen transfer. On the other hand, three studies of floral biology tested insect pollination in *D. strictus* a Paleotropical woody bamboo, *A. aristulata* and *M. riedeliana*, both Neotropical woody bamboos and found no evidence of insect pollination for those species (Nadgauda et al. 1993; Guilherme and Ressel 2001; Grombone-Guartini et al. 2011). However, those studies agree that insects play a role, though an indirect one, in pollination given that the bees produced a vibration in the anthers of the flowers, triggering pollen release and acting as devices for the dispersal of pollen.

Two different hypotheses have been proposed regarding the role of bees in bamboo flowers. The first states that the bees only feed on the pollen grains (Nadgauda et al. 1993). The second states that the bees could have an indirect biological role in wind pollination, because they induce the anthers to release pollen rapidly. These pollen grains are dispersed into the air, which increases the probability of their colliding with the stigmas. Even if the insects do consume some of the pollen grains, a huge number of pollen grains remain to be dispersed by the wind (Huang et al. 2002). In this study, we did not test these competing hypotheses directly with our field observations. However, if the first hypothesis was true, we would expect to see insects (bees) feeding on bamboo flowers, which we did not see. Our observations of *G. paniculata* and *G. inermis* support the second hypothesis in which bamboo species visited by bees have an increased probability of sharing their pollen grains with other plants, thus facilitating outcrossing and promoting gene flow among plants of the same populations or from different populations. It is remarkable that these polylectic bees somehow contribute to the pollination of bamboo, but above all, it must be noted that the pollen of bamboos is an important resource for these bees for feeding their offspring.

Acknowledgments We want to thank Tiburcio Laez of the Instituto de Ecología, A. C. for taking the scanning electron images of the insects and the pollen studied. Bianca Delfosse revised the English version of this manuscript. Enrique Ramírez García identified the fly species. We also thank two anonymous reviewers whose suggestions greatly improved the manuscript. This research was partially supported by a competitive Grant (215514) from the Consejo Nacional de Ciencia y Tecnología, México (CONACyT).

Compliance with ethical standards

Conflict of interest The authors have declared that there are no competing interests.

References

Adams DE, Perkins WE, Estes JR (1981) Pollination systems in *Paspalum dilatatum* Poir. (Poaceae): An example of insect pollination in a temperate grass. Amer J Bot 68:389–394

Ayala R (1999) Revisión de las abejas sin aguijón de México (Hymenoptera: Apidae: Meliponini). Folia Entomol Mex 106:1–123

Bamboo Phylogeny Group [BPG] (2012) An updated tribal and subtribal classification of the bamboos (Poaceae: Bambusoideae). Bamboo Sci Cult 1:1–10

Benton AJ, Weatherhead MA (1995) The flowering of three species of thorny bamboos in Hong Kong: 1993–1995. In: Proceedings of the V international bamboo workshop and the IV International Bamboo Congress Ubud, Bali, Indonesia 19–22 June 1995

Berniker LS, Szerlip S, Forero D, Weirauch C (2011) Revision of the *crassipes* and *pictipes* species groups of *Apiomerus* Hahn (Hemiptera: Reduviidae: Harpactorinae). Zootaxa 2949:1–113

Camargo JMF, Pedro SRM (2007) Meliponini Lepeletier, 1836. In: Moure JS, Urban D, Melo GAR (eds) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region. Available at: http://www.moure.cria.org.br/catalogue. Accessed 10 Nov 2015

Clark LG, Pohl RW (1996) Agnes Chase's first book of grasses. The structure of grasses explained for beginners. Smithsonian Institute Press, Washington

Clark LG, Londoño X, Ruiz-Sanchez E (2015) Bamboo taxonomy and habitat. In: Liese W, Köhl M (eds) Bamboo, tropical forestry 10. Springer International Publishing, Switzerland, pp 1–30

Filgueiras TS, Pereira BAS (1988) On the flowering of *Actinocladum verticillatum* (Gramineae: Bambusoideae). Biotropica 20:164–166

Franklin DC (2004) Synchrony and asynchrony: observations and hypotheses for the flowering wave in a long lived semelparous bamboo. J Biogeogr 31:773–786

Gonzalez VH, Engel MS (2012) A new species of *Geotrigona* Moure from the Caribbean coast of Colombia (Hymenoptera, Apidae). ZooKeys 172:77–87

Grombone-Guartini MT, do Nascimento AA, Santos-Gonçalves AP (2011) Flowering and fruiting of *Aulonemia aristulata*: a gynomonoecious woody bamboo species from Atlantic Forest in Brazil. Revista Bras Bot 34:135–140

Guerreiro C (2014) Flowering cycles of woody bamboos native to southern South America. J Pl Res 127:307–313

Guilherme FAG, Ressel K (2001) Biologia floral e sistema de reprodução de *Merostachys riedeliana* (Poaceae: Bambusoideae). Revista Bras Bot 24:205–211

Hamilton SW (1983) *Neortholomus*, a new genus of Orsillini (Hemiptera-Heteroptera: Lygaeidae: Orsillinae). Uni Kansas Sci Bull 52:197–234

Heiss EM (1938) A classification of the larvae and puparia of the Syrphidae of Illinois exclusive of aquatic forms. Univ Illinois Bull 36:1–142

Hernández ET, Roubik DW, Nates-Parra G (2007) Morphometric analysis of bees in the *Trigona fulviventris* group (Hymenoptera: Apidae). J Kansas Entomol Soc 80:205–212

Huang SQ, Yang CF, Lu B, Takahashi Y (2002) Honeybee-assisted wind pollination in bamboo *Phyllostachys nidularia* (Bambusoideae: Poaceae)? Bot J Linn Soc 138:1–7

Janzen DH (1976) Why bamboos wait so long to flower. Ann Rev Ecol Syst 1:347–391

Jones TM (2011) Why is the lawn buzzing? Biodivers Dat J 2:1–10

Judziewicz EJ, Clark LG, Londoño X, Stern MJ (1999) American bamboos. Smithsonian Institution, Washington

Kelchner SA, Bamboo Phylogeny Group [BPG] (2013) Higher level phylogenetic relationships within the bamboos (Poaceae: Bambusoideae) based on five plastid markers. Molec Phylogen Evol 67:404–413

Kellogg EA (2015) Flowering plants. Monocots: Poaceae, vol 13. Springer, New York

Koshy KC, Hairkumar D (2000) Flowering incidences and breeding system in *Bambusa vulgaris*. Curr Sci 79:1650–1652

Koshy KC, Harikumar D (2001) Reproductive biology of *Ochlandra scriptoria*, an endemic reed bamboo of the Western Ghats, India. Bamboo Sci Cult 15:1–7

Koshy KC, Harikumar D, Narendran TC (2001) Insect visits to some bamboos of the Western Ghats. Curr Sci 81:833–838

Melo GAR, Costa MA (2009) A new cluster-brood building species of *Plebeia* (Hymenoptera, Apidae) from eastern Brazil. Revista Bras Entomol 53:77–81

Metz MA, Thompson FC (2001) A revision of the larger species of *Toxomerus* (Diptera: Syrphidae) with description of a new species. Stud Dipterol 1:225–256

Nadgauda RS, John CK, Mascarenhas AF (1993) Floral biology and breeding behavior in the bamboo *Dendrocalamus strictus* Nees. Tree Physiol 13:401–408

Nunes-Silva P, Cordeiro GD, Obregon D, Neto JFL, Thompson FC, Viana BF, Freitas BM, Kevan PG (2010) Pollenivory in larval and adult flower flies: pollen availability and visitation rate by *Toxomerus politus* Say (Diptera: Syrphidae) on sorghum *Sorghum bicolor* (L.) Moench (Poaceae). Stud Dipterol 17:177–185

Ramanayake SMSD, Weerawardene TE (2003) Flowering in a bamboo, Melocanna baccifera (Bambusoideae: Poaceae). Bot J Linn Soc 143:287–291

Reemer M, Rotheray GE (2009) Pollen feeding larvae in the presumed predatory syrphine genus *Toxomerus* Macquart (Diptera, Syrphidae). J Nat Hist 43:939–949

Santana-Michel FJ (1992) Floración de *Guadua paniculata* (Bambusoideae: Gramineae), un bambú silvestre de la Reserva de la Biosfera de Manantlán. Bol Inst Bot 1:205–210

Soderstrom TR, Calderón CE (1971) Insect pollination in tropical rain forest grasses. Biotropica 3:1–16

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Davis JI, Morrone O (2015) A worldwide phylogenetic classification of the Poaceae (Gramineae). J Syst Evol 53:117–137

Sungkaew S, Stapleton CMA, Salamin N, Hodkinson TR (2009) Non-monophyly of the woody bamboos (Bambuseae; Poaceae): a multi-gene region phylogenetic analysis of Bambusoideae s.s. J Pl Res 122:95–108

Troup RS (1921) The silviculture of Indian trees, vol III. Lauraceae to Coniferae, Clarendon

Veller C, Nowak MA, Davis C (2015) Extended flowering intervals of bamboos evolved by discrete multiplication. Ecol Lett 18:653–659

Venkatesh CS (1984) Dichogamy and Breeding system in a tropical bamboo *Ochlandra travancorica*. Biotropica 16:309–312

Wong KM (1995) The morphology, anatomy, biology and classification of peninsular malaysian bamboos. Univ Malaya Bot Monogr 1:1–189

Wysocki WP, Clark LG, Attigala L, Ruiz-Sanchez E, Duval MR (2015) Evolution of the bamboos (Bambusoideae; Poaceae): a full plastome phylogenomic analysis. BMC Evol Biol 15:50

Zhang XZ, Zeng CX, Ma PF, Haevermans T, Zhang YX, Zhang LN, Guo ZH, Li DZ (2016) Multi-locus plastid phylogenetic biogeography supports the Asian hypothesis of the temperate woody bamboos (Poaceae: Bambusoideae). Molec Phylogen Evol 96:118–129