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Global chocolate supply is limited by low pollination and high temperatures

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Cocoa (*Theobroma cacao* L.) provides livelihoods for 5 million smallholder farmers, but the factors limiting cocoa yield are poorly understood. We present a global analysis of pollination, cocoa tree, plantation, and climate factors affecting cocoa yield, with experimental data from three major cocoa-producing countries: Brazil, Ghana and Indonesia. Hand-pollination increased yield by 20%, showing cocoa yield is limited by pollination, but not nutrients. Leaf litter and large cacao trees, measures of soil resource availability and access, increased yield by 9-19%. Cooler temperatures by 7 °C during the hot season increased yield by up to 31%, indicating substantial risks from climate warming. Agricultural production that enhances cocoa pollinator abundance, protects soils, and mitigates climate risks will be the most effective way to secure global cocoa production and support livelihoods into the future.

Cocoa (*Theobroma cacao* L.) is one of the most important cash crops produced by small-holder farmers in the tropics, with the global unprocessed cocoa bean market estimated to reach USD 16 billion by 2025[1], and the global chocolate industry estimated to be worth USD 100 billion per year[1–3]. Worldwide, four to six million small-holder farmers depend on the cocoa industry for their livelihoods[4,5]. Their income from cocoa helps to provide food, healthcare, and education[6], supporting progress towards the United Nations 2030 Sustainable Development Goals to eradicate poverty and hunger while securing good health and well-being for everyone[7].

The high economic value of cocoa provides an incentive to expand areas of cocoa production and intensify cocoa cultivation methods[8–10]. However, plantation expansion can drive deforestation, and intensively managed plantations are typically ecologically simplified and agrochemical-dependent, harbour reduced biodiversity, have diminished ecosystem services, including pest control and pollination, and are likely to be more vulnerable to climate change[9,11–14]. Thus, there is a trade-off between the short-term economic benefits of plantation expansion and intensive production on the one hand, versus, on the other hand, the resulting deforestation and losses of biodiversity, ecosystem services, ecological resilience, and the capacity for long-term, sustainable production.

A key approach to address this short-term yield vs. sustainability trade-off is to close the 'yield gap' in existing plantations using farming methods shown to protect ecosystem services while at the same time promoting crop production[15,16]. The yield gap of a crop is the difference between the achieved crop yield, *Ya*, and the potential yield, *Yp*, which is the field-demonstrated yield of a cultivar in its favoured conditions, or the theoretical yield, *Yt*, which is the model-predicted yield based on physiological parameters[17]. Our review of published literature found that cocoa *Ya* ranges from 39 to 3586 kg/ha, with wide variation both within and between major cocoa-producing countries. In some countries, *Yp* is double the current *Ya*, meaning the yield gap is equal to the current yield (Supplementary Table 1). Cocoa yield gaps have been linked to water availability[18], plantation age, soil nutrients[19,20], climate, plantation management[14,20,21], and pests and diseases[22]. In addition, because arthropod pollination is essential for fruit production in most cocoa varieties[23], low abundance or efficacy of available pollinators (pollinator limitation), lack of compatible pollen (pollen limitation), or cultivar selection can mean that the flowers on a cocoa tree do not receive sufficient pollen and do not set fruit, resulting in reduced yield[5,24–28]. Reducing the yield gap between current production levels (*Ya*) and estimated maxima (*Yp* or *Yt*) in existing plantations could improve farmer livelihoods and help meet market demands. In addition, yield increases could help protect ecosystem services in surrounding landscapes by reducing the incentive to expand plantations into areas of native vegetation, especially when implemented in combination with legal protections for

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native ecosystems[29]. However, a key knowledge gap is understanding the relative importance of pollination limitation compared to cocoa tree, plantation, or climate factors, as drivers of global cocoa yield gaps[26].

Here we present a global analysis of the factors affecting cocoa yield, with the rare advantage that the data are from methodologically consistent experiments in three major cocoa-producing countries: Indonesia, Brazil and Ghana. These three countries represent 33% of global cocoa production (Supplementary Table 1). Our study questions are: (i) How much effective natural pollination is occurring? (ii) Is there evidence of pollination limitation or physiological limitation to yield? (iii) What are the relative impacts of pollination, cocoa tree, plantation, and climate factors on cocoa yield? We find positive effects on pod yield from higher pollination percentage (+20%), cooler temperatures (+22–31%), and availability of and access to soil resources (+9–19%), suggesting cocoa production is pollination limited and threatened by loss of soil resources and rising temperatures.

Results and discussion

Natural cocoa pollination averages 16.7%

The hand pollination (HP) experiment was conducted at ten sites in Bahía, Brazil, during 2018–2019, eight study sites in the Western Region of Ghana during 2019–2020, and eight sites in Central Sulawesi, Indonesia, during 2017 (Supplementary Table 2). The data on fruit set and fruit development from the experiments in Brazil and Indonesia have been published in location-specific studies (see refs. 27,30), and are presented here in a planned, integrated, multi-continent comparison to identify global trends.

In each study site, a study plot was established, and one tree was selected for each of the six treatments: 0% (natural pollination), 20%, 40%, 60%, 80%, and 100% HP (Methods, Supplementary Table 2[27]). Natural pollination in cocoa is mainly by arthropods[23], but any occurrences of wind or water pollination would also be included in our definition of natural pollination. Only flowers below 2 m were included in the experiment, and the average number of flowers below 2 m on each tree before treatment was 226 (SD = 117).

The percentage of flowers per tree in the 0% HP treatment receiving effective natural pollination was calculated using a log-linked generalised linear model (GLM) of pods harvested against HP percentage (Methods, Supplementary Fig. 1). The model estimated 12% effective natural pollination occurred in the Brazilian sites, 27% in the Ghanaian sites, and 11% in the Indonesian sites (Table 1).

These estimated levels of natural pollination are similar to estimates from previous cocoa studies but also confirm substantial geographic variation. For example, Groeneveld[25] noted that pollination was a major factor limiting cocoa production in their sites in Indonesia, and both Groeneveld[25] and Toledo-Hernández[27] estimated that 10% of flowers were pollinated naturally. Similarly, Forbes[9] estimated that 10% of cocoa flowers in northern Australia were successfully pollinated. Vansynghel et al.[5] estimated in their study that 2% of flowers were effectively pollinated and went on to set fruit. Thus, the cocoa plant appears to be one of the approximately three-quarters of all plant species globally that produce more flowers than are converted to mature fruits, as part of an eco-evolutionary ‘bet-hedging’ strategy to maximise reproduction in a stochastic environment[24,25,31].

Having established that the percentage of cocoa flowers that mature into fruit is far below 100% in Question i, Question ii asks whether cocoa trees are producing as many pods as it is possible to produce at the study regions, or whether management interventions could increase pod production per tree.

Cocoa yield is pollination-limited

A student’s *t* test found that yield (i.e., pods per tree) in the 0% (natural pollination) treatment was significantly lower than yield in the 100% HP treatment in all three countries ($p = 3.95 \times 10^{-4}$, 1.66×10^{-9}, and 3.10×10^{-4} for Brazil, Ghana and Indonesia, respectively) (Table 1). We acknowledge that cocoa tree variety and age would also be expected to affect yield; for example, the higher overall numbers of pods in all treatments from the Indonesian sites compared to the Brazilian and Ghanaian sites may be influenced by the cocoa variety. However, in our study, cocoa variety and age correlated with the country (Supplementary Table 2), whereas the pattern of increasing pod number with increasing HP was consistent across countries. This result indicates that there was an effect of the pollination treatment, independent of any effects of variety or age. Question iii) investigates the impact of these and other factors on pod yield in more depth.

Our expectation is that if yield is generally limited by pollination, and if there is no physiological limitation, yield will increase linearly with the percentage of flowers pollinated. However, if yield is limited by pollination as well as physiological factors, yield will increase with percentage pollination up to a plateau or ‘breakpoint’ (a point at which the fitted linear model changes in slope), where physiological limitations would slow or stop the production of fruit (Fig. 1).

To determine whether the pod yield data exhibited a breakpoint, a self-exciting autoregressive (SETAR) model for a number of pods compared to pollination percentage was fitted for the data from each country. Breakpoint regression models are two coupled linear models which aim to find the plateau of a dataset where two lines provide a better fit for the data than one line. The SETAR models found no break points in the country-level data sets for Brazil and Ghana, and a breakpoint at 60% HP for Indonesia (Supplementary Table 3). In line with previous studies[25], this result suggests that pod yield is limited by pollination and not physiological limits in Brazil and Ghana, and that pod yield with pollination up to 60% would not exceed physiological limits in Indonesia.

In summary, results from Questions i and ii provide estimates of 11–27% natural pollination and evidence that cocoa trees in the study regions are not producing as many pods as it is physiologically possible for them to produce. These results provide strong evidence for pollination limitation in all three countries, with large variation between countries in the extent of pollination limitation, and in yield per cocoa tree. However, cocoa tree, plantation, and climate factors are also likely to affect cocoa yield[18–22]. Therefore, in Question iii we ask: How important is pollination compared to cocoa tree, plantation, or climate factors for cocoa yield?

Pollination, leaf litter, and cooler climate all positively affect cocoa yield

To address Question iii, we used three GLMs to determine the impact of pollination, cocoa tree, plantation, and climate factors on cocoa pod production. Model 1: We combined natural pollination (0% HP) data from all three countries to test whether cocoa tree, plantation, or climate factors explain patterns of natural pollination and pod production. Model 2: We combined 100% HP data from all three countries to determine whether cocoa tree, plantation, or climate factors explain pod production when there

Table 1 | Average number of mature pods produced per tree (pod yield) with natural pollination or increasing percentage hand pollination (HP) in the field experiment

Country	Estimated % effective pollination under natural pollination	Average pod yield (pods/tree)					
		(0% HP) natural pollination	20% HP	40% HP	60% HP	80% HP	100% HP
Brazil	12.2%	0.40	2.50	2.40	4.50	3.30	3.50
Ghana	27.1%	1.08	1.69	1.97	2.28	2.71	3.72
Indonesia	11.1%	5.38	6.75	7.50	7.42	8.92	10.00

is full pollination, i.e., no pollination limitation. Model 3: Data from all countries and all HP treatments except the 0% pollination treatment were used to understand the relative impact of cocoa tree, plantation, or climate factors compared to controlled levels of pollination on pod production (Supplementary Table 4).

The results of Models 1, 2 and 3 show the effects on pod yield from: higher pollination percentage (+20%), higher temperatures (higher temperatures in December, during the warm season in Brazil and Indonesia[32] (−22 to −31%), and the presence of shade trees (+3 to 9%)), and access to and availability of soil resources (larger cocoa trees (dbh (+19%), plantation age (+18%)), cocoa tree density (−6 to −14%), and leaf litter (+9%)) (Fig. 2, Tables S4 and S5). These results suggest that cocoa yield would be threatened by decreasing pollination, rising temperatures, and loss of soil resources. We discuss each of these factors below.

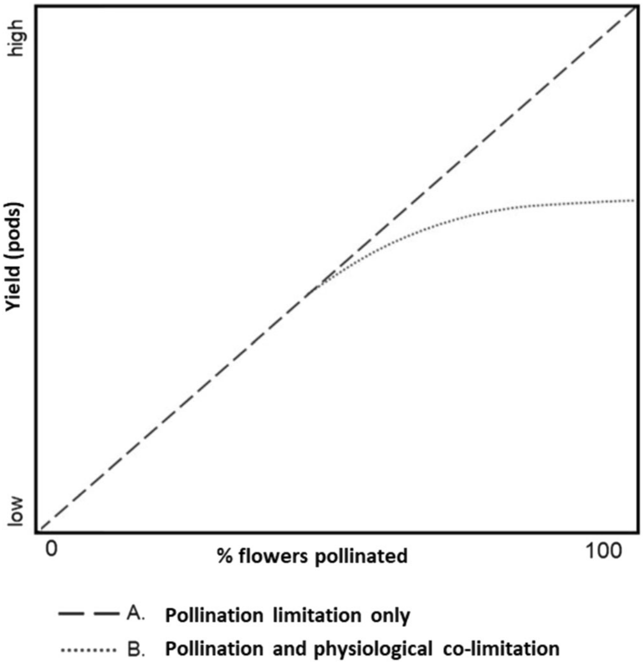


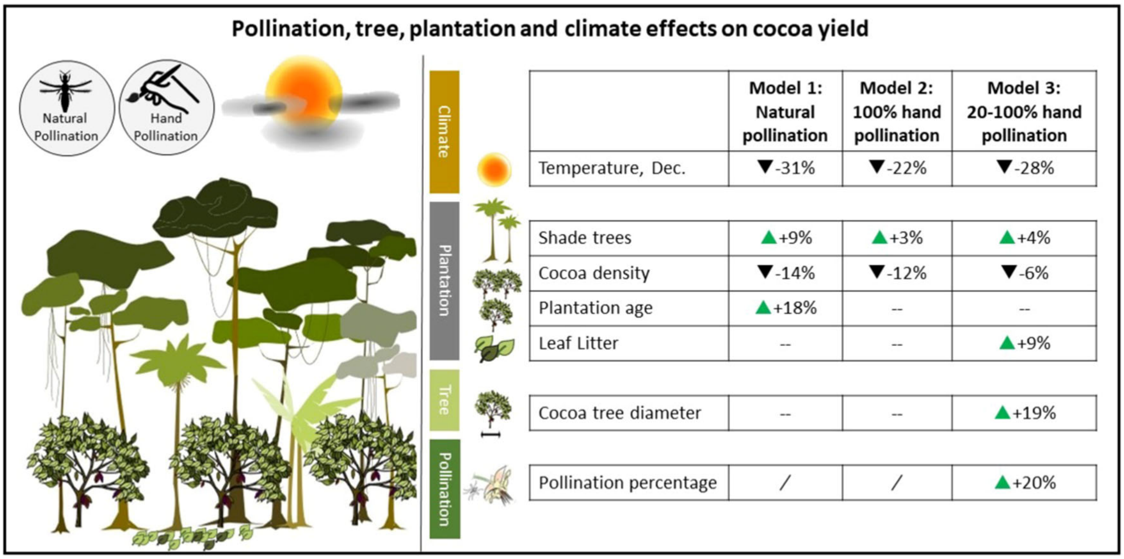
Fig. 1 | Expected relationships between pollination and cocoa yield with pollination limitation only, or pollination and physiological co-limitation (extended from ref. 25). The 'breakpoint' is the point at which the 'co-limitation' line diverges from the 'pollination limitation only' line.

Pollination

HP of cocoa flowers significantly increased yield in our study. Specifically, in Question i, pod yield in the 100% HP treatment was significantly higher than in the natural pollination treatment, where there was 16.7% pollination on average, and in Question iii, Model 3, increasing HP increased yield by up to 20%. HP can be extremely efficient, and is practiced for some crop species, but it is not generally an economically viable option for production at scale[33,34]. In addition, HP is often performed under poor working conditions by low-paid workers and children, and so can only be considered as a management approach in tandem with the implementation of production standards that ensure safe and just labour[27,30,34]. Thus, HP remains an area open for technological and socio-economic innovation.

If HP is not currently a viable strategy to increase cocoa yield, but there is evidence for pollination limitation in the field, and clear potential for increases in yield with even small increases in pollination (Table 1[9,35]), then it is crucial to consider land management interventions that may increase natural pollination. In the literature, the most common management interventions to increase cocoa pollinator abundance, with a view to increasing pollination, are the provision of pollinator habitat within the plantation through increasing leaf litter and soil organic matter[9,36,37], providing moderate shade[5,38,39], and reducing the use of agricultural chemicals[40]. In the wider landscape, management of neighbouring land for high biodiversity could also increase pollinator abundance. Data on agricultural chemicals and management of neighbouring land were not available at a suitable level of detail to allow analysis for our study regions, so here we focus on our data related to pollinator habitat provision, including the management of plantation shade levels.

Ceratopogonidae midges are the most widely recognised and best-studied cocoa pollinators. We note that a variety of arthropod taxa are thought to be cocoa pollinators, and some cocoa studies have found other dipterans and hymenopterans more abundant than, or in place of, the Ceratopogonidae when identifying cocoa flower visitors[5,26,41]. Unfortunately, most of the non-Ceratopogonidae cocoa flower-visiting taxa have not been studied in depth, so there is limited knowledge of their efficacy as pollinators or their ecology and habitat requirements[5,26]. We, therefore,



	Model 1: Natural pollination	Model 2: 100% hand pollination	Model 3: 20-100% hand pollination
Temperature, Dec.	▼-31%	▼-22%	▼-28%
Shade trees	▲+9%	▲+3%	▲+4%
Cocoa density	▼-14%	▼-12%	▼-6%
Plantation age	▲+18%	--	--
Leaf Litter	--	--	▲+9%
Cocoa tree diameter	--	--	▲+19%
Pollination percentage	/	/	▲+20%

Fig. 2 | Pollination, climate, and access to soil resources affect cocoa yield. The table (right side) shows estimates of percent change in cocoa pod production between the highest and the lowest values for each of the significant variables in the AIC selected models for Models 1–3 (Tables S4, S5). '--' indicates the factor was in the full model, but not significant in the AIC selected model. '/' indicates the factor was not included in the full model.

focus here on the Ceratopogonidae. The Ceratopogonidae are associated with average, but not excess, rainfall during the wet season and decomposing plant material on the plantation floor[42–45]. The latter is because many Ceratopogonidae lay eggs on, and their larvae develop on, decomposing organic matter[9,36]. Previous studies have also found that heterogeneous and 'moderate' shade, rather than dense shade, meets the needs of cocoa pollinators without compromising yield[5,35,38,39,46]. In summary, average rainfall, decomposing plant material, and moderate shade provide suitable conditions for Ceratopogonidae midges.

In agreement with the above, in our Model 1, the presence of shade trees positively impacted yield. Shade trees also positively impacted yield in Models 2 and 3, where pod production was the result of HP, suggesting the positive impact of shade trees may be a result of climate moderation as well as pollinator habitat provision. Precipitation was not significant in any of our Models, and leaf litter was only significant in Model 3, where pod production was the result of HP. This suggests that in contrast to previous studies[42–45], in our study, precipitation and decomposing plant material did not affect pollinator activity (Fig. 2, Supplementary Table 5), which may be, for instance, due to differences in pollinator communities in different localities and the sampling times.

Temperature

In Models 1–3, we found a negative relationship between cocoa yield and higher temperatures in December, during the warm season in Brazil and Indonesia[32] (Fig. 2, Supplementary Table 4). The study site with the warmest temperature in December was 7.2°C warmer than the coolest site, and had 22–31% lower yield (Fig. 2, Supplementary Table 5). These findings are in line with previous research which reported negative effects of increasing temperature on cocoa yields[38,47]. Yield in Model 1 is the result of natural pollination, so the effect may be a result of impacts on insect pollinators. As yield in Models 2 and 3 was the result of HP, the impact of temperature is likely to be an impact on tree physiology rather than pollinator abundance or behaviour. Given these results, cocoa growers will need to develop production strategies that moderate the temperature in the plantation to secure their cocoa production and livelihoods.

The use of non-cocoa shade trees is one method of decreasing plantation understory temperature, potentially counter-acting the negative impacts of higher ambient temperatures, and in our study, the presence of shade trees positively impacted yield by 3–9% (Fig. 2, Supplementary Table 4). We note that shade trees may also negatively impact yield by increasing humidity or lowering the temperature below optimal levels within the plantation, potentially promoting disease[14,22], and non-cocoa shade trees may also compete with cocoa trees for water, nutrients or light. However, non-cocoa shade trees can also provide economic diversification through crop diversity in agroforestry and other related systems[38,48], and may increase habitat diversity and biodiversity within the plantation[48,49]. Longer-term studies have also found longer productive lifetimes for cocoa trees under shade, which may compensate for reductions in yield per year[46]. Overall, it appears cocoa growers must make choices about shade tree management to balance potential crop diversity, biodiversity benefits, and temperature moderation[47]. The challenges of managing humidity, light and temperature in cocoa plantations are likely to increase in a changing climate[28,38,48,49].

Soil resources

In Model 3, access to and availability of soil resources was investigated indirectly through cocoa dbh, plantation age, and cocoa tree density, as indirect measures of inter-tree competition for soil resources, and depth of leaf litter as a measure linked to soil organic matter. Dbh and plantation age were positively associated with pod yield, which is likely to be a result of larger trees having greater access to light, water and soil resources, and so avoiding physiological limitations to yield[50]. Similarly, lower cocoa tree density was positively associated with pod yield, suggesting there may be reduced competition for soil resources in lower-density plantation (Fig. 2, Supplementary Table 5). Leaf litter does not appear to be affecting arthropod pollinators in our study, as it was not significant in Model 1, but its positive effect in Model 3 may be related to nutrient- or water-related soil effects. Organic matter, largely leaf litter, affects soil bulk density, water holding capacity, pH, carbon and nutrient concentrations, soil fauna and microbial communities, soil respiration, and soil temperature, all of which can affect plant growth and yield[51]. Conventional wisdom in cocoa management is to increase yield by increasing nutrient availability through fertiliser applications. Our study finds that management that maintains leaf litter, increasing soil organic matter, positively impacts cocoa growth and yield, potentially reducing the need for, and increasing the efficacy of, irrigation and fertiliser inputs. Soil resource availability also increases flower production in cocoa, which is related to fruit set via pollinator attraction[9,25,38,52,53].

Conclusions

In this study, we address a key knowledge gap regarding the relative importance of pollination, cocoa tree, plantation, and climate factors as drivers of global cocoa yield. Our analysis found that enhanced pollination increased yield, as did factors affecting cocoa trees' physiological capacity to produce pods, including cooler temperatures during the warm and wet season, and availability of and access to soil resources, measured as larger and older cocoa trees, lower planting density and thicker leaf litter (Fig. 2, Tables S4, S5). Thus, we find that cocoa tree and plantation management to avoid physiological limitations of pod production must be combined with increasing the percentage of cocoa flowers that are pollinated to effectively maximise cocoa yields.

Our study regions are on three different continents, and across a latitudinal range from −14.7 to +5.6, representing differences in cocoa variety, plantation management, local ecology, and climate (Supplementary Table 2). However, even with these country-level differences underlying the combined data, pollination, cocoa tree, plantation and climate factors all show significant effects on yield across countries. We therefore infer that our results are robust to country-level variation, and are likely to explain patterns of cocoa yield in cocoa-producing regions globally. Based on these findings, we propose three key recommendations for cocoa producers: (i) Increase the percentage of cocoa flowers that are effectively pollinated, either through positive management for pollinating arthropods or HP. Targeted land management for pollinator enhancement is important now and is expected to become even more critical as habitat loss, pollinator-insensitive land management, and climate change drive catastrophic losses of pollinating arthropods globally[28,54]. (ii) Manage cocoa tree density and shade trees to balance the photosynthetic requirements of the cocoa trees with moderation of the temperature in the plantation understory, especially during the warm and wet season. (iii) Manage plantation soils for nutrient and water retention. Maintaining leaf litter, in particular, appears to positively affect cocoa yield. Nutrient and water resources are not only critical for current cocoa production, but they can also help avoid future physiological limitations that might arise in a changing climate, or with management that increases cocoa yield per tree[13,20,21,47,50]. In summary, given the key role cocoa plays in the health, well-being, and economic livelihoods of millions of small-holder farmers, increasing the quantity and stability of cocoa yield through habitat-enhancing, biodiversity-centred, climate-resilient, diversified agriculture is imperative.

Methods

Study sites

The study was conducted at eight study sites near Tarkwa-Breman in the Wassa-Amanfi district in the Western region of Ghana during 2019–2020; ten study sites in Ilhéus, Southern Bahía, Brazil during 2018–2019[30], and eight study sites in the Napu Valley region near Lore Lindu National Park, Central Sulawesi, Indonesia during 2017[27] (Supplementary Table 2). Study plots in Brazil were separated by a minimum of 100 m, Ghana by 70 m, and Indonesia by 200 m. Tree spacing in Brazil and Indonesia was ~3.5 m (average 800 and 763 trees/ha, respectively), and in Ghana was ~6 m (average 280 trees/ha) (Supplementary Table 2). In Ghana each study plot was 40 × 40m, in Brazil each was 20 × 20m, and in Indonesia each was 10 × 10m.

Table 2 | Cocoa yield in Brazil, Ghana and Indonesia during the period 2010–2021

	Max yield 2010–2021 (t/ha)	Min yield 2010–2021 (t/ha)	Average yield 2010–2021 (t/ha)	SD	Study year	Yield study year (t/ha)
Brazil	0.503	0.297	0.397	0.051	2018	0.415
Ghana	0.564	0.395	0.512	0.047	2019	0.545
Indonesia	0.511	0.347	0.430	0.051	2017	0.356

Data from https://data.un.org/Data.aspx?d=FAO&f=itemCode%3A661

Data on the following site characteristics was recorded, as they were hypothesised to affect the abundance and species diversity of cocoa pollinators[26,39,49]: cocoa variety, grafting, and tree age were reported by the site owners (Supplementary Table 2). The average cocoa tree diameter at breast height (dbh) per plot was determined by measuring the dbh of all trees within 2 m left and right of a diagonal transect of the plot; dbh of all trees included in the experiment was also recorded. The density of cocoa trees was determined by counting all trees within the study plot and extrapolating to obtain the trees/ha value. Canopy cover in Ghana was measured using the canopy scope[55], and an average canopy cover score for each study plot was based on the measurements from the middle of the plot and the four corner points. In Brazil and Indonesia, average canopy cover per plot was calculated by taking four photographic images randomly located within each plot using a 13 mm wide-angle lens. The camera was held 4 m above the ground, and photos were taken under sunny conditions. The software *ImageJ* (https://imagej.net/ij/) was used to convert images to grey scale and calculate the canopy cover as the percentage of black pixels[56]. All sites in the three countries were categorised as either 'low' = 0–39% or 'high' = 40–100% canopy cover. The presence or absence of non-cocoa shade trees in the study plot was noted during the quantification of cocoa tree density. The complexity of vegetation surrounding each study plot was classified as: 'homogenous (simple)', when the plot was surrounded by a single species or human-simplified ecosystem (farm, single species plantation, or grass field); or 'heterogenous (complex)', when the vegetation surrounding a plot contained high floral diversity (primary or secondary forest or wetland). Litter depth was determined by averaging the depth of litter (cm) on the soil surface from the plot centre and near the four corners of the plot using a metre ruler.

Cocoa production during the study years was representative of cocoa production 2010–2021

Data was collected in Brazil during 2018–2019, in Ghana during 2019–2020, and in Indonesia during 2017, with pollination occurring during 2018, 2019, and 2017, respectively. Cocoa production can be variable year-to-year, but cocoa production, calculated as tons produced per hectare, was stable between 2010 and 2021 in all three countries, except for a small dip in production in Brazil in 2016. Moreover, cocoa production in each of the countries in the study years was near the 2010–2021 average for the country, within one standard deviation for Brazil and Ghana, and just marginally below one standard deviation for Indonesia (Table 2). We therefore suggest that the data collected for this study is representative of cocoa production in the study countries for the period 2010–2021.

Climate data

Post-processed ERA5-Land climate data for the year during which pollination occurred during the study (Brazil: 2018, Ghana: 2019, Indonesia: 2017) was downloaded from Copernicus (https://cds.climate.copernicus.eu). The pre-calculated monthly mean averages for the 0.1 × 0.1 degree squares of interest were imported to ArcMap (www.esri.com/) and then extracted for the study site point locations. The following data was downloaded: monthly averages for 'ground temperature' (°C at 2 m above ground level), temperature range, precipitation (mm/day), wind-U, wind-V (m/s), and surface pressure (kPa). Wind-U ('U') and wind-V ('V') were converted to wind speed with the standard calculation (wind speed = $\sqrt{(U^2 + V^2)}$). There were large correlation coefficients between the climate variables (Supplementary Fig. 2). Given these patterns of correlation, we selected two climate variables which did not correlate with the rest of the climate variables: temperature at 2 m above ground level in December, and precipitation in September, to include in Models 1–3. Temperature at 2 m above ground level in December correlated strongly with the 'Country' variable, so we excluded the 'Country' variable and included Temperature in December.

Soil data

Soil type is expected to affect cocoa yield, so for each study site soil data was extracted from the Global High-Resolution Soil Profile Database for Crop Modelling Applications[57]. The resolution of the soil data meant that all sites within each country were assigned the same soil classification: Brazil was Ferric Luvisol, Ghana was Xanthic Ferralsol, and Indonesia was Humic Acrisol. As soil type was highly correlated with the 'Country' variable, it was not included as a variable in the models and was not included in any analyses.

Pollination experiment

A standard protocol was used across all three countries to determine how much natural pollination was occurring and test for pollination-limitation[27]. In each study plot, one tree was selected for each of the six treatments: 0% (natural pollination), 20%, 40%, 60%, 80% and 100% HP. In Brazil, there was one tree in each of the six HP treatments and ten study plots, for a total of 10 trees per treatment and 60 trees total. In Ghana, we used six trees in each of the six HP treatments and eight study plots for a total of 36 trees per treatment and 288 trees in total. The Ghana experiment was repeated twice in successive years, using different trees, making a total of 576 trees over the two years. In Indonesia, there were eight trees in the 0% and 20% HP treatments, twelve trees in the 40–100% HP treatments, and eight study plots, for a total of 64 trees in the experiment. Thus, the number of trees used to calculate the average pod yield for each treatment was: Brazil = 10, Ghana = 48, Indonesia = 8 (0–20%) and 12 (40–100%); and a grand total of 700 trees were included in the experiment across all treatments and all three countries.

In the HP experiment, 0% HP (natural pollination) does not refer to pollinator exclusion; rather, natural pollination represents the control where all flowers are left undisturbed, and pollination occurs by arthropod pollinators, as well as any instances of wind or water pollination. For the 20–100% treatments, on each study tree, the total number of flowers present up to 2 m height from the base of the tree (~13% of the flowers on the whole tree[27]) was counted on the day of treatment, and the number to be pollinated calculated. For example, if the tree was in the 20% HP treatment, and 200 flowers were counted up to 2 m height from the base of a tree, 40 flowers would be hand pollinated and 160 would be removed, whereas, if the tree was in the 100% HP treatment, and 200 flowers were counted up to 2 m height from the base of the tree, 200 flowers would be hand pollinated and none would be removed. For the 20–80% HP treatments, all flowers that were not hand pollinated ('unpollinated') were removed from the tree to avoid the unpollinated flowers receiving natural pollination. Across all countries and all treatment, the average number of flowers below 2 m on each tree before treatment was 226 (SD = 117, min = 16, max = 700). Hand-pollinated flowers remaining on the tree were not covered after treatment, so may have received additional natural pollination, but as all flowers remaining on the tree had already been hand-pollinated, and this was not a test of HP technique, additional natural pollination would not have invalidated the results. Cocoa flowers open for 22–24hrs, after which, if unfertilised, they abscise[58]. Thus, each day the tree was visited during the HP experiment, the flower count, HP, and unpollinated flower removal was repeated. Flowers to be hand pollinated were randomly selected among the flowers present on the tree, and the pollen used to hand pollinate flowers came from a minimum of three separate cocoa flowers located in an adjacent area not included in the study[59]. In Brazil, HP was conducted from January to February 2019, and pods were counted from March to April 2019[27]. In Ghana, HP was conducted August to October 2019 and January to April 2020, and pods were counted from May to July and September to December 2020. In Indonesia flowers were hand pollinated from April to May 2017, and pods were counted from October to December 2017.

Statistical analyses

For Question I, the percentage of flowers that received pollen in the 0% HP ('natural pollination') treatment was calculated by creating a standard curve of number of pods harvested against HP percentage for the 20–100% treatments using a log-linked GLM with a Poisson error structure ($R^2 = 0.74$), and controlling for country by including it as a fixed effect. Goodness of fit was graphically checked using a q-q plot and residuals vs. fitted graphs. The statistical model fitted was: Pollination_Percentage ~ Intercept + Country + Number of Pods. The percentage of flowers per tree in the 0% HP treatment receiving effective natural pollination was calculated by locating the observed number of pods from the 0% HP treatment on the fitted line (Supplementary Fig. 1).

For Question ii, to determine whether the yield data exhibited a breakpoint, a SETAR for number of pods compared to pollination percentage was fitted per country (Supplementary Table 3). Whilst normally applied to time-series data, SETAR models are suitable when multiple possible trends are present in the model. A SETAR model is a series of linear models which compare the data before the chosen point to the data after the chosen point. Then the sum of the AIC for each of the pairs of models is determined, and the pair with the lowest total AIC value determines the breakpoint. In situations where there is no breakpoint, the model will return the first or last points of the dataset as the breakpoint.

General linear models

For Question iii, to test the impact of increasing percentage pollination, tree, plantation and climate factors on yield, we ran three GLMs with number of pods as the dependent variable. Each of them sought to answer a different fundamental question about cocoa yield and the role of pollination within it. Model 1: natural pollination (0% HP) data from all countries. This model tests whether tree, plantation, or climate factors explain patterns of natural pollination and pod production. Model 2: 100% HP data from all countries. This model tests whether tree, plantation, or climate factors explain pod production when there is no pollination limitation. Model 3: Data from all countries and all pollination treatments except 0% (natural pollination). This model was used to understand the relative impact of cocoa tree, plantation, or climate factors compared to known levels of pollination on pod production. A Poisson error structure was chosen for the GLMs because the pod count data is a count.

The pollination variable was percent HP (20%, 40%, 60%, 80% and 100%). The cocoa tree factor was diameter at breast height (dbh), a proxy for total tree size. The plantation factors were plantation age, average litter depth on the plantation floor, and two measures of the light environment: canopy cover and tree density. We were interested in both the light on top of the cocoa canopy (overstory), which affects photosynthetic activity, and the light underneath the cocoa canopy (understory), which affects factors such as fungal growth and pollinator habitat. Both the overstory and understory light environments are expected to be affected by cocoa tree density and the presence or absence of non-cocoa shade trees, so we included both factors in the models. Soil type and plantation management would also be considered plantation-level variables. However, soil type was consistent within each country, as discussed above, and there was a single main land owner/manager in Brazil and Ghana, meaning both variables strongly covaried with the 'Country' variable and so were not included in the models (Supplementary Table 2). For the climate factors we used ERA5-Land climate data[60] for ground temperature in December, and precipitation in September (Supplementary Tables 2 and 4).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The full field data have been deposited in the Oxford University Research Archive under the title "Field data—Global chocolate supply is limited by insufficient pollination". The data are under temporary embargo by Oxford University Library due to ongoing work on a PhD project. The dataset is available here: https://osf.io/krwxa (https://doi.org/10.17605/OSF.IO/UTM3E).

Code availability

The R code for the breakpoint analysis and Models 1–3 has been deposited in the Oxford University Research Archive under the title "R code—Global chocolate supply is limited by insufficient pollination". https://doi.org/10.5287/ora-nydjxadxq.

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Competing interests

The authors declare no competing interests.

Additional information

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