

# Coffee plant – pollinator interactions: a review

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**Abstract:** Coffee (genus *Coffea* L.) is one of the most critical global agricultural crops. Many studies have focused on coffee plants and their associated insects. This review will summarize work specifically relating to coffee plant – pollinator interactions. We review the current status of coffee as a worldwide commodity, botanical aspects of coffee, and insects associated with coffee pollination, and we assess the current understanding of the role of different pollinator taxa in increasing fruit set and yield.

**Résumé :** Le café (le genre *Coffea* L.) représente une des cultures agricoles globales les plus importantes. Plusieurs études se sont intéressées aux caféiers et aux insectes qui leur sont associés. Notre rétrospective résume les travaux reliés spécifiquement aux interactions caféiers–pollinisateurs. Nous examinons le statut actuel du café comme denrée mondiale, les aspects botaniques du café et les insectes associés à la pollinisation du café et nous évaluons la compréhension actuelle des rôles des différents taxons de pollinisateurs dans l'augmentation de la nouaison et du rendement.

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## Introduction

With approximately 2.28 billion cups consumed every day (Dicum and Luttinger 1999; Bacon 2005), coffee is the world's second most important legally traded commodity after oil (Daviron and Ponte 2005). Coffee is cultivated in approximately 80 tropical countries, and for some, it is their top source of foreign currency (Ridler 1983; Clay 2004; Schmitt 2006). The global coffee industry directly involves 25 million farmers and indirectly employs 125 million people (Donald 2004). Coffee is cultivated on approximately 11.5 million hectares of land, mainly owned by small-farm holders that usually have less than 10 ha of land each (Gresser and Tickell 2002; Lewin et al. 2004; FAO 2004, 2008). Because 70% of coffee producers are small-scale farmers, fluctuations in coffee prices greatly affect their livelihoods (Perfecto and Armbrecht 2003; Brown et al. 2001; Oxfam America 2005). The declining price of coffee over the last three decades has forced many farmers to sell coffee below cost or completely give up its cultivation (FAO 2003b; Lewin et al. 2004; Bacon 2005).

Commercial coffee production involves mainly two species, *Coffea arabica* L. (arabica coffee) and *Coffea canephora* Pierre ex. Froehner (robusta coffee), that make up nearly 66% and 34%, respectively, of the coffee market (Somarrriba et al. 2004; Camargo 2009). The other minor commercial coffee species, *Coffea liberica* Bull ex Hiern. (liberica) and *Coffea liberica* var. *dewevrei* (De Wild. & T. Durand) LeBrun (excelsa), together contribute less than 1%

of the coffee market (Davis et al. 2006). These ratios of coffee produced for consumption have not changed drastically since the 1950s when *C. arabica* and *C. canephora* were supplied at 75% and 25%, respectively (Meyer 1965).

The International Coffee Agreement (ICA), established in 1962 among coffee-producing countries, was responsible for maintaining coffee trade quotas and ensuring surplus coffee did not enter the market (Bacon 2005) and was indirectly responsible for stabilizing coffee prices (Marsh 2007). This agreement was suspended in 1989, leading to a de-stabilization of the market and coffee prices began to fall (Clay 2004). In 1988, the price of coffee was US\$1.24/lb, but this fell to US\$0.62/lb in 1989 (ICO 2004). Countries such as Vietnam flooded the market in the 1990s (Ha and Shively 2008), producing more than 160 times more coffee than it did in 1961 (Donald 2004), and it is now the second highest coffee-producing country in the world (Ramirez-Vallejo 2002).

The temporary coffee glut followed by the precipitous decrease in coffee prices did not slow down global coffee production (Ha and Shively 2008): the annual rate of growth in coffee production from 1999 until 2010 was forecast to be approximately 0.5% (FAO 2003a). Countries such as India, Vietnam, and Indonesia are increasing coffee output by 2% or more annually, while countries such as Brazil, a major coffee producer, is projected to decrease production by 4.4% (FAO 2003a). Asia increased its contribution of coffee exports (volume) by almost 7-fold (Rice 2003) from 1961 to 2000. Global coffee production is projected to grow annually

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at a rate of 1.2% up until 2030 (FAO 2003*b*), while global coffee consumption is also projected to rise 1.2% (per capita), which is 1.1 kg/person annually by 2030 (FAO 2003*b*).

Many aspects of the biology of *Coffea* have been studied and reviewed: ecophysiology (Maestri and Barros 1977; Barros et al. 1995, 1997; Beining 2007; DaMatta et al. 2008), seed physiology (Eira et al. 2006), fruit development (De Castro and Marraccini 2006), root competition (Ronchi et al. 2007), chemical composition (including caffeine content) (Baumann 2006; Spiller 1998; Campa et al. 2005), growing regimes (Beer 1987; Beer et al. 1998), diseases (Souza 2008; Waller et al. 2007), and taxonomy (Chevalier 1947; Davis et al. 2006).

We begin by briefly reviewing botanical aspects of coffee and management practices. We focus only on the four coffee varieties that are produced for the commercial market: *C. arabica*, *C. canephora*, *C. liberica*, and *C. liberica* var. *dewevrei*. We then review the current knowledge of coffee pollination, mainly concentrating upon coffee-pollinator information.

## Production systems and coffee botanics

*Coffea* belongs to the family Rubiaceae and originated in tropical Africa (DaMatta 2004*b*). There are approximately 103 species of *Coffea* (Hatanaka et al. 1999; Davis and Rakotonasolo 2001*a*, 2001*b*; Davis et al. 2006), with new species still being discovered (Davis and Rakotonasolo 2001*a*, 2001*b*; Stoffelen et al. 2009) and even more varieties being bred (Mazzafera and Carvalho 1991; Nagai et al. 2008). They are classified in two subgenera: *Coffea* (with 95 species) and *Baracoffea* (J.-F. Leroy) J.-F. Leroy (with 8 species) (Maurin et al. 2007). All the commercial species belong to the nominate subgenus (Berthou et al. 1983; Maurin et al. 2007). *Coffea* is a tropical, perennial woody shrub that usually grows to 3–12 m in height if left unpruned (Clay 2004; Mengistu 2007; Belitz et al. 2009). Coffee is grown in approximately 85 tropical and subtropical countries (Berthoud and Charrier 1988; Bridson and Vercourt 1988; Rice 2003). *Coffea* is a short-day plant (Masarirambi et al. 2009), requiring a certain length of dark period (night time) to initiate flowering (Glimn-Lacy and Kaufman 2006). The coffee root system is extensive and contained mostly in the first 60 cm of the soil layer but can extend down to 3 m in depth (Rena and DaMatta 2002; Vieira 2008). Almost all coffee species have persistent leaves (Vieira 2008), leaves that remain on the plant after maturity or past the time of the flowers withering. *Coffea* typically have a single main trunk but can be grown using a multiple trunks system (Kimani et al. 2002). Orthotropic (vertical) branches extend from the main trunk (Vieira 2008), and from them, plagiotropic (near horizontal) branching occurs (Davis et al. 2006). Inflorescences are present in clusters, or serial buds, at the axils of the plagiotropic branches (Vieira 2008). There are anywhere from 2 to 20 flowers at each of these axils (Free 1993).

The structure of the coffee flower, pollen, and fruit are well known (Cheney 1925; Stoffelen et al. 1997; Davis et al. 2006). Pollen morphology of 26 coffee species has been described (Stoffelen et al. 1997). Cheney (1925) summarizes coffee flower morphology. Briefly, the flowers are supported by a short pedicel and have a rudimentary five-petal calyx, a

white corolla, and relatively short anthers (Cheney 1925; McGregor 1976; Free 1993).

Coffee fruits are “drupes” (fleshy fruits that have a hard nut) (Peterson and McKenny 1998; De Castro and Marraccini 2006) and normally develop with two ovules (Klein et al. 2003*b*). “Pea berries” form during coffee fruit development when only one ovule matures and one is aborted, resulting in one seed (Raw and Free 1977; Van der Vossen 1985; Free 1993). Pea berries are normally undesirable (McGregor 1976; Ricketts et al. 2004), being deformed or misshapen (Muschler 2001), but there is a small market for pea berry coffee (Ricketts et al. 2004). From the time of seed germination, coffee shrubs take anywhere from 3 to 5 years to flower and bear fruit (Clay 2004; Belitz et al. 2009; Wintgen 2004).

Five different categories of coffee farms have been described by Moguel and Toledo (1999); these are separated by levels of management and floristic complexity. Briefly, coffee farms can range from traditional rustic systems, where most of the original canopy and plant diversity is maintained while coffee is planted into this system, to highly modernized monoculture “sun coffee” farms (Rice and Ward 1996; Moguel and Toledo 1999). A “sun coffee” farm, also referred to as an unshaded monoculture system, has only coffee shrubs that are exposed to direct sunlight (Moguel and Toledo 1999). For a more detailed method of separating coffee farm production systems see Mas and Dietsch (2003).

## *Coffea arabica*

Beans of *Coffea arabica* are produced and sold for higher quality coffees (DaMatta et al. 2007). All varieties of *C. arabica* are self-fertile (i.e., autogamous, receiving pollen from its own stamen) (Manrique and Thimann 2002) and allotetraploid (having four sets of chromosomes not two,  $2n = 4x = 44$ ) (Krug 1935; Charrier and Berthoud 1985; Clarindo and Carvalho 2008), whereas all other coffee species, including *C. canephora*, are self-incompatible diploids ( $2n = 22$ ) (Charrier and Berthoud 1985). The diploid progenitors of *C. arabica* are *Coffea eugenioides* Moore and either *Coffea congensis* Froehner or a very close relative (Raina et al. 1998; Lashermes et al. 1993).

*Coffea arabica* originated from the rainforests of the Ethiopian highlands around 850 CE (common era) (Monaco 1968; Somarriba et al. 2004; Schmitt 2006; Vieira 2008), where it grows naturally in the understory of montane rainforests between 1000 and 2800 m above sea level (DaMatta 2004*a*; Schmitt 2006). Arabica plants thrive best in environments that have between 1200 and 1800 mm of rainfall annually and temperature ranges of 18–21 °C (Alègre 1959).

The flowering period of *C. arabica* can vary from region to region but is generally from January to April. The flowering events are in synchronous flushes after a heavy rainfall following a dry period (Vieira 2008). In one coffee reproductive period, there is usually more than one flowering event (Wormer 1964; Alvim 1977). Mature flowers of *C. arabica* are hermaphroditic, white, and have a scent similar to jasmine (Krug 1935). Flowers open at dawn and pollen starts shedding soon after. At this time, the stigma is receptive and pollination can occur until noon (Alvim 1985). Flowers of *C. arabica* usually wither in 1 or 2 days after pollination (Free 1993; Aga 2005), but if not pollinated, they can remain open for up to 5 days (Jiménez-Castano and Castillo-Zapata

1976; Free 1993). With other coffee species, anthesis (the flowering period), normally lasts slightly longer, 1–3 days (Wormer 1964; Alvim 1977). Upon completion of the flowering period, fruits develop over the next 7–10 months (De Castro and Marraccini 2006; Eira et al. 2006). Most literature report that the percentage of flowers that eventually develop into beans ranges from 20% to 40% (Purseglove 1968; Free 1993). More recently, Klein et al. (2003a) reported natural fruit set (i.e., the proportion of fruits formed) of *C. arabica* in Costa Rica to be 75.2%.

**Coffea canephora**

The other important commercially grown *Coffea* species is lowland *C. canephora*, commonly known as “robusta” coffee. *Coffea canephora* is mostly used for instant coffees (Moncada and McCouch 2004). The beans are lower in quality (i.e., with less flavour and more acidity) (Reiger 2006) but have approximately double the amount of caffeine per bean (2%–3% of the total bean mass) compared with *C. arabica* (Willson 1999; DaMatta 2004b). Even though *C. canephora* sells for less, farmers often choose to cultivate *C. canephora* over *C. arabica* because of its greater resistance to pests and diseases and potential for higher yields (Moncada and McCouch 2004; Reiger 2006).

Robusta coffee originated from the lowlands of west Africa (DaMatta 2004b; Clay 2004), where it was discovered in 1895 (Spiller 1998) and is mainly grown in Africa and Asia. It is generally grown in humid, evergreen forests from sea level to 1200 m (Willson 1999), requires 1800–2000 mm of rainfall per year (more than required by *C. arabica*) (Alègre 1959), and prefers a hotter climate with optimal temperatures ranging between 24 and 30 °C (Hicks 2001).

The flower morphology of *C. canephora* has been described (Purseglove 1968), and the formation of its reproductive buds has been studied (Piringer and Borthwick 1955; Went 1957). This coffee species is grown with a multiple trunk system (Vieira 2008). *Coffea canephora* can grow up to 30 m in height but usually only to 2–3 m when pruned (Luttinger and Dicum 2006). The flower and shrubs of *C. canephora* tend to be larger compared with *C. arabica*; its leaves are slightly larger and paler green in colour (Klein et al. 2003b; Sureshkumar et al. 2010). Otherwise, the general structure of the shrub, roots, and flowers are similar to those of *C. arabica* (Willmer and Stone 1989).

There is a difference in flowering patterns between *C. arabica* and *C. canephora*. With *C. canephora*, the flowers grow on the branches of the present year, whereas with *C. arabica*, the flowering happens on branches from the previous year (Dean 1939; Moens 1968; Vieira 2008). Otherwise their flowering phenologies are similar (Willmer and Stone 1989). Willmer and Stone (1989) have observed 0900 to be the time where pollen viability is the highest for *C. canephora*. The pollen grains of all diploid *Coffea* species, including *C. canephora*, are relatively light and airy (Free 1993; Willmer and Stone 1989) (Table 1).

After pollination, the fruits of *C. canephora* take approximately 2 months longer to mature (i.e., 9–11 months) than those of *C. arabica* (Wellman 1961; De Castro and Marraccini 2006). Percentage of fruit set for *C. canephora* is around 78.1% (Klein et al. 2003a). Compared with *C. arabica*, the

**Table 1.** A summary of the botanical information of the four *Coffea* species.

	<i>C. arabica</i> ( <i>arabica</i> )	<i>C. canephora</i> ( <i>robusta</i> )	<i>C. liberica</i> var. <i>liberica</i> ( <i>liberica</i> )	<i>C. liberica</i> var. <i>deweyrei</i> ( <i>excelsa</i> )
Pollination	Self-fertile or autogamous	Self-incompatible	Self-incompatible	Self-incompatible
Ploidy level	Allotetraploid (44 chromosomes)	Diploid (22 chromosomes)	Diploid (22 chromosomes)	Diploid (22 chromosomes)
Origin	Ethiopia	West Africa	West Africa (Guinea, Liberia, Ivory Coast)	Central Africa
Altitudinal range (m)	1000–2800	0–1200	0–1000	200–1300
Required rainfall (mm)	1200–1800	1800–2000	1000–1800	
Optimal temperature range (°C)	18–21	24–30		
Flowering period	January–April	February–March	September–March	March–July
Fruit development time (months)	7–10	9–11	12–14	11–12
Time highest pollen viability (h)		0900		
Pollen	Relatively heavy and sticky; variable shape; 6 morphological variations; 30–47 µm long and 28–38 µm wide	Light and airy; size range 23–35 µm and almost spherical	Light and airy; radially symmetrical and spheroidal; 19–24 µm long and 21–26 µm wide	Light and airy; radially symmetrical; 24–27 µm long and 22–25 µm wide
Mean wet fruit mass (g)	1.3–1.64	1.28		
Mean dry fruit mass (g)	0.325		0.3	



resulting bean of *C. canephora* is slightly smaller and rounder (Eira et al. 2006) (Table 1).

### *Coffea liberica* and *Coffea liberica* var. *dewevrei*

*Coffea liberica* (liberica) and *C. liberica* var. *dewevrei* (excelsa) are the other two coffee types that are commercially traded (Davis et al. 2006). *Coffea liberica* var. *dewevrei* is a variety of *C. liberica* (Lebrun 1941; Bridson 1985).

*Coffea liberica* was first described by Hiern (1876) and originated from western Africa, whereas *C. liberica* var. *dewevrei* came from central Africa (N'diaye 2005, Charrier and Berthaud 1985; Campa et al. 2005). Like *C. canephora*, both *C. liberica* and *C. liberica* var. *dewevrei* grow in humid or seasonally dry evergreen forests (Davis et al. 2006; Waller et al. 2007). *Coffea liberica* has a widespread distribution, similar to that of *C. canephora*, from Guinea to Angola (west Africa) (Anthony et al. 1993; Reddy and Narayan 1981; Waller et al. 2007). *Coffea liberica* is found and cultivated in altitudes from sea level up to 1000 m (Eskes 1989) (Table 1).

*Coffea liberica* var. *dewevrei* was described by Lebrun (1941). It is also found growing in humid evergreen forests at elevations ranging from 200 to 1300 m (Bridson 1982; Davis et al. 2006). Both *C. liberica* and *C. liberica* var. *dewevrei* have relatively large fruit and flowers compared with those of *C. canephora* (Cramer 1957; Reddy and Narayan 1981). The main flowering period for *C. liberica* is from September until March, although flowerings can happen sporadically throughout the year (Cramer 1957). The major coffee flowering months for *C. liberica* var. *dewevrei* are from March to July (Dagoon 2005), but this may vary according to region and annual weather conditions. Mature beans of *C. liberica* (both varieties) are large and orange to orange-red in colour (Chinnappa 1970). *Coffea liberica* takes 12–14 months to mature, while *C. liberica* var. *dewevrei* takes 11–12 months (De Castro and Marraccini 2006; Wintgen 2009).

### Pollination mechanism

#### Wind

Anemophily, or wind pollination, is important for species in approximately 18% of angiosperm families (Ackerman 2000; Culley et al. 2002). The importance of wind for coffee pollination varies among species. With *C. arabica*, Le Pelley (1973) noted, based on the structure of pollen grains (i.e., heavy and sticky), that wind would not carry pollen very far and that cross-fertilization can mostly be attributed to insects. A more recent study (Klein et al. 2003a) tested the importance of different pollinating mechanisms for both *C. arabica* and *C. canephora*. For *C. arabica*, they found fruit set to be 62.9% when exposed to only wind and autogamy (self-fertilization). The control treatment excluded wind and just tested for the percentage of fruit set based on autogamy, which was 47.9%. Therefore, wind was responsible for a 1.31-fold increase in fruit set of *C. arabica*.

*Coffea canephora* and all other self-incompatible *Coffea* species have light and dry pollen, therefore wind is assumed to be the major pollinating vector (Le Pelley 1973; McDonald 1930; Free 1993). Ferwerda (1948) reported that pollen travelled up to 100 m, concluded that wind was the main

pollination vector for *C. canephora*, and that insects played an “insignificant” role in cross-pollination. Furthermore, wind and gravity transfer of pollen were sufficient to meet adequate pollination levels in *C. canephora*. Other studies also looked at wind transfer of pollen of *C. canephora*. In attempts to see how efficient wind is as a pollinating agent, Charrier (1971) tracked pollen with radioactive phosphorus and sulphur. He noted, in the absence of insects, that within 6 m of the source, 50%–100% of all stigmas received radioactive pollen, whereas beyond 24 m, no radioactive pollen was transferred by wind. Klein et al. (2003a) also studied effectiveness of wind for pollination of *C. canephora*. They found fruit set to be 62.3% in treatments with wind and autogamy. With wind excluded (i.e., only autogamy), the fruit set in *C. canephora* was only 8.9%. Therefore, wind did play a significant role in increasing pollination of *C. canephora* by increasing fruit set by a factor of more than 7. The discrepancies among studies regarding how far pollen of *C. canephora* can travel likely depend on the specifics of the environmental conditions at the study sites.

No information on wind pollination of *C. liberica* or *C. liberica* var. *dewevrei* could be found.

#### Bees

##### *Coffea arabica*

Bees have long been recognized for their important role in pollination of *C. arabica* (McDonald 1930; Krug 1935; Amaral 1952, 1960, 1972; Smith 1958; Nogueira-Neto et al. 1959; Raw and Free 1977; Badilla and Ramírez 1991; Manrique and Thimann 2002; Roubik 2002a, 2002b; Klein et al. 2003a, 2003b, 2003c; De Marco and Coelho 2004; Ricketts 2004). Similar conclusions have also been made for *C. canephora* (Willmer and Stone 1989; Klein et al. 2003a, 2003b).

In Brazil, Amaral (1960) found that bees were important pollinators of *Coffea arabica* var. *caturrea*. With exclusion experiments, Amaral (1960) found fruit set in treatments with bee visits to be 1.22 times higher than in treatments where bee visitors were excluded. Amaral (1960) identified the most frequent visitors (i.e., number of flowers visited per unit time) of coffee flowers to be honey bees (*Apis mellifera*). Amaral (1972) studied insect visitors of *C. arabica* var. *Mundo Novo* in Brazil. He observed that honey bees were the main visitor of coffee flower, whereas the stingless bees *Trigona spinipes* and *Partamona testacea*, as well as carpenter bees (*Xylocopa* sp.) were minor visitors.

In Jamaica, Raw and Free (1977) conducted an experiment with honey bees caged with *C. arabica* var. *caturrea*. Pollination by honey bees resulted in almost a doubling in the mass yield of coffee fruit compared with treatments without honey bees. Nogueira-Neto et al. (1959) singled out *A. mellifera* as being the bee species that frequented coffee flowers (*C. arabica* var. *bourbon*) the most for both nectar and pollen. The peak time of activity of *A. mellifera* on coffee flowers was in the middle of the day when temperatures reached 30–32 °C. Other bees visiting flowers were the stingless bees *Nannotrigona testaceicornis*, *Plebeia* sp., *Tetragonisca angustula* (reported as *Tetragona jaty*), and *Melipona quadrifasciata* (Raw and Free 1977).

Badilla and Ramírez (1991) investigated insect pollination of *C. arabica* var. *catuái rojo* in Costa Rica. The most fre-

quent visitor of coffee flower was again the honey bee. They conducted a bagging experiment where some flowers were exposed to insect pollination and some were not. The flowers exposed to open pollination by insects had a 15.85% higher fruit set than those flowers from which insect visitors were excluded.

More recently, Roubik (2002a) reported that the African honey bee (*Apis mellifera scutellata*) increased production of *C. arabica*, measured by final crop yield, by 50% in Panama. Over 95% of flower visits came from this bee. Other visitors of coffee flowers observed in the same study were *Trigona* spp., *Melipona* spp., *Bombus* spp., and *Centris* sp.; all of which are social bees with the exception of the genus *Centris*. Roubik (2002a) noted that solitary bees visited coffee flowers, but visits were infrequent compared with those of social bees.

Ricketts (2004) studied the effects of distance from large forest fragments on pollinator activity in farms of *C. arabica* in Costa Rica and observed that the top 10 most common visitors were stingless bees and *A. mellifera*. Klein et al. (2003b) confirmed that social bees were frequent visitors of *C. arabica* in Indonesia and found that native honey bees (*Apis nigrocincta*, *Apis dorsata*, and *Apis cerana*) were the most frequent visitors.

Veddeler et al. (2006) studied visitors of flowers of *C. arabica* in Ecuador. They found that 19 morphospecies of social bees made the majority of visits to coffee flowers (2743 visits), whereas 10 morphospecies of solitary bees made almost negligible visits to coffee flowers (29 visits). The most dominant visitor to coffee flowers was the Africanized honey bee, followed by the stingless bee *Partamona peckolti*.

Vergara et al. (2008) studied pollinators of farms of *C. arabica* of varying management intensity in Mexico. One unshaded farm, one monoculture farm, and two rustic coffee farms were used in their study. A total of 15 species of insects were observed to visit coffee flowers, 7 of which were bees. Across all sites, *A. mellifera* was the most frequent flower visitor, accounting for approximately 84% of total flower visits. The second most frequent coffee visitor was the stingless bee *Scaptotrigona mexicana*, making up 7% of the total observed flower visits.

Social bees have been recognized as the primary pollinators of coffee (Ricketts 2004; Veddeler et al. 2006; Bos et al. 2007; Vergara et al. 2008). For *C. arabica*, there is overwhelming evidence that honey bees are an important pollinator, if not the most important pollinator of coffee, at least throughout the introduced, managed range of its various cultivars.

Not only do bees provide a pollination service for coffee plants, but coffee plants are also a nectar source for bees. In a review, Ramalho et al. (1990) reported that *C. arabica* was identified as an important bee plant in the neotropics, providing nectar (pollen was not noted) specifically for bees of the highly eusocial tribe Meliponini and the Africanized honey bee.

Klein et al. (2003b) emphasized that solitary bees should not be overlooked as efficient pollinators of *C. arabica*. They bagged virgin flowers and studied the effect of single bee visits. A single visit by a solitary bee lead to a higher fruit set than a single visit by a social bee (yielding fruit sets

of 87.3% and 74.7%, respectively). Furthermore, they found increased fruit set of *C. arabica* was correlated to the diversity of bee fauna and not the abundance. Successful pollination was therefore improved by a species-rich community and not dependent solely on the frequency of flower visits by social bees.

#### *Coffea canephora*

Previous information on the pollination of *C. canephora* stated that it was mainly wind-pollinated (Le Pelley 1973; Free 1993), but it is now regarded as a entomophilous crop with bees being the primary pollinator (Willmer and Stone 1989). Willmer and Stone (1989) studied pollinators of *C. canephora* in detail in Papua New Guinea. Visual observations were made to assess which insect visitors were important to crops of *C. canephora*. During massive synchronous flowering events, *Apis* spp., stingless bee species, and the leaf-cutter bee *Megachile frontalis* were the main coffee visitors. With the exception of *M. frontalis*, social bees seem to also be the main pollinator of *C. canephora*. Flowering of single coffee flowers outside of the massive flowering events was also observed and *M. frontalis* and *Amegilla* sp., both solitary bees, were the most frequent visitors in this situation. These solitary bees are thought to be more efficient as pollinators than the social bee species even though the visitation rates of social bees to coffee flowers were higher (Willmer and Stone 1989; Klein et al. 2003b). The synchronous flowerings attract social bees, but because of the high concentration and density of flowers, bee movement between plants is rather limited and the potential for out-crossing is poor (Willmer and Stone 1989).

Klein et al. (2003a) conducted pollination studies on *C. canephora* in Indonesia. In bagging experiments, they found pollination by bees to increase fruit set by 25% compared with the control (wind pollination and autogamy combined). The bees that visited *C. canephora* most frequently were *Apis* spp. (*Apis nigrocincta* and *Apis dorsata*), *Lepidotrigona terminata* (= *Trigona terminata*), and *Trigona* sp. 1. An earlier study by the same team (Klein et al. 2002) is the only study of coffee pollination that did not find *Apis* spp. to be the most common visitor of coffee flowers. They observed stingless bees of the tribe Meliponini to be the most frequent visitors of coffee flowers followed by *Apis* spp. (Klein et al. 2002).

Despite solitary bees being observed and collected in coffee systems (Raw and Free 1977; Carvalho and Krug 1996; Willmer and Stone 1989; Klein et al. 2002; Veddeler et al. 2006) (Table 2), no one has highlighted their importance in coffee pollination with the exception of Klein et al. (2002, 2003b). Willmer and Stone (1989) did observe *Megachile frontalis* to be the most regular visitor of flowers of *C. canephora*. The foraging behaviour (i.e., shorter visits between many coffee flowers) of *M. frontalis* may make this solitary bee the “most important pollinating agent” of *C. canephora* (Willmer and Stone 1989).

#### *Ants*

There has only been one study on ants as pollinators of coffee (Philpott et al. 2006) even though they have long been known to visit the flowers (Willmer and Stone 1989). Philpott et al. (2006) studied the efficiency of ants as

**Table 2.** Major and minor pollinators of *Coffea arabica* and *Coffea canephora*.

Country	<i>C. arabica</i>		<i>C. canephora</i>		References
	Major	Minor	Major	Minor	
Brazil	Common bee, small wild bees, wasps, butterflies <i>Apis mellifera</i> L., 1758, <i>Nannotrigona testaceicornis</i> (Lepeletier, 1836), <i>Plebeia</i> sp.	<i>Tetragonisca angustula</i> (Latreille, 1825) (formerly <i>Trigona jaty</i> ), solitary bees, <i>Xylocopa</i> sp., <i>Trigona hyalinata</i> (Lepeletier, 1836) <sup>1</sup> , ants, Diptera, Lepidoptera, Hemiptera			Krug 1935  Nogueira-Neto et al. 1959*
Brazil	<i>Apis mellifera</i> , <i>Trigona spinipes</i> (Fabricius, 1793), <i>Partamona testacea</i> (Klug, 1807), <i>Xylocopa</i> sp.				Amaral 1972
Costa Rica	<i>Apis mellifera</i>				Badilla and Ramírez 1977
Jamaica	<i>Apis mellifera</i>	<i>Centris dirrhoda</i> Moure, 1960, <i>Exomalopsis</i> sp., <i>Dialictus</i> sp., Vespidae, Lepidoptera			Raw and Free 1977
Jamaica			<i>Trigona</i> sp., <i>Apis</i> sp., <i>Amegilla sapiens</i> (Cockerell, 1911), <i>Megachile frontalis</i> (Fabricius, 1804) (formerly <i>Creightonella frontalis</i> ), Syrphidae	Other solitary bees, <i>Brachygastra augusti</i>	Willmer and Stone 1989
Panama	<i>Apis mellifera scutellata</i> Lepeletier, 1836	<i>Lasioglossum</i> sp., <i>Augochlora</i> sp., <i>Centris festiva</i> Smith, 1854, <i>Centris</i> sp., <i>Epicharis rustica</i> (Olivier, 1789), <i>Eulaema polychroma</i> (Mocsáry, 1899), <i>Bombus pullatus</i> Franklin, 1913, <i>Bombus volucelloides</i> Gribodo, 1891, <i>Bombus ephippiatus</i> Say, 1837, <i>Apis mellifera</i> , <i>Melipona panamica</i> Cockerell, 1919, <i>Nannotrigona perilampoides</i> (Cresson, 1878), <i>Scaptotrigona subobscuripennis</i> (Schwarz, 1951), <i>Paratrigona ornaticeps</i> (Schwarz, 1938), <i>Partamona bilineata</i> (Say, 1837), <i>Trigona amalthea</i> (Olivier, 1789), <i>Trigona corvina</i> Cockerell, 1913, <i>Trigona fulviventris</i> Guérin-Méneville, 1845, <i>Trigona nigerrima</i> Cresson, 1878, <i>Tetragona dorsalis</i> (Smith, 1854) (formerly <i>Trigona dorsalis</i> ), <i>Tetragonisca angustula</i> , <i>Brachygastra</i> sp., Trochilidae, Syrphidae, Lepidoptera (family Hesperidae and Nymphalidae: Ithomiinae, Danaidae, Heliconiinae)			Roubik 2002a

Table 2 (continued).

Country	<i>C. arabica</i>		<i>C. canephora</i>		References
	Major	Minor	Major	Minor	
Indonesia			<i>Lepidotrigona terminata</i> (Smith, 1878) (formerly <i>Trigona terminata</i> ), <i>Heterotrigona</i> sp., <i>Apis cerana</i> Fabricius, 1793, <i>Apis dorsata</i> Fabricius, 1793, <i>Amegilla samarensis</i> (Cockerell, 1925), <i>Xylocopa dejeanii</i> Lepeletier, 1841	<i>Nomia fulvata</i> (Fabricius, 1804), <i>Nomia thoracica</i> Smith, 1875, <i>Lipotriches</i> sp., <i>Patellapis</i> sp., <i>Euaspid</i> sp., <i>Megachile frontalis</i> (formerly <i>Creightonella frontalis</i> ), <i>Megachile terminalis</i> Smith, 1858, <i>Coelioxys smithii</i> Dalla Torre, 1896, <i>Apis nigrocincta</i> Smith, 1861, <i>Heterotrigona</i> sp. 2, <i>Trigona</i> sp.‡, <i>Ceratina rugifrons</i> Smith, 1879, <i>Ceratina</i> sp. (formerly <i>Pithitis</i> sp. 2), <i>Ceratina unimaculata</i> Smith, 1879 (formerly <i>Pithitis unimaculata</i> ), <i>Thyreus nitidulus</i> (Fabricius, 1804)	Klein et al. 2002
Indonesia	<i>Apis nigrocincta</i> , <i>Apis dorsata</i> , <i>Apis cerana</i> , <i>Lepidotrigona terminata</i> (formerly <i>Trigona terminata</i> ), <i>Heterotrigona</i> sp. 2, <i>Megachile frontalis</i> (formerly <i>Creightonella frontalis</i> ), <i>Heriades</i> sp. 1, <i>Nomia thoracica</i>	<i>Heterotrigona</i> sp. 1, <i>Trigona</i> sp.‡, <i>Amegilla samarensis</i> , <i>Amegilla whiteheadi</i> (Cockerell, 1910), <i>Ceratina rugifrons</i> , <i>Thyreus nitidulus</i> , <i>Xylocopa aestuans</i> (L., 1758), <i>Xylocopa dejeanii</i> , <i>Xylocopa smithii</i> Ritsema, 1876, Halictidae spp., <i>Lipotriches</i> sp., <i>Patellapis</i> sp., <i>Coelioxys ducalis</i> Smith, 1854 (formerly <i>Torridapis ducalis</i> ), <i>Coelioxys smithii</i> , <i>Heriades</i> sp. 2, <i>Megachile bakeri</i> Cockerell, 1918, <i>Megachile</i> sp.,	<i>Apis dorsata</i> , <i>Apis cerana</i> , <i>Apis nigrocincta</i> , <i>Lepidotrigona terminata</i> (formerly <i>Trigona terminata</i> ), <i>Heterotrigona</i> sp. 2, <i>Heriades</i> sp. 1, <i>Megachile frontalis</i> (formerly <i>Creightonella frontalis</i> )	<i>Heterotrigona</i> sp. 1, <i>Trigona</i> sp.‡, <i>Amegilla samarensis</i> , <i>Amegilla zonata</i> (L., 1758), <i>Amegilla whiteheadi</i> , <i>Ceratina rugifrons</i> , <i>Thyreus nitidulus</i> , Halictidae, <i>Lipotriches</i> sp., <i>Nomia thoracica</i> , <i>Patellapis</i> sp., <i>Xylocopa aestuans</i> , <i>Xylocopa dejeanii</i> , <i>Xylocopa smithii</i> , <i>Coelioxys ducalis</i> (formerly <i>Torridapis ducalis</i> ), <i>Coelioxys smithii</i> , <i>Heriades</i> sp. 2, <i>Megachile bakeri</i> , <i>Megachile</i> sp.	Klein et al. 2003
Indonesia	<i>Apis nigrocincta</i> , <i>Apis dorsata</i> , <i>Apis cerana</i> , <i>Lepidotrigona terminata</i> (formerly <i>Trigona terminata</i> ), <i>Heterotrigona</i> sp. 2, Halictidae, <i>Megachile frontalis</i> (formerly <i>Creightonella frontalis</i> ), <i>Heriades</i> sp.	<i>Trigona</i> sp. 3‡, <i>Heterotrigona</i> sp. 1, <i>Amegilla</i> sp., <i>Ceratina</i> sp., <i>Xylocopa aestuans</i> , <i>Xylocopa dejeanii</i> , <i>Megachile clotho</i> Smith, 1861 (formerly <i>Chalicodomo clotho</i> )			Klein et al. 2003
Brazil	<i>Apis mellifera scutellata</i>	<i>Dialictus</i> sp., (formerly <i>Chloralictus</i> sp.) <i>Trigona spinipes</i> , <i>Xylocopa</i> sp., <i>Tetragonisca angustula</i> , “wasps”, Diptera, Lepidoptera			Malerbo-Souza et al. 2003 <sup>§</sup>
Brazil	<i>Apis mellifera</i>	<i>Dialictus</i> spp. (formerly <i>Chloralictus</i> spp.), <i>Melipona quadrifasciata</i> Lepeletier, 1836, <i>Tetragonisca angustula</i> , <i>Trigona spinipes</i> , <i>Xylocopa</i> spp.			De Marco and Coelho 2004

Table 2 (concluded).

Country	<i>C. arabica</i>		<i>C. canephora</i>		References
	Major	Minor	Major	Minor	
Costa Rica	<i>Apis mellifera</i> , <i>Plebeia jatiformis</i> (Cockerell, 1912), <i>Plebeia frontalis</i> (Friese, 1911), <i>Trigonisca</i> sp.	<i>Melipona fasciata</i> Latreille, 1811, <i>Nannotrigona mellaria</i> (Smith, 1862), <i>Partamona cupira</i> (Smith, 1862), <i>Tetragona clavipes</i> (Fabricius, 1804), <i>Tetragona dorsalis</i> (formerly <i>Trigona dorsalis</i> ), <i>Trigona angustula</i> , <i>Trigona corvina</i> , <i>Trigona fulviventris</i> , <i>Trigona fuscipennis</i> Friese, 1900			Ricketts 2004
Mexico	Ants ( <i>Brachymyrmex</i> spp., <i>Crematogaster</i> sp., <i>Solenopsis</i> sp.), <i>Trigona</i> spp. <i>Apis mellifera</i> , <i>Ceratina</i> spp., Vespidae, Diptera	Ants ( <i>Azteca</i> spp., <i>Camponotus senex</i> (Smith, 1858), <i>Dolichoderinae</i> sp., <i>Pheidole</i> sp., <i>Solenopsis geminata</i> (Fabricius, 1804), <i>Wasmannia auropunctata</i> (Roger, 1863), Coleoptera, Bombyliidae, Dolichopodidae, Lepidoptera, Odonata			Philpott et al. 2006 <sup>ii</sup>
Ecuador	<i>Apis mellifera scutellata</i> , <i>Cephalotrigona capitata</i> (Smith, 1854), <i>Melipona mimetica</i> Cockerell, 1914, <i>Nannotrigona mellaria</i> , <i>Nannotrigona perilampoides</i> , <i>Partamona peckolti</i> (Friese, 1901), <i>Tetragonisca angustula</i> , <i>Trigona amalthea</i>				Veddeler et al. 2006, 2008
Mexico	<i>Apis mellifera</i> , <i>Scaptotrigona mexicana</i> (Guérin-Méneville, 1845)	<i>Augochlora</i> sp., <i>Ceratina</i> sp., <i>Plebeia frontalis</i> , <i>Trigona nigerrima</i> , <i>Trigona corvina</i> , Polistinae, Syrphidae, Calliphoridae, Bibionidae, Scarabaeidae			Vergara et al. 2008

**Note:** Minor pollinators were those insects that visited coffee less than 5% of the total insect visits. This was calculated when information on total insect visits was given. Updated names of species are used.

\*Data on hybrids of *Coffea dewevrei* and visiting insects are not included (i.e., *Melipona quadrifasciata* and *Cephalotrigona capitata*). Also not included in this list of pollinators are bees observed on old flowers collecting nectar, after anthesis, or those bees that were observed collecting nectar from holes made at the base of the corollas (i.e., *Trigona ruficus*, *Trigona hyalinata*, and *Brachygastra augustii*).

<sup>†</sup>Observations made of *Trigona hyalinata* visiting flowers was during preliminary observations and not part of the observations of insect visitation for the data set.

<sup>‡</sup>This genus has now been broken up into a number of genera and it is not known which generic name applies to the bees included in this study. However, *Trigona*, as now defined, does not occur in Indonesia.

<sup>§</sup>Results of insect visitors may be confounded by the attractant Bee-Here, which was sprayed in several treatments.

<sup>||</sup>Presence-absence of ants was used to determine if they were major coffee visitors (>5% encounter rate for “Major pollinator”—pollination was not determined, only based on visitation (presence) frequency).



pollinators of *C. arabica* var. *typica* in Mexico in both a low-shaded and a high-shaded coffee farm. There was no difference in the number of flower buds, total number of fruit per branch, or final fruit set among their three treatments of flying insects and ants, no ants, and no insects (control). However, in the high-shaded coffee farms, fruit mass was significantly higher in treatments exposed to ant and flying insect pollinators compared with those exposed to just flying insect pollinators. This increase occurred only in replicated blocks in the high-shade sites and was not observed in the low-shade sites. The mechanism by which ants increased fruit mass in high-shade coffee farm was not determined.

### Vespid wasps

The role of vespid wasps in coffee pollination has not yet been explored in detail. They have been collected in coffee farms and observed visiting coffee flowers (Klein et al. 2002, Roubik 2002a; Willmer and Stone 1989; Free 1993). Roubik (2002a) observed the social “honey wasp” *Brachygastra* sp. visiting coffee flowers. However, it may not have acted as a coffee pollinator as a species of this genus—*Brachygastra augusti* (de Saussure, 1854)—has been observed biting holes at the bottom of coffee flowers (nectar robbing) (Nogueira-Neto et al. 1959). Other researchers have reported *B. augusti* as an “intermittent” visitor of coffee flowers (Raw and Free 1977; Free 1993; Willmer and Stone 1989). However, these social wasps may play an important role in pest control, which may indirectly affect successful coffee production. For example, *Brachygastra lecheguana* (Latreille, 1824) prey on the larvae of coffee leaf miners (*Leucoptera coffeella* (Guérin-Méneville, 1842) (Parra et al. 1981). Vespid wasps are present in coffee farms, but it is unclear whether or not they contribute directly to coffee pollination.

### Non-hymenopteran insect pollinators

Syrphid (hover) flies have been observed visiting coffee flowers (Klein et al. 2008; Willmer and Stone 1989). During isolated flowering events in Papua New Guinea, Willmer and Stone (1989) noted hover flies to be the second most common flower visitor next to *Amegilla* sp. Hover flies were observed eating coffee pollen. Roubik (2002a) also observed that hover flies occasionally visited coffee flowers but noted that they were not important pollinators because of their low rates of visitation.

Other minor visitors of coffee flower have included several species of Lepidoptera in the families Hesperidae and Nymphalidae, Dictyoptera, and Coccinellidae (Roubik 2002a; Willmer and Stone 1989; Free 1993). Some Lepidoptera have been recognised as coffee pests (Le Pelley 1968, 1973; Parra et al. 1981). None of these insect groups have been studied in detail with regards to coffee pollination.

## Summary and knowledge gaps

Different species of coffee are pollinated in distinct ways—*C. arabica* is self-pollinating and *C. canephora* is thought to be wind-pollinated because it is self-sterile (i.e., it is incapable of self-pollination). In both species of coffee, research has shown that social bees are important for increasing fruit set. Both honey bees and stingless bees are common visitors of coffee flowers in all studies. From an economic standpoint,

social bees are extremely important for coffee production (Roubik 2002b; Ricketts 2004; Veddeler et al. 2008). Veddeler et al. (2008) found that an 80% increase in coffee yield accompanied a 4-fold increase in the density of social bees visiting coffee flowers. The resulting increase in coffee production equated to an 800% increase in revenues for small-scale farmers. Solitary bees (10 species) only made up approximately 10% of the observed coffee visits. Coffee fruit set and yield was not reported to be related to the richness of bee species. This is contrary to previous findings in which the relative efficiency of single solitary bee visits to coffee was higher than single visits by social bees (Klein et al. 2003a). Perhaps these discrepancies exist simply because these studies were conducted in different countries (Ecuador and Indonesia, respectively) or because of different *Coffea* species. Nonetheless, there has only been one study completed on solitary bee pollination of coffee (Klein et al. 2003a). Studies of other crops that highlight the contribution of native bees to successful production include watermelon (Kremen et al. 2002), canola (Morandin and Winston 2005), tomatoes (Greenleaf and Kremen 2006), eggplant (Gemmill-Herren and Ochieng 2008), and indeed, some whole agricultural systems as in parts of Kenya (Kasina et al. 2009). Some of these studies have shown that bee diversity is more important than the absolute abundance of all bees (Klein et al. 2003a). Further studies examining the relative importance and contribution of all pollinators to coffee production are needed. Solitary bees, ants, wasps, and other insects have not been examined thoroughly as potential pollinators of coffee even though they are present in coffee farms and frequent coffee flowers (Willmer and Stone 1989; Free 1993; Roubik 2002a).

The contribution of pollinators, including solitary bees, may potentially be important for other *Coffea* spp. aside from *C. arabica* and *C. canephora*. Pollinators of other *Coffea* spp. such as *C. liberica* and *C. liberica* var. *dewevrei* have not been examined at all. Both shrubs of *C. liberica* and *C. liberica* var. *dewevrei* have larger flowers and fruit compared with those of *C. canephora* and *C. arabica* (Wintgen 2009). Additionally, these coffee species tend to flower asynchronously and at irregular time intervals (A. Mojica, personal observation). Studies that focus on the pollination of, as well as the bee fauna that visit, flowers of *C. liberica* and *C. liberica* var. *dewevrei* are worthwhile and interesting because of the differences in flowering phenology.

Surprisingly, there have been no studies conducted on pollinators of *Coffea* spp. in Africa, the native range of all coffee species. Rather, pollination studies of *Coffea* have been conducted in Brazil (Nogueira-Neto et al. 1959), Papua New Guinea (Willmer and Stone 1989), Venezuela (Manrique and Thimann 2002), Panama (Roubik 2002a), Indonesia (Klein et al. 2003a, 2003b), Costa Rica (Ricketts 2004), and Ecuador (Veddeler et al. 2008). We are missing a critical piece of information by not having looked at coffee in its natural setting with its natural pollinators. No one knows what pollinates coffee in the highlands of Ethiopia or the lowlands of west Africa. Preliminary observations of major insect pollinators of *C. arabica* in Ethiopia were highland honey bees (*Apis mellifera monticola* Smith, 1961) and solitary native bee species (Martins 2007). Other visitors of coffee flowers included *A. m. scutellata*, *Xylocopa* sp., and two species of diurnal

hawk moths (*Cephanodes hylas* (L., 1771) and *Macroglossum* sp.) (Martins 2007). Just south of Ethiopia, in Kenya, a study was investigated bee diversity and abundance in conventional and organic coffee farms (Karanja et al. 2010). Bee species richness was positively correlated with plant diversity in both farm types (conventional and organic farms,  $R^2 = 0.6744$  and  $0.5918$ , respectively). Major and minor visitors of coffee flowers were not specified in this study.

Lastly, there have been inconsistencies in reporting the importance of anemophily (wind pollination), geitonogamy, and autogamy by gravity in coffee pollination. Geitonogamy is the transfer of pollen between flowers within the same plant (Fox et al. 2001). De Marco and Coelho (2004) noted that the relative importance of wind and gravity in pollination changes depending on the number of flowers produced by the plant and on various branches. Similarly for geitonogamy, if the plant produces more flowers, then there is a higher probability of within plant pollen exchange. Wind plays an important role in the pollination of *C. canephora* but not in the pollination of *C. arabica*. Wind pollination was studied with *C. canephora* (Ferwerda 1948; Klein et al. 2003a). The percentage of coffee flowers receiving adequate pollination by wind ranged from 53.4% (Klein et al. 2003a) to 100% (Ferwerda 1948). Wind speeds were not recorded in either study, therefore conclusions about relative importance of wind for coffee pollination cannot be made. The only way to determine the true importance of wind in coffee pollination is to conduct a controlled experiment in which wind speeds are controlled and varied, and the resulting fruit set for every speed is recorded.

Spacing schemes of coffee farms can affect the relative importance of wind and insect pollination. In some coffee farms, there is a high density of coffee plants (planted in a 1 m × 1 m grid). Even at low speeds, wind may be an important pollen vector in such situations, whereas farms with plants more widely spaced may depend less on wind pollination and more on insect pollination. Different microclimatic conditions, different spacing schemes, different plant ages, and quality of coffee shrubs may all affect the relative importance of wind and insect pollination, as well as the relative importance of different insect visitors.

Currently, there are over 850 pests that attack coffee (Le Pelley 1973; Vega et al. 2006) and over two dozen diseases that affect coffee plants (Wintgen 2004) and decrease crop productivity. Pollination studies on *Coffea* sp. can help improve crop productivity by aiding our understanding of the relative importance of each pollen vector and the mechanism of pollen transfer. Management and conservation strategies focused on enhancing and preserving recognized pollinator communities are important. The role of artificially augmenting pollinator density through management of nest densities of stingless bees or solitary bees remains to be investigated. We reviewed the work relating to coffee pollinator interactions in hopes of bringing together all the recent work that has been done on coffee pollinator interactions. In reviewing this, we have also recognised that there are many gaps in our knowledge regarding coffee pollination.

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