

Reporting Summary

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

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|-------------------------------------|-------------------------------------|--|
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | The statistical test(s) used AND whether they are one- or two-sided
<i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i> |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | A description of all covariates tested |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals) |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
<i>Give P values as exact values whenever suitable.</i> |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> | For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> | For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> | Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection	Data was not collected through code.
Data analysis	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". Doi: http://dx.doi.org/10.5287/ora-nydjxadxq .

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

Data Availability

The field data has been deposited in the Oxford University Research Archive under the title "Field data – Global chocolate supply is limited by insufficient pollination". The data is under temporary embargo. However, datasets generated during and/or analysed during the current study are available from the

corresponding author on reasonable request.

Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

Reporting on sex and gender

Population characteristics

Recruitment

Ethics oversight

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description

Cocoa (*Theobroma cacao* L.) provides livelihoods of 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.

Research sample

Study plots in Brazil were separated by a minimum of 100 m, Ghana by 70m, and Indonesia by 200m. 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 40x40m, in Brazil each was 20x20m, and in Indonesia each was 10x10m.

Data on the following site characteristics was recorded, as they were hypothesized 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 2m left and right of a diagonal transect of the plot; dbh of all trees included in the experiment was also recorded. 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 gray-scale and calculate the canopy cover as the percentage of black pixels 56. All sites in the three countries were categorized 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. 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 meter ruler.

Sampling strategy

Statistical analyses

For Question i, the percentage of flowers that received pollen in the 0% hand pollination ('natural pollination') treatment was calculated by creating a standard curve of number of pods harvested against hand pollination (HP) percentage for the 20-100% treatments using a log-linked generalised linear model (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: $\text{Pollination_Percentage} \sim \text{Intercept} + \text{Country} + \text{Number of Pods}$. 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 Figure 1).

For Question ii, to determine whether the yield data exhibited a break point, a self-exciting autoregressive model (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 break point. 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 general linear models (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% hand pollination) data from all countries. This model tests whether tree, plantation, or climate factors explain patterns of natural pollination and pod production. Model 2: 100% hand pollination 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 hand pollination (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 Table 2, Supplementary Table 4).

Data collection

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 in 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 x 0.1 degree-squares of interest was 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 2m 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 ($\text{wind speed} = \sqrt{U^2 + V^2}$). There were large correlation coefficients between the climate variables (Supplementary Figure 2). Given these patterns of correlation, we selected two climate variables which did not correlate with the rest of the climate variables: temperature at 2m above ground level in December, and precipitation in September, to include in Models 1-3. Temperature at 2m 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 soils 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 six treatments: 0% (natural pollination), 20%, 40%, 60%, 80% and 100% hand pollination (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 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 and 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 hand pollination 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 2m 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 2m height from the base of 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 2m height from the base of 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 2m 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 hand pollination technique, additional natural pollination would not have invalidated the results. Cocoa flowers open for 22-24hrs, after which, if unfertilized, they abscise 58. Thus, each day the tree was visited during the hand pollination experiment, the flower count, hand pollination, 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,

hand pollination was conducted from January to February 2019, and pods were counted from March to April 2019 27. In Ghana, hand pollination 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.

Timing and spatial scale	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 Bahia, 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).
Data exclusions	No data were excluded.
Reproducibility	The study design, data collection methods, and analysis procedures are described in detail in the methods section. All statistical analyses, including sample sizes, are clearly reported. We have made every effort to ensure our results can be independently verified and reproduced by other researchers.
Randomization	We randomly selected the flowers used for the hand pollination experiments.
Blinding	NA
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	All details about the sites are provided in Supplementary Table 2: Study sites. Private plantation owners/managers are anonymized as 'A'-'J', with owner 'A' managing multiple sites in Ghana. In Indonesia the farms were each owned by separate small-scale producers, but from one month before data collection started until the end of the experiments, the farmers agreed not to apply agrichemicals to the study sites to improve comparability across sites (see 9). 'Mean dbh' is the average diameter at breast height (dbh) of all trees within 2m either side of a diagonal transect of the study plot. Canopy cover is percent canopy cover measured below the cocoa canopy: L (low = 0-39%) or H (high = 40-100%). 'Shade trees' is a binary indication of the presence or absence of non-cocoa shade trees within the cocoa plantation. 'Veg' is a binary classification of neighbouring land-use: S (simple: farm, single species plantation, or grass field), or C (complex: high floral diversity, primary or secondary forest or wetland). 'Mean pods/tree, open poll' is the average number of pods per tree in the natural pollination treatment. 'Mean pods/tree, all poll' is the average number of pods per tree in all of the pollination treatments combined, including natural pollination.
Location	Lat Long coordinates of each site in Ghana, Brazil and Indonesia are provided in Supplementary Table 2
Access & import/export	Permission to access the sites was given directly by the farmers. We did not import or export any samples.
Disturbance	The pollination techniques used were useful for the farmers. For instance in Indonesia, we trained farmers in the technique and they later even stated in a BBC documentary how useful hand pollination techniques are for their livelihoods.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems		Methods	
n/a	Involved in the study	n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies	<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines	<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology	<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms		
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data		
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern		