Why is arabica coffee visited by so few non-\textit{Apis} bees in its native range?

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The current knowledge about pollinators in sub-Saharan Africa is extremely scarce. General pollinator distributions and resource usages are mainly unknown, as are the main pollinators of different crops (Timberlake and Morgan 2018). In early 2011, I went to an Afromontane area of Ethiopia, where arabica coffee, \textit{Coffea arabica} L., has its origin, to survey coffee pollinators. I surveyed 19 coffee sites, most managed with organic practices, across a gradient from state-owned, shaded semi-plantation coffee to coffee grown sparsely, more or less wild, in the understory of disturbed natural forests (Fig. 1A, B). I was surprised to find that native honey bees, \textit{Apis mellifera} L., were the almost exclusive visitors. Out of 1,226 collected potential coffee pollinator individuals, 1,200 were bees, and 98\% of these were honey bees (Samnegård et al. 2014). The dominance of honey bees in Ethiopian coffee pollination has also been found by Geeraert et al. (2019). Even though both studies found the proportion of alternative pollinators to increase in less disturbed forests (Samnegård et al. 2014, Geeraert et al. 2019), nonetheless honey bees dominated the pollinator assemblage in those areas and visiting rates of alternative pollinators were low. Like \textit{C. arabica}, honey bees are native to Ethiopia (Fig. 2A). In the introduced range of coffee, honey bees and other eusocial bees, i.e., bees that live together in perennial colonies, are the most frequent visitors (reviewed in Ngo et al. 2011), but solitary bees, i.e., bees that nest solitarily and have non-overlapping generations, also account for a significant proportion of visits in some systems. For example, in Indonesian coffee fields that varied in shade level and distances to forest, 44\% of the visits to arabica coffee were made by 22 species of solitary bees, and the rest of the visits divided between seven different eusocial bee species (Klein et al. 2003). In a study from sun-coffee sites in Brazil, where the honey bee was the most common visitor, 12 species of other eusocial bees (stingless bees from the tribe Meliponini) were present and accounted for 71\% of the sampled bees (Saturni et al. 2016). These coffee systems seemed, according to the description in the papers, either similar (Indonesia; Klein et al. 2003) or more simplified (Brazil; Saturni et al. 2016), than the coffee systems I surveyed in Ethiopia. Since crops grown within their biogeographic region of origin in general are visited by a higher number of bee genera (Brown and Cunningham 2019), and the native Ethiopian coffee is grown in heterogeneous, organic systems, I found the total dominance of one visiting bee species very surprising.

The bee fauna in sub-Saharan Africa is described as moderately diverse, including 13\% of the world’s described bee species, but the real number is probably much higher (Eardley et al. 2009). To investigate if the low numbers of non-\textit{Apis} bee pollinators of coffee could be explained by a general low diversity or abundance of other bees, I also surveyed pollinators of the African senna, \textit{Senna} didymobotrya (Fresen.) H.S.Irwin \& Barneby, that flowered abundantly simultaneously with coffee in the same landscape. African senna, a shrubby herb in the Fabaceae family, is native to Ethiopia and tropical east Africa (Dulberger 1981; Fig. 2B). Herbs and shrubs that bore flowers were sparse during this period, probably because of the dry season and high grazing pressure. However, the landscape was not empty of food resources for pollinators; because most native trees and fruit trees flower during the dry season, floral tree resources were patchily distributed across the landscape. African senna favors disturbed areas, such as grazed landscapes, but is avoided by grazing cattle. Hence, it is quite common in the landscape, especially along roads, water courses, and in villages.

The two plant species, arabica coffee and African senna, differ in their flowering patterns and flower morphologies. While arabica coffee flowers three to four
times during the dry season in day-long synchronous flushes after heavy rains, African senna flowers more or less throughout the year. Arabica coffee has fragrant, white, open, generalist flowers that provide both nectar and pollen apparently easily accessible for pollinators (Fig. 2A), while the African senna has yellow, open, nectarless flowers that only provide pollen as a pollinator reward (Fig. 2B). The African senna requires specialized pollinators that can sonicate, “buzz,” the anthers to discharge the pollen through terminal pores (Dulberger 1981). Since honey bees are not among the 58% of bee species that are able to buzz, they are not major pollinators of African senna (Dulberger 1981, Cardinal et al. 2018). The white color and strong fragrance of coffee flowers may suggest attraction of nocturnal pollinators. Even though the opening of flowers at dawn and the short receptiveness of coffee stigmas indicate that mainly day-active pollinators affect the pollination (Ngo et al. 2011), the presence of nocturnal or dawn active pollinators cannot be excluded without further studies.

Fig. 1. The Ethiopian coffee production systems are mainly recognized as semi-forest or semi-plantation coffee. (A) The semi-forest coffee is grown in the understory of more or less dense natural moist evergreen afro-montane forests and has low annual forest management, whereas (B) the semi-plantation coffee is recognized by its higher forest management intensity and lower shade tree and plant diversity.

Fig. 2. Three species native to Ethiopia: (A) a honey bee worker visiting the generalist flowers of arabica coffee and (B) flowers of the buzz pollinated African senna.
I surveyed visitors to African senna flowers across the time period of two major coffee flowering events (about 1.5 months) in 18 sites close to my coffee sites (distance to closest coffee site ranged from <80 m to 10 km), with similar sampling effort as for the coffee (64 sampling hours on African senna and 57 h on coffee). More bee species visited senna (28 bee species) than coffee (17 bee species) with 8 bee species observed on both plants (Appendix S1: Table S1). The abundance of the shared bee species differed between senna and coffee; on coffee, I collected only one or two individuals of each of the observed non-\textit{Apis} bee species, while many more individuals of some of the species were collected from the African senna (Appendix S1: Table S1). Honey bees, the dominant bee visitors of coffee, represented only a small fraction (11\%) of the total abundance of bees visiting African senna, which instead was predominantly visited by solitary bees. In another landscape-wide bee survey with traps that we conducted in the open part of the landscape the following year, we found 61 bee species (Samnegård et al. 2015). Taken together, we found 71 bee species active during the dry season in this landscape. Hence, the low numbers of non-\textit{Apis} bee pollinators of coffee did not appear to be explained by a general low diversity or abundance of other bees in the landscape.

Could the high densities of honey bees displace other coffee pollinators (see Herbertsson et al. 2016)? Honey bees are very good utilizers of mass-flowering resources since they can recruit foraging workers from their colonies and quickly build high densities on attractive flowering plants, possibly competing or disturbing other bee species. Yet, honey bees are present in other coffee systems that still include high abundances of other bee species (Saturni et al. 2016), and further observations during a visit to the same Ethiopian landscape two years later (2013) suggested that honey bees might not displace non-\textit{Apis} pollinators. During this later visit, it was dry and hot earlier than usual, and the onset of the first coffee flowering events was earlier than expected. In most years, local beekeepers have placed traditional bee hives in the flowering trees around the coffee, to be colonized by semi-wild honey bees. However, at this time, the hives were not in place yet and I did not see any honey bees active around the coffee flowers. Yet even without honey bee activity, the activity of other bees was again extremely low. In addition, the coffee flowers remained open for an extended time, a response that indicates lack of pollination (Ngo et al. 2011). Even though a mismatch in timing with other potential pollinators cannot be excluded, this observation indicates a pollination system highly sensitive to changes in climate and environmental conditions.

Why are so few bees utilizing an abundant resource like coffee in its native range, where many of these bee species should have coevolved and been adapted to utilize the resource? Arabica coffee is considered attractive to a diverse range of pollinators, with its apparent generalist flowers, and its heavy, sticky pollen grains indicating the need for cross-fertilization by animals (Le Pelley 1973). Possibly, disturbance could have led to disrupted interactions. Brown and Cunningham (2019) recently introduced the “agricultural tolerance” hypothesis, proposing that specific traits (being social, soil nesting, and specializing on plant groups that includes crop species) make some bee taxa more tolerant to agricultural environments. These traits are more common in the New World and Neotropical bee fauna, compared to the Old World bee fauna (Brown and Cunningham 2019). Even though coffee production in Ethiopia has been demonstrated to conserve forest cover, the widespread conversion from natural forests to managed coffee forests causes degradation and decreased biodiversity (Hylander et al. 2013). If the bee fauna associated with coffee in sub-Saharan Africa is by its nature more sensitive to disturbance than bee faunas in other regions, the current coffee production system, even though it is organic and heterogeneous, may no longer support the non-\textit{Apis} pollinators involved in the original coffee–pollinator interactions. On the other hand, the African senna is growing in its natural habitat (i.e., disturbed areas), which may be reflected in its rich pollinator diversity, relative to coffee.

My observations of a poor pollinator community on coffee concur with another result from this region where we found poor pollination services in a widespread common oil crop, rapeseed, \textit{Brassica napus} L., (Samnegård et al. 2016). Altogether, this highlights highly sensitive crop pollination systems. To meet the need for more studies on Afrotropic pollinator communities and pollination services, a first approach may be to evaluate the support for the “agricultural tolerance” hypothesis and how that may apply to Afrotropic pollinator communities. Further, assessment of the impact of different type of disturbances, including deforestation, forest degradation and grazing pressures, on pollinator communities and pollination services is needed. Building this knowledge is urgent since the area of pollinator-dependent crops is steadily increasing, despite scarce knowledge of pollinator ecology and species distributions, which may lead to severe yield gaps (Knight et al. 2018, Aizen et al. 2019).

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