# The value of biotic pollination and dense forest for fruit set of *Arabica* coffee: A global assessment

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## ABSTRACT

Animal pollinators are globally threatened by anthropogenic land use change and agricultural intensification. The yield of many food crops is therefore negatively impacted because they benefit from biotic pollination. This is especially the case in the tropics. For instance, fruit set of *Coffea arabica* has been shown to increase by 10–30% in plantations with a high richness of bee species, possibly influenced by the availability of surrounding forest habitat. Here, we performed a global literature review to (1) assess how much animal pollination enhances coffee fruit set, and to (2) examine the importance of the amount of forest cover, distance to nearby forest and forest canopy density for bee species richness and coffee fruit set. Using a systematic literature review, we identified eleven case studies with a total of 182 samples where fruit set of *C. arabica* was assessed. We subsequently gathered forest data for all study sites from satellite imagery. We modelled the effects of open (all forest with a canopy density of ≥25%), closed (≥50%) and dense (≥75%) forests on pollinator richness and fruit set of coffee. Overall, we found that animal pollination increases coffee fruit set by ~18% on average. In only one of the case studies, regression results indicate a positive effect of dense forest on coffee fruit set, which increased with higher

forest cover and shorter distance to the forest. Against expectations, forest cover and distance to open forest were not related to bee species richness and fruit set. In summary, we provide strong empirical support for the notion that animal pollinators increase coffee fruit set. Forest proximity had little overall influence on bee richness and coffee fruit set, except when farms were surrounded by dense tropical forests, potentially because these may provide high-quality habitats for bees pollinating coffee. We, therefore, advocate that more research is done to understand the biodiversity value of dense forest for pollinators, notably assessing the mechanisms underlying the importance of forest for pollinators and their pollination services.

## 1. Introduction

The rapid growth of the global human population challenges humanity to simultaneously increase food production while protecting biodiversity, if the current distribution of resources remains unchanged (Crist et al., 2017). Coffee is among the most intensively traded soft commodities in the world. The coffee industry accounts for more than 10 million hectares of cultivated land and USD 11.6 billion in gross revenues (during 2000–2012), and builds an economic foundation for roughly 25 million smallholder farmers in tropical countries (Perfecto et al., 2014; Pham et al., 2019). In recent decades, global coffee production suffered significant declines due to price instabilities, changing climatic conditions and pests (Avelino et al., 2015; Cheng, 2007; Jaramillo et al., 2011; Pham et al., 2019). New strategies are therefore needed to secure and increase coffee yields.

Animal pollinators, notably insects, fulfil important ecological functions in natural ecosystems and many crop production systems, including coffee. One strategy to increase coffee yield could therefore be to integrate the protection and promotion of biotic pollinators within and around coffee farmland (Egan et al., 2020). Animal pollinators play a vital role in the reproduction of thousands of plant species: depending on the biome, about 78–94% of all flowering plant species are animal pollinated (Ollerton et al., 2011; Rech et al., 2016). In agricultural systems, over 80% of the world's leading food crops depend to a certain degree on animal pollination, which corresponds to 5–8% of the global production volumes (Garibaldi et al., 2009; IPBES, 2016; Klein et al., 2007). With steeply increasing production volumes and producer prices for pollinator-dependent crops, financial values of pollination services are expected to increase further in the future (Garibaldi et al., 2009; IPBES, 2016; Lautenbach et al., 2012). Coffee is able to self-pollinate, but it significantly benefits from biotic pollination with reported fruit set increases of 10–30% in *Coffea arabica* L., as compared to self-pollination (Hipólito et al., 2018; Klein et al., 2003a; Saturni et al., 2016). Besides the quantitative output, animal pollination can also improve coffee quality, measured by berry size, weight and coffee cup quality (Classen et al., 2014; Karanja et al., 2013; Philpott et al., 2006). However, not just the abundance of pollinators but also pollinator species richness has been shown to positively affect the fruit set of coffee (Garibaldi et al., 2013; Klein et al., 2003b; Munyuli, 2012), although available results of the effect of pollinator richness for crops are mixed (Cardinale et al., 2006; Saturni et al., 2016). Positive relationships may be the consequence of interacting factors, such as complementary pollination among species and thus better coverage of temporal and spatial resources (Hoehn et al., 2008; Klein et al., 2003b; Ricketts et al., 2004), 'sampling effects' that occur when increases in the diversity of animal communities enhance the likelihood that highly effective pollinators are present (Cardinale et al., 2006), synergistic effects between pollinating species (Greenleaf and Kremen, 2006; Sapir et al., 2017).

As part of the global biodiversity crisis, insect pollinators and the ecosystem functions they provide are also increasingly at threat (Garibaldi et al., 2009; Klein et al., 2007; Potts et al., 2010). In a global study, two-thirds of the assessed insect species were identified to be reduced in abundance by at least 45% over the last 40 years (Dirzo et al., 2014). Numerous local studies have found similar alarming values (Hallmann et al., 2017; Thomas et al., 2004). Although multiple factors cause this defaunation, land use change and habitat fragmentation are the main drivers of biodiversity loss, including pollinator loss (Aguilar et al., 2006; Dicks et al., 2020; Klein et al., 2018; Potts et al., 2010). Such negative impacts of land use change, for instance, due to agricultural intensification, can be exemplified by the dynamics of the coffee industry. To counter income losses from coffee production, many farmers abandon their fields (Perfecto et al., 2005), cultivate new farmland or switch to monocultures to accelerate growth, leading to reduced forest cover, habitat fragmentation, biodiversity loss and soil degradation (Campanha et al., 2004; Hipólito et al., 2018; Philpott et al., 2008). However, more intensified land use may not provide the desired increase in coffee yield. On the contrary, monocultures may decrease production outputs and economic value per hectare due to lower pollinator richness and decreased fruit set in fields far from forest, as forest provides nesting sites and floral resources for many social and solitary bees pollinating coffee (González-Chaves et al., 2020; Klein et al., 2003b; Machado et al., 2020; Ricketts et al., 2004). In contrast, well-preserved natural habitats may enhance the diversity of pollinator assemblages (Menz et al., 2011; Senapathi et al., 2015). Studies identified bee species richness to be affected by landscape composition (Andersson et al., 2013), resource availability (Peters and Carroll, 2012) and the accessibility of natural habitat such as forests (Brosi et al., 2008; Klein, 2009; Nemésio and Silveira, 2010; Ricketts, 2004). However, tropical forests are among the most severely human-modified biomes and require urgent protection (Green et al., 2020; Kremen et al., 2007; Rosenzweig, 1995), especially as tropical species may be more susceptible to habitat loss than temperate species (Melo et al., 2018). Over recent decades, tropical forests received increasing attention for their potential to preserve pollinators, particularly bees. Roubik (2002a, 2002b) hypothesised that tropical forests provide high-quality habitats for bee pollinators and that yields of *C. arabica* might be higher near forest habitats. Many following studies reported increases in pollinator diversity and richness as well as coffee yield in fields near forest fragments (e.g. Boreux et al., 2013; Bravo-Monroy et al., 2015; Caudill et al., 2017; De Marco and Coelho, 2004; Klein et al., 2003c; Krishnan et al., 2012; Munyuli, 2014; Ricketts et al., 2004; Saturni et al., 2016; Vergara and Badano, 2009). However, in these studies, forest was often identified on the ground according to local criteria rather than by international standards. The definition of forest in such cases remains unclear, which complicates the comparison of results as well as drawing overall conclusions on the role of forest on pollinators and their pollination functions (see for instance Bauer and Sue Wing, 2016; Campanha et al., 2004; Klein et al., 2003a).

Here, we perform a worldwide macroecological assessment of the role of pollinators for coffee fruit set and the effects of amount of forest cover, distance to forest patches, and forest canopy density on bee pollinators and coffee fruit set, using international forest definitions supplemented with remote sensing techniques to characterise forest structures. This remote sensing approach allowed us to include coffee pollination studies, in which forest was not originally recorded. Based on the existing literature, we expected to find positive effects of both bee pollinator richness and forest on the fruit set of *C. arabica*. To examine these effects at the global scale, we first conducted a systematic literature review to create a comprehensive data set of suitable studies. Then, we used satellite imagery to synthesise data on forest cover and distance to forest at three different levels of canopy density. We defined forest cover as the proportion of forest that covers a given area (buffers)

around the coffee samples. Distance to forest specified the distance in kilometres between a coffee plot and the edge of the nearest forest of a given patch size. Finally, canopy density was defined as the proportion of the forest floor that is covered by tree canopies (Jennings et al., 1999). We used these data to examine the following research questions:

Q1. Is there a positive effect of biotic pollination on *C. arabica* fruit set when comparing pollinator exclusion experiments?

Q2. Does local bee pollinator richness correlate positively with the fruit set of *C. arabica*?

Q3. Do forest cover and distance to forest from the coffee plantations correlate with bee species richness and/or coffee fruit set?

Q4. Does a potential correlation with forest in Q3 differ depending on the canopy density of the forest patch?

## 2. Materials and methods

### 2.1. Systematic literature review

From May to September 2019, we conducted a systematic review of the literature on biotic pollination of *C. arabica* (Okoli, 2015; Pullin and Stewart, 2006). Initially, the study included another common cultivar, *Coffea canephora* Pierre ex A.Froehner, which was later removed from the analysis since it has another reproductive system, and we could not identify enough studies to include this species in a separate analysis. The review was structured using the four phases of the PRISMA guidelines (Preferred Reporting Items for Systematic reviews and Meta-Analysis): identification, screening, eligibility, and inclusion of case studies (Moher et al., 2009). We selected the following combination of search terms: '*coffee OR coffea*' AND '*pollinat\* OR bee OR bees*' AND '*fruit set OR fruit-set OR yield*'. We searched within the title, abstract and keywords in the search engines CAB Abstracts, Scopus, and Web of Science. To include grey literature, we used Google Scholar as a fourth search engine with the slightly different search terms '*coffee OR coffea*' AND '*pollination OR pollinator OR bee OR bees*' AND '*"fruit set" OR fruit-set OR yield*'. Here, we limited the review to the first 200 entries as recommended in the literature, to restrict the share of grey literature to the results (Haddaway et al., 2015).

In the identification and screening phase, we selected studies which conducted pollinator exclusion experiments and appeared to be suited for the analysis based on their titles and abstracts. Studies had to fulfil the requirements of having geographic coordinates for their sample sites, measurements of initial or final fruit set of *C. arabica* for open and closed pollination treatments (more on the terminology in 2.2.1) and, ideally, having recorded data on environmental variables, notably forest. If coffee management strategies were recorded by authors, these were also noted. In the eligibility phase, we removed duplicate papers and repeated the review in greater detail on full manuscripts. Finally, in the inclusion phase, we included studies with full and accurate data sets and authors were contacted to receive the raw data. In addition to published studies retrieved from the literature, we included an unpublished data set from Brazil and our own unpublished data set from Jamaica (see Supplementary Material S1). In a few cases, authors could not be reached. It is also possible that some pollination treatment data were not yet published and could thus not be identified through the literature review. Therefore, we acknowledge that the final selection may not represent a complete data set.

### 2.2. Preparation of variables for the statistical analysis

We collected the data of selected studies in a single database. Here, we defined a *coffee plant* as one plant where both open and closed pollination treatments were conducted. We defined a *sample* as a group of closely situated coffee plants (usually 4–10 coffee plants, depending on the study) centring on a geographic coordinate. For Q1 on pollination success, we compared the difference in fruit set between open and closed pollination experiments across and within studies. In these analyses,

each data point represented a single coffee plant (in average $79 \pm 37$ plants per study).[1] For questions Q2-Q4, we calculated means across all plants in a sample, as defined above. These means were calculated to ensure independent data points and to avoid pseudo-replication (in average $16.5 \pm 9.4$ samples per study). Two parameters were used as response variables: *pollination success (logOR)* and *bee pollinator richness (Chao1)*. Seven parameters were used as predictors: three *forest cover* variables, three *forest distance* variables, and *bee pollinator richness*; all are described in detail below. To answer Q2, we estimated a simple linear regression for each individual study investigating how pollinator richness impacted pollination success. Richness data were gathered at the sample level, and the data were analysed within each study. The questions Q3 and Q4 were addressed by estimating simple linear regressions for each individual study on the effect of forest cover and distance to forest on pollination success at different levels of tree canopy density.

### 2.2.1. Pollination success (logOR)

To investigate how biotic pollinators affect coffee yields, pollinator exclusion experiments usually consist of (at least) two treatments: 'open' and 'closed' pollination. 'Open' pollination treatments refer to non-manipulated flowers, which are accessible to pollinators, and can be either animal, wind and/or self-pollinated. 'Closed' pollination treatments allow for wind and self-pollination only, excluding pollinators with physical barriers such as coarse gauze. For each treatment, the fruit set is determined as the proportion of flowers developing into fruit from a total number of sampled flowers (De Marco and Coelho, 2004). The difference in fruit set between open and closed treatment is then interpreted as the contribution that biotic pollinators make to fruit set, here coffee yield. Coffee fruit set is commonly measured at two points in time: around five to eight weeks after pollination (initial fruit set) and immediately before harvest of the fruit (final fruit set; Badano and Vergara, 2011; Klein et al., 2003b). We gathered data on both the initial and final fruit set, as well as the total number of sampled flowers. Fruit set levels commonly differ between initial and final sampling due to fruit abortion (Bos et al., 2007). Eight studies estimated either initial or final fruit set. Three studies estimated both initial and final fruit set data. In these cases, we used initial fruit set data for the analysis. We additionally used a *t*-test to examine whether the difference between treatments differed significantly between the initial and final fruit sets and found no significant differences (p-values of 0.775, 1, and 0.129). We therefore concluded that results from the participating studies could be directly compared, regardless whether the authors had calculated initial or final fruit set. Furthermore, although some of the included studies already analysed the difference in fruit set between the treatments, they calculated the fruit set variable in different manners (see e.g. Badano and Vergara, 2011; Classen et al., 2014; Hipólito et al., 2018). To facilitate the comparison of results from different local assessments, we, therefore, used a joint variable to apply the same methodology across studies.

For this purpose, we calculated the number of pollinated flowers that developed fruit ('success') and unpollinated flowers ('failure') for each treatment and for each coffee plant. In rare cases, one of these variables turned out zero, so a Haldane-Anscombe correction was applied by adding a value of 0.5 to all variables (Anscombe, 1956; Lawson, 2004). To analyse the effects of forest variables on biotic pollination of coffee, the association between the two treatments had to be reflected in the response variable. We did this using odds ratios (OR), which indicate whether the presence or absence of a property A (here, the pollinator exclusion) affects a property B (here, the share of pollinated flowers or pollination success; Rudas, 1998). We defined the response variable *pollination success* as the ratio of the odds for pollination success in the

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[1] In the study by Hipólito et al. (2018), authors did not sample a fixed number of coffee plants, but sampled a fixed number of 200 flower buds per sample. Thus, the number of coffee plants varied between samples.

open treatment to the odds of pollination success in the closed treatment in each sample *s*:

$$logOR_s = \log\left(\frac{odds_{open,s}}{odds_{closed,s}}\right) = log\left(\frac{pollflowers_{open,s}/unpollflowers_{open,s}}{pollflowers_{closed,s}/unpollflowers_{closed,s}}\right)$$
(1)

The above calculations involved three steps: Firstly, we calculated the odds of pollinated flowers to unpollinated flowers for each treatment (odds for pollination success). Then, we calculated the ratio of the odds from open and closed treatments (OR) and, finally, we calculated the log of the OR to simplify the subsequent analysis so that the resulting response variable *pollination success (logOR)* was centred on zero. A $logOR > 0$ indicated higher odds for pollination success in open than in closed treatments, a $logOR = 0$ implied no association between treatments, and a $logOR < 0$ indicated higher odds for pollination success in closed than in open treatments. After the log transformation, the resulting variable followed a normal distribution (Bland and Altman, 2000).

### 2.2.2. Bee pollinator richness (Chao1)

The abundance and richness of pollinators were assessed in nine out of eleven studies, using flower visitor observations, sweep netting on plants and transects, as well as pan traps (Classen et al., 2014; Hipólito et al., 2018; Saturni et al., 2016). The remaining two studies did not assess such data. The approaches differed in sampling duration, frequency, sample sites, and targeted pollinator species. Three studies sampled bee pollinators only. Across studies, bee species accounted for an average of 70% of all recorded species (richness) and 87% of all recorded individuals (abundance). Bees are widely believed to be the main pollinators of coffee (e.g. González-Chaves et al., 2020; Klein et al., 2003a; Roubik, 2002a, 2002b). Therefore, we focused our richness estimates on bee pollinators by estimating species richness only based on the identified bee species in the samples. We included the honey bee *Apis mellifera* L. in the data set, whereas non-bee taxa were not included. To receive a comparable species richness estimate for the bee pollinator community at the sample level, we calculated the widely used abundance-based Chao1 estimator as (Chao and Chiu, 2016):

$$\widehat{S}_{Chao1} = S_{obs} + F^2/(2*G), \text{if} \quad G > 0$$
(2)

$$\widehat{S}_{Chao1} = S_{obs} + F(F-1)/2, \text{if} \quad G = 0$$
(3)

$S_{obs}$ is the number of observed bee species in the sample, $F$ is the number of singletons (species with one individual in the sample), and $G$ is the number of doubletons (species with two individuals in the sample). In this way, $\widehat{S}_{Chao1}$ indicates the expected number of bee species if all species are included in the sampling.

### 2.2.3. Forest variables

To identify possible effects of forest on pollination success for coffee (Q3 and Q4), two types of forest variables were synthesised from satellite data: *forest cover*, which defines the percentage of forest within a given buffer surrounding the sample, and *forest distance*, which describes the distance from a sample to the nearest forest patch. Each of these variables was synthesised at three levels of tree canopy density of the surrounding forest (i.e. the proportion of forest floor covered by tree canopies): open forest (all forest with a canopy density of $\geq$25%), closed forest ($\geq$50%) and dense forest ($\geq$75%).

Forest definitions in national or international assessments often differ in minimum patch size, tree canopy density and management intensity (Chazdon et al., 2016). In order to conduct a comprehensive analysis across continents based on remote sensing, a standardised definition of forest is therefore required. In this study, we defined forest as an area of minimum 0.8 ha with trees above 5 m height and categorised it as open, closed and dense forest at minimum tree canopy

densities of $\geq$ 25%, $\geq$ 50% and $\geq$ 75%, respectively, as described above. This was based on the forest definitions by the Food and Agriculture Organization (FAO) and the United Nations Framework Convention on Climate Change (UNFCCC), as well as the resolution of the available satellite data (FAO, 2015; Sasaki and Putz, 2009; UNFCCC, 2006). It must be noted that common forest definitions such as those from FAO and UNFCCC are criticised as being too simplistic and not distinguishing plantations from natural forests (Chazdon et al., 2016; Sasaki and Putz, 2009). Using these definitions may therefore lead to erroneously classifying highly degraded landscapes as forest and falsely indicating that canopy density thresholds are met, which are required for maintaining the integrity of biotic communities (Banks-Leite et al., 2014; Lima and Mariano-Neto, 2014; Saturni et al., 2016). Furthermore, many habitat features, which are relevant for defining forest integrity, such as forest age, patch size, height of trees, tree canopy density canopy layers, and tree species diversity (Green et al., 2020; Hill et al., 2019), are not reflected in the applied definition. It is therefore feasible that our definition cannot fully provide the required level of information on the forest's integrity, which may generate imprecisions in the available data and conclusions (Chazdon et al., 2016; Green et al., 2020; Harris et al., 2019).

We retrieved global forest or *tree canopy density* data at 30 m/pixel resolution from the Landsat-based Global Forest Cover Change (GFCC) archive of the University of Maryland (Sexton et al., 2013; *tree canopy density* is referred to as 'tree cover' by GFCC). The data were available for the years 2000, 2005, 2010 and 2015. We retrieved the forest cover at the three levels of canopy density closest to the date in which each pollination study was conducted (on average, these data were $1.6 \pm 0.8$ years away from study dates). For the variable *forest cover*, we used ArcMap 10.5 to create circular buffers of 500, 1000 and 2000 m radius around each sample coordinate (Environmental Systems Research Institute, 2016). Radii were chosen based on previous assessments of pollinator foraging distances from coffee and other crop plantations to cover both field and landscape levels (Benjamin et al., 2014; Kremen et al., 2004; Ricketts et al., 2004; Saturni et al., 2016). We calculated the proportion of forest in the buffers for each sample at the three canopy density levels. We also included the variable *forest distance*, which was calculated as the distance (in metres) from the sample coordinate to the edge of the nearest forest patch using the gdistance package in RStudio 1.2.5042 (R Core Team, 2020; van Etten, 2017). The maximum distance to a forest patch that was considered relevant for bees was defined at 3 km distance. Based on a literature review on foraging distances of solitary and social bees (see selected citations in footnote 2), distances greater than 3 km were therefore not recorded, and samples were not included in the analysis.[2] The *forest distance* variable was log-transformed for the regression analyses. As the size of the forest patch may influence the magnitude of the effect of forest on coffee pollination (Ricketts et al., 2004), we conducted the analyses at four minimum patch sizes assumed relevant for bee pollinators: 0.8, 5, 15 and 25 ha. Finally, the data for both forest cover and distance variables were synthesised for all buffer and forest patch sizes at the three above described levels of canopy density: open, closed and dense forest.

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[2] Solitary bees, who are particularly dependent on forest habitat for nesting, and some species of *Bombus* ssp. Latreille are commonly found to fly maximum distances of 2.6 km (Araújo et al., 2004; Gathmann and Tscharntke, 2002; Osborne et al., 1999; Zurbuchen et al., 2010). While some carpenter bees (*Xylocopa* ssp. Latreille) and *Apis mellifera* L. were found to fly up to 6 and 10 km respectively (Beekman and Ratnieks, 2000; Cresswell et al., 2000; Valk et al., 2012), their foraging distances are commonly limited to one-third to half of this maximum distance (Somanathan et al., 2019; Visscher and Seeley, 1982).

## 2.3. Statistical analyses

We used a one-tailed Wilcoxon signed-rank test for each study to determine whether fruit sets of open treatments were significantly greater than fruit sets of closed treatments at the coffee plant level (for the definition of a coffee plant, see 2.2). This test addressed the question whether there is an overall effect of pollinators on *C. arabica* fruit set (Q1).

Further, for those studies where pollinator richness data was available, we estimated simple linear regressions between *pollination success* and the predictor variable *bee pollinator richness* at the sample level (for the definition of a sample, see 2.2) to assess whether local bee richness positively associates with fruit set of *C. arabica* (Q2). Predictors of regression analyses were normalised to zero mean and unit variance (z-score standardisation).

Finally, to test the impact of forest on the richness of bee pollinators and coffee fruit set (Q3), we regressed the response variables *pollination success* and *bee pollinator richness* against the forest predictor variables *forest cover* and *forest distance* for all buffer and forest patch sizes (see 2.2.2 and 2.2.3). For both response variables, we estimated simple linear regressions against the individual predictor variables, as the sample size did not allow for multiple regression models. We only estimated regressions for data sets with six or more samples, and only if a majority of the forest cover values were above zero. Additionally, to assess whether the effect of forest differs depending on the canopy density (Q4), we performed the above analysis for each study at the three density levels ($\geq$25%, $\geq$50% and $\geq$75%).

All regressions were carried out at the level of the individual studies. As we ran between 14 and 22 regressions for each response variable and study, we controlled for a potential false discovery rate (FDR) by applying the Benjamini-Hochberg procedure on the number of analyses for each data set (Benjamini and Hochberg, 1995; Waite and Campbell, 2006). We used the stats package in RStudio 1.2.5042 for all analyses (R Core Team, 2020).

## 3. Results

In the systematic literature review, we screened a total of 556 articles from the four databases. After the PRISMA review steps, only eleven studies met all criteria for the final analyses (Table 1). Nine of these studies were located in the Americas, one in East Africa, and one in South-East Asia (Fig. 1A). The entire data set included a total of 869 coffee plants, distributed over 182 samples from the eleven studies. More detailed results of the literature review and a discussion thereof can be found in Supplementary Material S2.

In the analysis for Q1 of pollination treatments across studies, we found that the fruit set of open pollination had an average of ~65% ($\pm$22% SD) whereas the fruit set of closed pollination averaged at ~55% ($\pm$25% SD). These results show that biotic pollination increased fruit set by ~18% on average across all studies (Fig. 1B), and a one-tailed Wilcoxon signed-rank test confirmed that this difference between the treatments was significant. The within-study analyses for Q1 indicated that fruit set was significantly greater in open than in closed pollination treatments in eight out of eleven studies (Fig. 1B). In three studies, there were no statistical differences between the treatments. For approximately 30% of the coffee plants, the fruit set from closed treatments was about the same or slightly higher than from open treatments. Most of these plants were located in Mexico 1 (38% of coffee plants), Ecuador (43%) and Tanzania (45%), the three studies with the highest fruit set (>80%) in both treatments (Fig. 1B), as well as Mexico 2 (42%). The *pollination success* variable supports these findings: the odds for pollination success were 2.3 times higher in open than in closed treatments and negative values reflecting greater pollination success in closed compared to open treatments were clustered in the four above mentioned studies (the grey area in Fig. 2A).

The Chao1 estimator of bee species richness varied between one and 46 species per sample, with an average of 8.4 species (Fig. 2B). The third quantile of this estimator lay at 10.6 species per sample. The regression analyses applied to assess associations between *bee pollinator richness* and *pollination success* of coffee indicated no significant relationships between these variables in any study (Q2).

Next, we analysed whether forest influences pollinator communities and coffee fruit set and assessed at which canopy density this effect can be measured (Q3 and Q4). Between studies, *forest cover* varied between 0% and 100% in the small buffer (500 m). However, data variability within most studies was moderate for open forest ($\geq$25% canopy density), meaning that available data did not cover a large part of the possible data range (Fig. 2C). For dense forests ($\geq$75% canopy density), data variability was very low within most studies, except for Indonesia, where dense forest cover ranged between 4% and 51% in the 24 samples

**Table 1**

Table showing the eleven studies on *Coffea arabica* pollination identified in the literature review with information on location, geographic coordinates, study year, the number of samples (cluster of coffee plants), information on initial or final fruit set, the total number of coffee plants (collectively for all samples), and if flower visitor data was collected.

| Study | Location | Coordinates at centre | Year | No. of samples | No. of coffee plants | Flower visitor data |
|---|---|---|---|---|---|---|
| Meireles et al. unpublished data | **Brazil 1** Minas Gerais | 18°44'39.3"S 47°58'50.3"W | 2017/18 | 30 IFS | 140 | ✗ |
| Hipólito et al. (2018) | **Brazil 2** Bahia | 13°14'56.3"S 41°22'31.4"W | 2013/14 | 31 FFS | 31 | ✔ |
| Saturni et al. (2016) | **Brazil 3** Minas Gerais / São Paulo | 21°37'15.1"S 46°35'47.3"W | 2013 | 9 IFS | 118 | ✔ |
| González-Chaves et al. (2020) | **Brazil 4** Minas Gerais | 21°46'06.9"S 46°27'29.8"W | 2014 | 24 FFS | 72 | ✔ |
| Bravo-Monroy et al. (2015) | **Colombia** Santander | 6°22'46.9"N 73°07'37.5"W | 2011 | 12 FFS | 112 | ✔ |
| Veddeler et al. (2008) | **Ecuador** Manabí | 1°34'24.6"S 80°24'07.9"W | 2003/04 | 18 IFS | 88 | ✔ |
| Klein et al. (2003b) | **Indonesia** Central Sulawesi | 1°34'06.4"S 120°29'01.0"E | 2000/01 | 24 IFS | 96 | ✔ |
| Moreaux et al. unpublished data | **Jamaica** St. Andrew | 18°08'09.1"N 76°48'09.4"W | 2018 | 4 IFS | 25 | ✗ |
| Vergara and Badano (2009) | **Mexico 1** Veracruz | 19°19'23.6"N 96°55'34.9"W | 2003 | 16 IFS | 64 | ✔ |
| Philpott et al. (2006) | **Mexico 2** Chiapas | 15°10'30.0"N 92°19'30.0"W | 2002 | 2 FFS | 28 | ✔ |
| Classen et al. (2014) | **Tanzania** Mount Kilimanjaro | 3°15'41.5"S 37°20'48.4"E | 2011/12 | 12 IFS | 95 | ✔ |

IFS = Initial fruit set; FFS = Final fruit set.
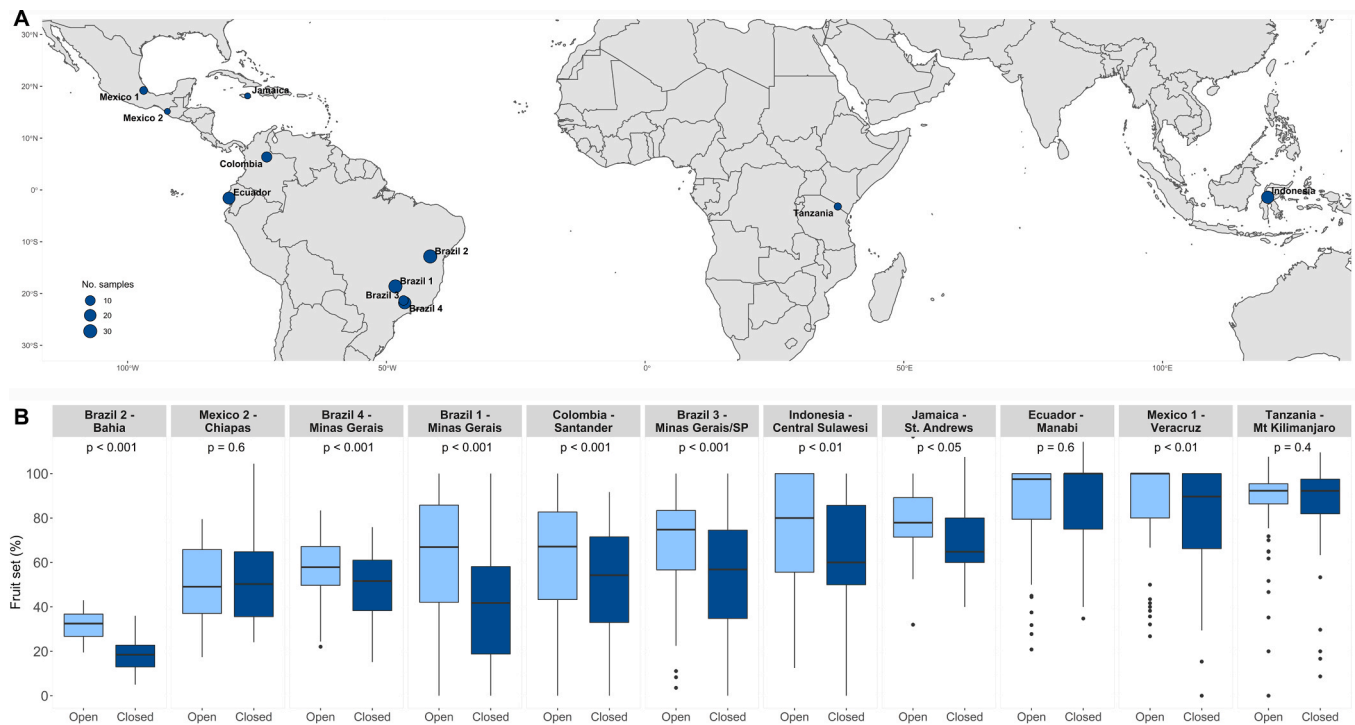
**Fig. 1.** (A) Location and sample size of included coffee studies. (B) Fruit set proportion in each study after 'Open' and 'Closed' treatment, sorted in ascending order by fruit set of open treatments. The p-values indicate Wilcoxon signed-rank test results examining whether 'Open' is significantly greater than 'Closed' treatments.

(Fig. 2D). Open forest was located within ca. 1 km distance from all samples (Fig. 2E). Data variability of the *forest distance* variable was low for open forest. Distance to dense forest varied more between studies, and no dense forest was located within a 3 km distance from the sample location in three studies (Fig. 2F). Due to the plurality of forest variables, we present only selected levels here. Data variability for all levels of the forest predictors is provided in Supplementary Materials S3 (*forest cover*) and S4 (*forest distance*).

For open forest, we found no significant association between the two forest variables *forest cover* and *forest distance* with *pollination success* at any buffer or patch size (Supplementary Material S5A-B). For closed forest (≥50% canopy density), only one regression analysis was significant, indicating a negative association between forest cover in the 2000 m buffer and *pollination success* in Tanzania. With increasing forest cover in the buffer, the odds of pollination success in open treatments decreased with a factor of 0.71 (i.e., 29%) per unit of forest cover, as compared to closed treatments (Table 2). Noticeably, the fruit set of open and closed treatments in Tanzania was among the highest of all recorded studies (>80%; Fig. 1B). For dense forest, we only identified significant relationships in Indonesia, where dense forest cover was positively correlated with *pollination success.* Here, the odds of pollination success in open treatments increased with a factor of 1.37 (i.e., 37%) per unit of forest cover in the 500 m buffer, as compared to closed treatments (Table 2). Also, in Indonesia, the distance to dense forest correlated negatively with *pollination success* for forest patch sizes of at least 0.8, 5 and 15 ha respectively. Depending on the patch size, the regression analyses indicated a reduction of 0.73–0.75 (i.e., 23–25%) in the odds of pollination success in the open treatments with increasing distance to forest, as compared to closed treatments (Table 2). We identified no significant effect of forest variables on *bee pollinator richness* at any canopy level. Results of all analyses, including the effect of *forest cover* in all buffers, all forest patch sizes for *forest distance* and canopy density levels, can be found in Supplementary Material S5A-C.

## 4. Discussion

This study provides the first global literature review assessing the importance of animal pollination for fruit set of *C. arabica*, and, most importantly, indicates whether the density of forest habitat influences the relationship between forest and animal pollination. Our main findings confirm the importance of animal pollination for coffee yield in a majority of the included studies, by showing an average increase of ~18% in fruit set across studies as compared to wind and self-pollination. This result is consistent with previous studies, which found a fruit set increase of up to 30% in *C. arabica* plants being animal pollinated (e.g. Hipólito et al., 2018; Klein et al., 2003b; Krishnan et al., 2012; Munyuli, 2012). However, the extent of this biotic effect on the coffee fruit set largely differs between the studies we analysed, ranging from 9% to 74% for the studies with significant results (Fig. 1B). The reason may lie in differences in the cultivars grown in different parts of the world, the biogeographic location and local environmental factors, such as shade, which have been shown to affect both the quality and quantity of the coffee produced (see e.g. Aristizábal and Metzger, 2019; Classen et al., 2014; Munyuli, 2014; Philpott et al., 2006). Farm management strategies, such as shading, management intensity and pesticide application are also known to impact coffee yields (Hipólito et al., 2018; Munyuli, 2014; Vergara and Badano, 2009). This information was therefore recorded as part of the data collection, if available. However, as documentation on management strategies was not consistent and only available for a few of the included studies, these factors were not included in the analyses. Accounting for them would likely result in more accurate models and should preferably be considered in future large-scale analyses.

For around 30% of the coffee plants, the fruit set from closed treatments was about the same or slightly higher than under open treatments. These cases were mostly clustered in the three studies with the highest overall fruit set, on average > 80% for both treatments. Therefore, it is possible that the similar or marginally higher fruit set observed in closed treatments were caused by a pollinator saturation effect or even an "over-pollination" effect in the open treatment where too many bee
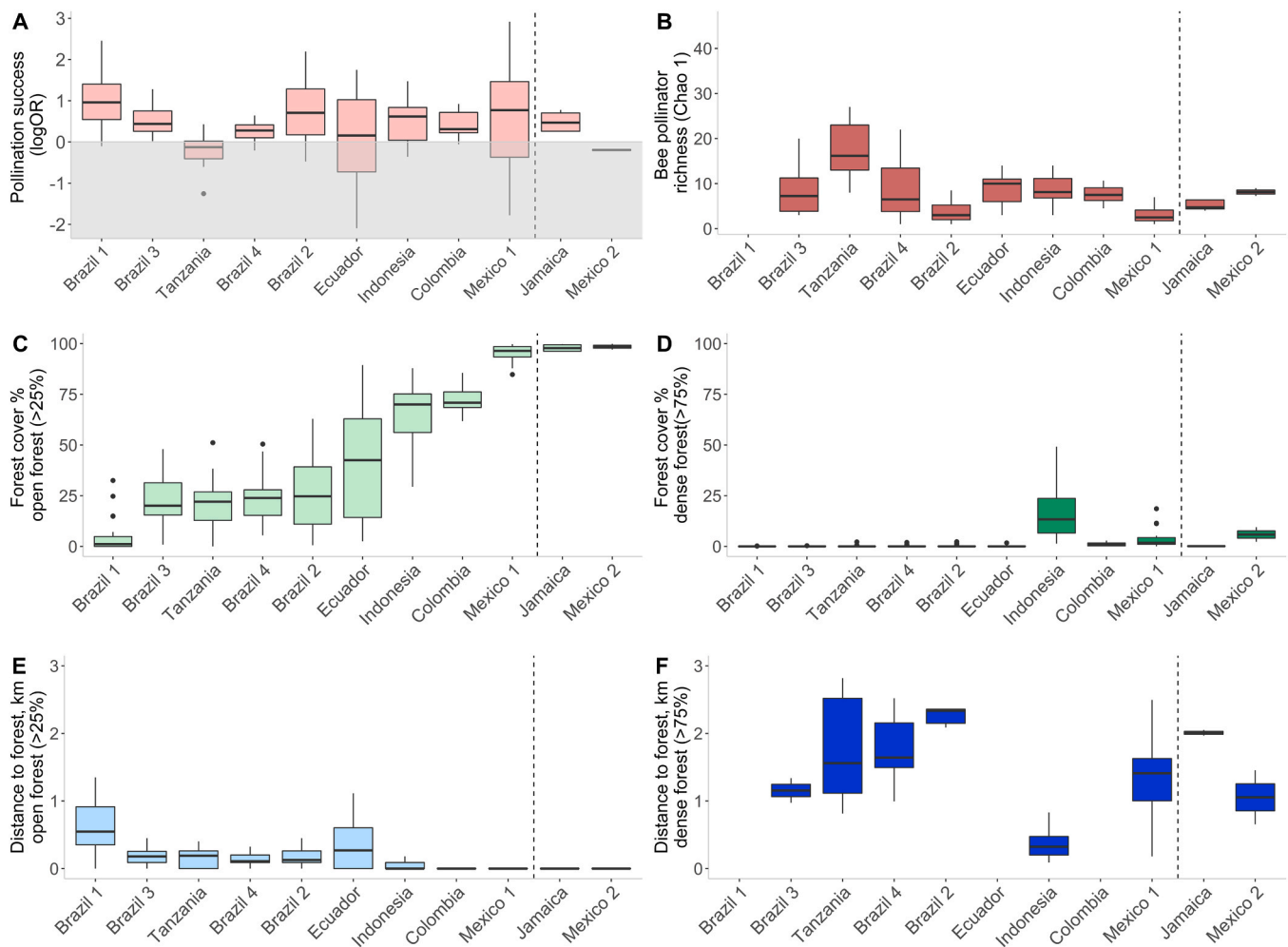
**Fig. 2.** Overview of response and selected predictor variables included in this study. (A) *logOR* of pollination success in open vs. closed treatments, with positive values indicating a positive impact of pollinators on fruit set. The grey area below zero indicates the odds of a closed treatment resulting in a higher fruit set than open treatment; (B) Bee pollinator richness (*Chao* 1) for the studies where data was available; (C) Forest cover in 500 m buffer with canopy density of $\geq$ 25%; (D) Forest cover in 500 m buffer with a canopy density of $\geq$ 75%. (E) Distance to forest of min. patch size (0.8 ha) with a canopy density of $\geq$ 25%; (F) Distance to forest of min. patch size (0.8 ha) with a canopy density of $\geq$ 75%. In all panels, the dashed line separating the studies Jamaica and Mexico 2 indicates that they were excluded from regression analyses due to too small sample size (n = 4 and n = 2, respectively). Studies on all panels are sorted by the mean in Fig. 2C.

visits have negative effects on fruit set (Aizen et al., 2014). Alternatively, flowers exposed to pollinators are also exposed to an array of potential antagonists, which may harm flowers and thus lower fruit set. Still, in the majority of the samples, fruit set increased considerably when flowers were exposed to pollinators.

The analysis of the effects of bee pollinator richness on coffee fruit set revealed that increasing bee species richness did not positively influence fruit set in any study, as compared with fruit development in closed pollination experiments (Q2). Previous assessments of bee diversity effects (including variables such as abundance and richness) on coffee fruit set showed mixed results for this relationship. Some studies documented positive effects (Boreux et al., 2013; Garibaldi et al., 2013; Klein et al., 2003b). Notably, Klein et al. (2003b) found strong positive effects of bee richness on coffee fruit set in Indonesia. However, whereas Klein et al. (2003b) assessed pollinator success based on fruit set of open flowers and subsequently compared it to the fruit set of manually cross-pollinated flowers, we estimated the role of pollinators by examining the ratio of pollination success in open versus closed (wind) pollination treatments. Thus, we assessed the potential positive effects of pollinators on fruit set, rather than identifying the upper limits of possible pollination levels using manual cross-pollination. Our results do therefore not stand in direct comparison to the findings by Klein et al. (2003b). Our overall findings are in line with several previous studies,

which likewise did not identify positive correlations between bee species richness and fruit set (González-Chaves et al., 2020; Philpott et al., 2006). One reason that those bee pollinator communities may not affect coffee fruit set, is if the community is dominated by few species, particularly social bees, which are less effective pollinators (Saturni et al., 2016). Thus, pollinator abundance and evenness of the pollinating community might be other important factors to predict the effects of bee pollinators on coffee fruit set (Veddeler et al., 2008). Effects might further vary depending on the sampling design (sampling times and duration, number of samples taken, etc.), the spatial scale (Jha and Vandermeer, 2009; Saturni et al., 2016; Veddeler et al., 2006), competitive interactions with domesticated honey bees (Badano and Vergara, 2011; Garibaldi et al., 2013; Valido et al., 2019), coffee cultivars, biogeographic location and other environmental conditions (Ngo et al., 2011; Peters and Carroll, 2012; Philpott et al., 2006), including the proximity of forest ecosystems (Hansen et al., 2020; Klein et al., 2003b; Ricketts, 2004). Nevertheless, no matter the forest density, we found no correlation between forest cover or distance with bee species richness in any of the studies (Q3 and Q4).

With regards to the effect of forest on pollination success (Q3 and Q4), we found that results differed depending on the density of forest habitat surrounding coffee farms. While we found no effects of open forest ($\geq$25% canopy density) on pollination success, we identified

**Table 2**
Results from regression analyses of the forest variables on the response variables *pollination success (logOR)* and *pollinator richness (Chao1)*. Only results significant after the Benjamini-Hochberg (BH) procedure are shown. For the remaining studies, we identified no statistically significant associations. P-values indicate significance levels before BH corrections. 25/50/75 in predictor names indicate canopy densities of $\geq 25\%$, $\geq 50\%$ and $\geq 75\%$, respectively. Distance to forest was measured in metres (min. forest patch size in parentheses), forest cover was measured as the proportion of a buffer (buffer size in parentheses). Predictors were normalised.

| Response | Predictors | Estimate | Std. error | Pr (>\|z\|) | $R^2$ | After BH procedure |
|---|---|---|---|---|---|---|
| Pollination success (logOR) | **Indonesia** | | | | | |
| | Forest cover 75 (500 m) | 0.312** | 0.089 | 0.002 | 0.357 | * |
| | Forest distance 75 (0.8 ha) | -0.298** | 0.091 | 0.004 | 0.326 | * |
| | Forest distance 75 (5 ha) | -0.292** | 0.092 | 0.004 | 0.314 | * |
| | Forest distance 75 (15 ha) | -0.314** | 0.089 | 0.002 | 0.362 | * |
| | **Tanzania** | | | | | |
| | Forest cover 50 (2000 m) | -0.344** | 0.087 | 0.003 | 0.612 | * |

\* $P < 0.05$, \*\* $P < 0.01$, \*\*\* $P < 0.001$

positive correlations with forest variables for dense forest ($\geq 75\%$) in one study and a negative correlation for forest cover for closed forest ($\geq 50\%$) in another study. For dense forest, pollination success increased with increasing forest cover and decreasing distance to forest at multiple forest patch sizes in Indonesia (Table 2). It must be noted that data variability for dense forest cover was very low within most studies, meaning that available data covered a minor part of the possible data range between 0% and 100% forest cover (Fig. 2D). Similarly, except for Indonesia, distance to dense forest was > 1 km in many studies, or in some cases, no dense forest existed within the 3 km threshold (Fig. 2F). This lack of data variability could therefore have masked associations between dense forest and fruit set variables (Hansen et al., 2020). As the Indonesian study of Klein et al. (2003) is the only one within the database with wide variability for dense forest cover (Fig. 2D; Supplementary Material S3C, F, I), this may well explain why we do not detect a wider impact of dense forest on pollinator richness and fruit set in other sites. Although the positive trend was restricted to one site, the result suggests that dense forest in close vicinity of coffee farms may be beneficial for biotic pollinators, to obtain high coffee fruit set, compared to more open or disturbed forests. This would be consistent with what we expected because forest systems with higher intactness and more diverse plant communities are important for pollinators, notably social bees, as they host an elevated array of pollen food resources and nesting grounds (Boreux et al., 2013; Bravo-Monroy et al., 2015; Klein et al., 2004). While higher canopy density is not synonymous with a higher quality of the forest habitat, dense forests are more likely to reflect low disturbance levels and 'true' forests (reducing confusion with tree plantations). Thus, to better understand if dense forest has particular biodiversity value for pollinators, more case studies are needed to substantiate these findings beyond a single study. In contrast, more open forests can often not be distinguished clearly from agroforests and tree plantations using the available satellite imagery. These prevailing limitations in remote sensing techniques may generate imprecisions in the available data (Chazdon et al., 2016; Green et al., 2020; Hill et al., 2019). This might contribute to the discrepancies in results between our study and the original studies, which found positive correlations between forest cover and pollination success, as well as negative correlations between distance to forest and pollination success. Although the assessments are based on the same biological data, authors could determine distances to forest on the ground and distinguish it from other, potentially more degraded land use types. Therefore, despite the great potential of remote sensing methodologies, its use is restricted due to the level of detail of forest data available, which needs to be improved in future assessments.

For closed forest ($\geq 50\%$), there appears to be a negative correlation between forest cover and pollination success in Tanzania, contrasting our hypothesis. This effect is limited to Tanzania and to the large buffer size (2000 m), which is beyond the foraging range of many solitary bee species, which were identified on the coffee farms in Tanzania (Classen et al., 2014) and are important for crop pollination (Araújo et al., 2004;

Roubik and Aluja, 1983). As the amount of forest cover increases with elevation in this study area (pers. comm. Alice Classen), it seems likely that fruit set was affected by temperature (either directly or indirectly via reduced pollinator visitation rates in cooler climates, see Lehmann et al., 2019). Alternatively, other landscape-scale factors, such as the availability of floral resources closer to nesting sites and the fragmentation level of natural habitats (Brosi, 2009; Saturni et al., 2016) might be the underlying driver of such effect. Finally, fruit set of both open and closed treatments in this study was on average > 80%, which may have caused a saturation effect, such as described above.

Finally, the level of landscape fragmentation and deforestation is an important factor, which might have confounded the effect of forest on the response variables. Landscape complexity was found to be an influencing variable in other studies on coffee pollination (e.g. Hipólito et al., 2018; Jha and Vandermeer, 2009; Saturni et al., 2016) as well as the pollination of other crops (e.g. Andersson et al., 2014; Brittain et al., 2010; Chateil and Porcher, 2015; Sritongchuay et al., 2019). Pollination limitation, resulting from changes in the abundance or composition of pollinating communities due to habitat fragmentation, can consequently affect plant reproductive success and seed production (Aguilar et al., 2006; Aizen and Feinsinger, 1994). This is important because habitat loss and fragmentation are the primary drivers of the biodiversity crisis, threatening insects and other pollinators at accelerating rates. Those threats are also reflected in our data, and the remote sensing techniques disclose the alarmingly low cover and high fragmentation of tropical forests around the studies we included in our analyses: With the exception of the Indonesian study, dense forest covered only up to 18% in the 500 m buffer, 11% in the 1000 m buffer and 9% in the 2000 m buffer around sample sites (Supplementary Material S3). Distance to dense forest averaged at 4.7 km for all patch sizes and a staggering 17.5 km for forest patches of at least 25 ha size. Thus, most dense forests lie beyond our defined threshold of 3 km, which is often considered to be relevant for the maximum foraging ranges of most bees (Araújo et al., 2004; Gathmann and Tscharntke, 2002; Osborne et al., 1999; Roubik and Aluja, 1983; Zurbuchen et al., 2010). This supports the assumption that a lack of dense forest may prevent the identification of associations between the forest variables and pollinator richness or fruit set in other sites than Indonesia. Therefore, we support the call for more studies on the effects of landscape heterogeneity and forest fragmentation on pollinators (Boreux et al., 2013; Brosi et al., 2008).

Taken together, we have shown that bees and other pollinators make a significant contribution to the fruit set of *C. arabica*. Their conservation can therefore be used as a strategy to increase coffee yields and revenues while strengthening on-farm biodiversity. Our results further suggest that forest habitats at high canopy density may have positive effects on biotic pollination success and that more research is needed to confirm these findings. However, the satellite data reveals that dense forest habitats are scarce and highly fragmented around coffee farms. As this landscape degradation and forest loss continue to occur at an alarming rate, notably in many tropical regions, it is important to conserve the

well-preserved forests left on earth (Rosa et al., 2021). We warn that focusing purely on the economic benefits via ecosystem services bears the risk of designing isolated initiatives with little conservation value (Kleijn et al., 2015; Senapathi et al., 2015). Instead, we suggest that an ecosystem-level approach must be applied, which takes into account foraging ranges, connectivity of restored sites (e.g. through corridors) and minimum habitat areas to direct pollinator conservation towards improved ecosystem resilience and connectedness, not only to the benefit of crop pollination but also wild plants (Kremen et al., 2007; Menz et al., 2011; Senapathi et al., 2015). This is particularly relevant under already changing climate regimes, which together with land use changes pose some of the major global challenges for biodiversity and food production systems alike (Díaz et al., 2018).

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## CRediT authorship contribution statement

**Bo Dalsgaard, Céline Moreaux, Niels Strange**: Conceptualization. **Céline Moreaux**: Data curation, Investigation, Project administration, Visualization, Writing – original draft. **Céline Moreaux, Jesper Sonne, Tuanjit Sritongchuay**: Formal analysis. **Niels Strange, Carsten Rahbek, Bo Dalsgaard**: Funding acquisition. **Céline Moreaux, Desirée A. L. Meireles, Pietro K. Maruyama, Jesper Sonne, Tuanjit Sritongchuay, Carsten Rahbek, Niels Strange, Bo Dalsgaard**: Methodology. **Céline Moreaux, Desirée A.L. Meireles, Pietro K. Maruyama, Juliana Hipólito, Blandina F. Viana, Fernanda T. Saturni, Jean Paul Metzger, Adrian González-Chaves, Liliana Bravo-Monroy, Teja Tscharntke, Alexandra-Maria Klein, Ernesto I. Badano, Carlos H. Vergara, Stacy M. Philpott, Shinsuke Uno, Alice Classen, Niels Strange, Bo Dalsgaard**: Resources. **Carsten Rahbek, Niels Strange, Bo Dalsgaard**: Supervision. **Céline Moreaux, Desirée A.L. Meireles, Pietro K. Maruyama, Jesper Sonne, Tuanjit Sritongchuay, Carsten Rahbek. Juliana Hipólito, Blandina F. Viana, Fernanda T. Saturni, Jean Paul Metzger, Adrian González-Chaves, Liliana Bravo-Monroy, Teja Tscharntke, Alexandra-Maria Klein, Ernesto I. Badano, Carlos H. Vergara, Stacy M. Philpott, Shinsuke Uno, Alice Classen, Niels Strange and Bo Dalsgaard**: Writing – review & editing. All authors have read and agreed to the published version of the manuscript.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107680. Textbox S1: Methodology and results of the data collection on biotic coffee pollination in St. Andrews, Jamaica. S2: Further results and discussion of the systematic literature review. Fig. S3: Forest cover (%) with tree canopy density of $\geq$ 25%, $\geq$ 50%, and $\geq$ 75% for the three buffer sizes of 500 m (A-C), 1000 m (D-F) and 2000 m (G-I). Fig. S4: Distance to forest (km) with tree canopy density of $\geq$ 25%, $\geq$ 50%, and $\geq$ 75% at minimum 0.8 ha, (A-C), 5 ha (D-F), 15 ha (G-I) and 25 ha (J-L) forest patch size. Table S5: Model results from all linear regression models using pollinator richness (Chao1) and forest predictor variables at $\geq$ 25% (A), $\geq$ 50% (B) and $\geq$ 75% (C) tree canopy density.

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