Global malnutrition overlaps with pollinator-dependent micronutrient production.

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Title: **Global Malnutrition Overlaps with Pollinator-Dependent Micronutrient Production**

Short title: Malnutrition and Pollination Dependence

Author affiliations: Rebecca Chaplin-Kramer\(^a,1\), Emily Dombeck\(^b\), James Gerber\(^b\), Katherine A. Knuth\(^b\), Nathaniel D. Mueller\(^b\), Megan Mueller\(^c\), Guy Ziv\(^a,d\), Alexandra-Maria Klein\(^e\)

\(^a\)Natural Capital Project, Woods Institute for the Environment, Stanford University, 371 Serra Mall, Stanford, CA 94305. \(^b\)Institute on the Environment, University of Minnesota, 1954 Buford Ave, St. Paul, MN 55108. \(^c\)School on Public Health, University of Minnesota, 420 Delaware St SE Mmc88, Minneapolis, MN 55455. \(^d\)School of Geography, University of Leeds, Leeds, LS2 9JT, United Kingdom. \(^e\)Institute of Earth and Environmental Sciences, University of Freiburg, Tennenbacherstraße 4, 79106 Freiburg, Germany.

\(^1\)To whom correspondence should be addressed. Rebecca Chaplin-Kramer, Natural Capital Project, Woods Institute for the Environment, Stanford University, 371 Serra Mall, Stanford, CA 94305. 831-331-6015. bchaplin@stanford.edu
Summary

Pollinators contribute around 10% of the economic value of crop production globally, but the contribution of these pollinators to human nutrition is potentially much higher. Crops vary in the degree to which they benefit from pollinators, and many of the most pollinator-dependent crops are also among the richest in micronutrients essential to human health. This study examines regional differences in the pollinator-dependence of crop micronutrient content and reveals overlaps between this dependency and the severity of micronutrient deficiency in people around the world. As much as 50% of the production of plant-derived sources of vitamin A requires pollination throughout much of Southeast Asia, while other essential micronutrients such as iron and folate have lower dependencies, scattered throughout Africa, Asia and Central America. Micronutrient deficiencies are three times as likely to occur in areas of highest pollination dependence for vitamin A and iron, suggesting that disruptions in pollination could have serious implications for the accessibility of micronutrients for public health. These regions of high nutritional vulnerability are understudied in the pollination literature, and should be priority areas for research related to ecosystem services and human well-being.

Keywords: ecosystem services, agriculture, pollination, global, spatial, nutrition

Introduction

Reliable and high quality crop yields are critical to food security, and are underpinned by natural processes often not considered in global agricultural forecasts. Pollination is one of these important processes, supporting 75% of the 115 major crop species grown globally, and up to 35% of global annual agricultural production by weight [1]. Pollination also improves the quality of fruit produced, leading to higher-value crops for the same yields [2]. Many ecosystem services operate over broader spatial scales, creating flexibility to reduce greenhouse gases or nitrogen pollution in one location by enhancing carbon sequestration or water purification in other locations. Pollination, in contrast, is a smaller-scale process; while managed pollinators can be transported to crop fields, wild pollinators from natural and semi-natural habitats cannot, and landscape-level habitat factors such as homogeneity and fragmentation impact pollinator nesting and foraging behaviours and can ultimately reduce pollination and fruit set [3,4]. Therefore, it is
important to identify where pollination is most critical to agricultural production, in order to 
prioritize regions for pollinator conservation. Furthermore, the pollinators most important to 
agriculture, mainly the domesticated honey bee, *Apis melifera* L., and a wide array of wild bees, 
are in decline, likely due to land-use intensification (deficiencies of resources and high risk of 
poisoning by pesticides) at field and landscape scales [5-8]. Evidence of this decline and 
susceptibility to further threat has raised concern among both national and international policy-
makers [9-12], with calls to prioritize conservation of pollinators and the services they provide. 
Making actionable policy out of these general concerns requires an understanding of the areas 
most vulnerable to further declines in pollination services, and the possible ramifications to 
human well-being.

The importance of wild pollinators to agriculture has been demonstrated in many local studies 
documenting the contribution of pollination to production of target crops (reviewed by [13,14]) 
as well as several global assessments of the economic value of pollination. Estimates of the 
contribution of animal-mediated pollination to total world agricultural production used for 
human food range from 5-8% [15] to 9.5% [16], depending on the metric considered (total 
production or economic value) and annual variability. Spatial analysis shows that agriculture’s 
dependence on pollinators is not uniform across the globe, with several hotspots of up to 20- 
30% [15]. Furthermore, pollinator-dependent crops have slower-growing and less stable yields 
than pollinator-independent crops [16]. The relatively small contribution of pollinators to total 
agricultural revenues is explained by the fact that the nine highest revenue-generating crops, 
which together account for nearly half of global agricultural production value (Table S1 in the 
Electronic Supplementary Material; [17]), are all either wind-pollinated or predominantly self-
pollinating. However, economic value of crop production is only one facet of its importance to 
human well-being; more holistic assessment should include the value of nutrition to human 
health, and such an assessment will provide a different estimate of relative importance or value 
of pollination services than for economic valuation alone.

Crops that are at least partially dependent on animal-mediated pollination comprise the vast 
majority of crop types grown, and therefore help maintain the diversity of human diets and the
resilience of our food supply. While the cereals that drive the main trends in agricultural revenues can meet the bulk of our caloric needs, overall nutrition relies upon a much broader set of crops. Significant portions of global micronutrient supplies come from pollinator-dependent crops [20,21]. As is the case for economic value, pollinator contributions to micronutrient supply are not expected to be uniform across the globe, and such spatial heterogeneity may have important implications for regional nutrition patterns that are constrained by purchasing power and food access. Here, we map the micronutrients supplied by pollinator-dependent crops globally, and examine overlap between pollinator-dependence and malnutrition. The results highlight priority locations for future research on pollination services by identifying agricultural regions where pollination is most critical to micronutrient production.

Methods

Spatial datasets for crop yields and harvested area at 5 min resolution [22] were used to calculate production of 115 food crops. Proportional areas of harvested acreage for each crop in each 5 min grid cell were first multiplied by the area of that grid cell to calculate total ha of each crop harvested, and then multiplied by the yield (tons/ha) in each grid cell to calculate production (tons) for each crop. These production values were reduced to reflect only the amount used as human food based on national-level data compiled by the Food and Agriculture Organization [23]. This food-only production was then multiplied by the proportion of each crop that is edible (leaving aside refuse such as peels, pits, shells, ends, and stems) derived from a database cataloguing the composition of food created by the U.S. Department of Agriculture [24]. All production in this analysis therefore comprises only that contributing to human nutrition.

Production values were reduced by the fraction of their pollination dependence, according to Klein et al.’s [1] classification of 124 crops, which designated animal-mediated pollination as “essential,” for instance, if its absence decreases yields by 90% or more. The averages for the ranges of pollination dependence (0.95 for “essential”, 0.65 for “great”, 0.25 for “modest,” 0.05 for “little”) were used to multiply by the corresponding crop’s production to calculate pollinator-dependent production in each pixel for the crops analysed here that are dependent to some
degree on animal-mediated pollination. Some mismatches occurred between the Klein et al. [1] and Monfreda et al. [22] datasets; 22 of the crops reported by Klein et al. [1] were grouped into broader categories (e.g., different types of pulses, tropical fruits, and other uncommon crops). In this case an average of the pollinator-dependence and nutrient value of the component crops was used. Pollinator-dependence for 13 crops reported by Monfreda et al. [22] but not by Klein et al. [1] was estimated from additional literature review [25-28].

Following the approach set out by Eilers et al. [20], nutritional content was collected for each crop from the USDA database referenced above [24]. Micronutrients examined include minerals (calcium, iron, magnesium, phosphorus, potassium, sodium, zinc, copper, manganese, selenium, and fluoride), water-soluble vitamins (vitamin C, thiamine, riboflavin, niacin, vitamin B5, vitamin B6, folic acid), and fat-soluble vitamins (E, including tocopherol precursors, K, A, and related carotenoids: carotenes, cryptoxanthins, lycopene, lutein, and zeaxanthin). The database includes nutritional information for nearly 8,000 food items, both processed and whole, prepared in a variety of manners; all nutrients considered for this analysis were taken from the values listed for the raw, fresh food crop. Micronutrient content was converted to g per ton values and multiplied by total crop production and pollinator-dependent crop production for each crop. Micronutrient production was summed across all crops per pixel for each micronutrient. We limit our examination of results here to three plant-derived micronutrients particularly important to nutritional health: vitamin A, iron, and folate. The remaining micronutrients can be seen in the Electronic Supplementary Material (Figure S1). Iron and vitamin A are two of the three micronutrient deficiencies of greatest public health significance in the developing world [29-30]; plant content of iodine, the third of these, is highly dependent on the abiotic environment and thus not as easily mapped. Folate is essential for the prevention of birth defects, and is thus increasingly considered a public health concern [30].

Pollinator-dependence was derived for each of the tracked nutrients by dividing pollinator-dependent nutrient production by total nutrient production in each pixel. This ratio varies according to the mix of crops grown in that pixel, the amount of nutrients in those crops, and the dependence of those crops on pollination. As this measure of pollinator-dependence approaches
1, the nutrient produced in a pixel comes from crops increasingly dependent on pollination. Each nation was ranked by the maximum value for pollinator-dependence occurring in that nation to formalize identification of "hotspots" of pollinator-dependence. We excluded from this designation of "hotspot" nations whose mean pollinator-dependence values were < 2 %, as this indicated the maximum values were outliers and not representing a large area of pollinator-dependence.

In order to understand the nutritional context for these hotspots of pollinator-dependent micronutrient production, we examined the overlap between pollinator-dependence and nutritional deficiency. The observed values of the distributions of different levels of prevalence for these micronutrient deficiencies between nations designated hotspots and the remaining nations were compared using a chi-squared test for independence. The expected values were taken from the total distribution of nations into categories of "severe," "moderate," "mild" deficiency and "no known deficiency" categories established by World Health Organization (WHO) [31] for Vitamin A, and the categories of >50%, 25-50%, <25% and 0 incidence of iron-deficiency anaemia among pregnant females [32], then scaled in the same proportions to the total number of nations in hotspots and non-hotspots. No deficiency incidence data were available at the global level for folate, so overlaps with pollination dependency are considered more qualitatively for this micronutrient.

A third of the total number of nations were selected as pollinator-dependent hotspots, so as to obtain an adequate sample size for statistical comparison within different categories of nutrient deficiency, as described above. For vitamin A, this designation of hotspots corresponded to >38% maximum pollinator-dependence within a nation, which defined 52 hotspots of a total of 157 nations ranked by the WHO for severity of vitamin A deficiency [31] and for which we were able to obtain crop production data to derive pollinator-dependence. For iron, the hotspots corresponded to >15% maximum value for pollinator-dependence within a nation, designating 51 hotspots out of 152 nations with data on the prevalence of iron-deficiency anaemia [32].

To aid in the interpretation of our results concerning pollination dependency of micronutrient production, micronutrient demand was also calculated for each country. Male and female age-
structure population data were gathered from the UN Population Division [33]. Micronutrient recommended daily allowances (RDAs) and adequate intake data specific to each sex and age class were gathered from the Institute of Medicine (IOM) Dietary Reference Intake Report [34]. The age-structure breakdown of the IOM RDAs was modified to be consistent with UN age classes where necessary. The population within each sex and age class was multiplied by the appropriate RDA and 365 days to determine annual demand within each class. Summing across all sex and age classes determined the annual total micronutrient demand for each country.

**Results and Discussion**

**Patterns of pollination dependence**

Areas of highest dependence on pollination services are different for different nutrients. Production of vitamin A, the most pollinator-dependent nutrient of the those examined here, approaches 50% dependence on pollination in Thailand, north central and south-eastern India, western Iran, Romania, eastern and south-western Australia, and scattered throughout Mexico, parts of the US and Argentina (Fig. 1a). Iron and folate have lower pollinator-dependence, reaching 12-15% in western China, Central African Republic, north-eastern South Africa, northern Mexico and the Yucatan, and scattered throughout Brazil for iron (Fig. 1b), and throughout South East Asia for folate (Fig. 1c). These relative hotspots of pollination dependence show where local micronutrient production is most vulnerable to pollinator declines, but does not capture the overall contribution of pollination to global micronutrient production. For example, while iron production is highly dependent on pollination across Africa (in Fig. 1), the lower productivity overall in that region means the pollination dependence ranks fairly low on a global scale (Fig. 2).

The crops responsible for the bulk of production of each nutrient also vary by region and by nutrient (Table S2 in the ESM). Pumpkin, melon, and mango are among the top crops for production of Vitamin A in many of the pollination dependence hotspots, but other crops are equally or more important in different regions. Okra in India, tropical fruits (e.g., cherimoya, guava, jackfruit, passion fruit, etc.) in India and Thailand, apricot and sour cherry in Iran, apricot and plum in Romania, and peach in Mexico are important sources of vitamin A highly dependent
on pollinators. Carrot and sweet potato are two common pollinator-independent crops contributing highly to vitamin A production in all regions. In China, in particular, where there is high vitamin A production but low pollination dependence (bright green area in Fig. 2a), the top crops contributing to vitamin A production are sweet potato, carrot, lettuce, and spinach, all pollinator-independent (although all require pollination for seed production, which suggests declines in pollination could still damage propagation of these crops, a consideration not included in this analysis). Most of the pollinator-dependent production of iron is attributed to pumpkin, sesame, and avocado, along with anise in Brazil and China, buckwheat and watermelon in China, melon seed in Central African Republic, and lupin in South Africa. Wheat, groundnut (peanuts), rice, and maize produce the bulk of plant-derived iron in these regions, without requiring pollination. For folate, coconut is the only top crop shared among all regions, with nutmeg providing the highest production of this micronutrient in Malaysia and Indonesia, and other important contributors including pumpkin in Malaysia, avocado and soybean in Indonesia, and tropical fruits in Papua New Guinea. Important crops that contain folate and do not require pollination include groundnut and banana.

Hotspots for micronutrient dependence on pollination and malnutrition

Interestingly, the areas of highest micronutrient dependence on pollination do not match up with the areas of greatest economic value for pollination. This study identified India, Southeast Asia, and central and southern Africa as recurring hotspots for pollinator-dependence of micronutrient production, rather than the US, Europe, China, and Japan that Lautenbach and colleagues [18] demonstrated to be of greatest importance to overall agricultural and economic value. This disparity in micronutrient and economic importance means that different places would experience the impact of pollinator losses to different degrees and in very different ways. Micronutrient dependence on pollination coincides more with areas of poverty, which suggests that they will be less resilient to shocks to crop production due to possible decline or fluctuations in pollination services [29,35].

In fact, hotspots for micronutrient dependence on pollination correspond with areas of high deficiency for some nutrients. Vitamin A deficiency is nearly three times as likely to occur in
regions of high (>30%) pollination dependence of this micronutrient, compared to more pollinator-independent regions (Table 1). Vitamin A deficiency can cause severe visual impairment and blindness, especially in children, significantly increases the risk of fatality from common childhood infections, and may increase the risk of maternal mortality [36]. Occurrence of iron-deficiency anaemia in pregnant women is over three times higher in regions of at least 15% pollination dependence for plant-derived iron (Table 1). Iron-deficiency anaemia has been linked to complications in pregnancy (contributing to 20% of maternal deaths), impaired physical and cognitive development, increased risk of morbidity in children and reduced work productivity in adults [37]. Global folate deficiencies have not been mapped, but folate requirements increase significantly during pregnancy and deficiencies are one of the leading causes of neural tube defects (NTD) such as spina bifida and anencephaly [30,38]. Vulnerability of folate production may be of particular concern in nations with high rates of NTDs and limited resources for fortification and supplementation programs. The World Health Organization recommends intervening in nations where NTD rates exceed 0.6/1,000 live births [39]. Many of the regions with high pollinator-dependent folate production also have high rates of NTDs, including Guatemala (where NTD rates reached 2.8/1,000 live births in 2001; [40]) and in the Sarawak region of Malaysia (1.09/1,000 live births; [41]). One caveat to identifying such overlaps is that regions that are too deficient in certain micronutrients will likely not be impacted by a disruption in pollination, if the health problem is already so extreme that additional micronutrient shortage cannot cause any additional deterioration in conditions.

Regions with high micronutrient dependence on pollination and high nutrient deficiencies may be even more vulnerable to pollinator losses if pollinator-dependent production constitutes a major part of regional demand. While plant-derived micronutrients are only one source of nutrition, comparing the amount of pollinator-dependent micronutrient production relative to the amount demanded based on population and demographics can provide a sense of how the importance of this source of nutrition may vary regionally. For folate (Fig. 2c), the pollinator-dependent production alone exceeds global demand by 13 times, suggesting that access to rather than availability of these micronutrients would be a cause of deficiencies. In contrast, pollinator-dependent iron production (Fig. 2b) meets only 31% of global demand, but in central
Africa around one major pollinator-dependent hotspot, production and demand align more closely. Pollinator-dependent production is $7 \times 10^{10} \text{ mg}$, or 93% of regional demand for Central African Republic, Sudan, and Cameroon. Regional patterns for vitamin A production (Fig. 2a) also buck global trends; whereas total global pollinator-dependent production is five times global demand, locally vitamin A production can be much more limiting. In Southeast Asia (India, Bangladesh, Myanmar, Cambodia, Laos, Vietnam, Thailand, and Malaysia), pollinator dependent production of vitamin A is $1.5 \times 10^{14} \mu g \text{ RAE}$, which is 48% of demand for that region. While global trade obviously plays a large role in determining how local demand for nutrition is met, this mismatch is in stark contrast to another area of high pollination dependence, Central America, where pollinator-dependent production of vitamin A is nine times the demand for that region. This is not meant to suggest that local production of nutrition is necessary or even possible in these regions, but only to highlight differences across regions and across scales. For example, while both Mexico and India present public health concerns for vitamin A deficiencies, Mexico is in a region that follows the broader global pattern of higher production of vitamin A than is needed to meet dietary guidelines. This overproduction at the global and regional level may buffer the nutritional impacts of possible declines in pollination. India, on the other hand, being part of the region where pollinator-dependent production of vitamin A meets only half of demand, may be much more vulnerable to pollinator declines.

Adaptations to reduce nutritional dependence on pollination

There are many aspects of nutrition that this global analysis was unable to capture, and which deserve further scrutiny at finer scales, especially for regions that are highly dependent on pollination and known to have high nutrient deficiencies. The value of pollination services, whether economic or nutritional, is generally considered to be the replacement value or the difference between the current situation and a possible future without any pollination services [42]. It is therefore important to note that regions that are vulnerable to changes in micronutrient production due to pollinator declines could adapt by reducing their overall dependency on pollination services. Such adaptations may involve utilising other forms of pollination than wild pollinators and finding novel ways of meeting nutritional needs if pollinator-
dependent crops were not available, including crop switching, nutrient supplementation and other (non-crop) sources of nutrition, and access to global markets for nutrition via trade.

Wild pollinators are obviously not the only form of pollination available to crop growers. Managed pollinators like the honeybee currently meet most of our pollination needs, and while they may benefit from the same landscape resources that support wild pollinators, they are also able to be transported when and where they are needed [43]. However, as previously noted, the massive die-offs of honeybee colonies in recent years have underscored the precariousness of relying on one managed species, and there may be increasing occurrences of honeybee scarcity in the future that result in price spikes for honeybee rentals, as was seen in the case of almonds in California in the late 2000s [44]. Additionally, wild pollinators have been shown to increase the effectiveness of pollination in honeybees, and we do not know the extent to which this phenomenon operates in many systems [45]. Hand pollination can provide an effective substitute for insect pollinators, as has been shown in apple in China, but this certainly comes at higher cost [46]. For malnourished regions that are typically also impoverished, the cost of such additional inputs as managed pollinators or additional labour for hand pollination may simply not be bearable.

Shifting local production from pollinator-dependent to pollinator-independent crops could reduce the reliance on pollination to some degree. However, pollinator-dependent crops are the primary sources of certain micronutrients in several regions (Table S2), suggesting that fully transitioning this micronutrient production to new pollinator-independent crops would require significant changes to growing and eating habits. Some such transitions, such as from pumpkin to sweet potato as a source of Vitamin A in India or Thailand, may be culturally feasible if the crops occupy similar flavour and texture profiles. Diet preferences are often deeply ingrained in different cultures and acceptable substitutes may not always be easily identified [47]. Furthermore, even crops that are not reliant on pollination to produce the part of the plant that is consumed (like tubers and leafy greens) may still require pollination for seed production [1]. Finally, certain pollinator-dependent crops provide high sources of several nutrients in a single serving. For example, pumpkins, tropical fruits, and melons appear as top crops for two or all
three of the nutrients examined here; this is not the case for any of the pollinator-independent crops.

Other sources of nutrients, especially animal products and fortified food or supplements, can and do contribute to meeting nutritional requirements, and including these sources of nutrients would provide a more complete picture of the total nutritional profile produced from region to region. Pairing this nutrient production data with information on actual nutrition deficiency would require dietary assessments such as 24-hour dietary recalls or food frequency questionnaires, which are not available on a global scale. This is an important next step when focusing on areas that are particularly pollinator-dependent, in order to better understand the vulnerability of the local population to declines in particular sources of micronutrients.

A true vulnerability assessment would require a much more in-depth analysis of trade patterns and consumer purchasing power, to track how much of nutrient production is locally consumed and what flexibility there may be in transitioning to global markets if local nutrient supply declines. However, the pollinator-dependent regions that overlap with malnutrition in places like Iran, the Democratic Republic of Korea, and throughout much of Africa are further challenged by high (>30%) incidence of undernourishment and/or high food price index (>2, meaning it costs twice as much to buy food as in the United States, relative to other goods), which suggests little flexibility to adapt in these pollinator-dependent, malnourished areas [48]. Despite the simplicity of this approach to valuing the contribution of pollination to human nutrition, it is still able to reveal the implications for pollinator-dependence in regions of high micronutrient deficiency and low purchasing power, where any further reduction in availability of already scarce sources of certain nutrients could directly impact human well-being.

**Nutrient dependence can focus pollination research where it matters for human health**

This analysis was a preliminary step in understanding the relative importance of pollination to micronutrient production in different regions of the world, and as such, it provides a global screen for prioritizing where to devote resources to more intensive local study. The identification of high pollination dependence does not indicate the degree to which crop pollination needs are met, by either wild or managed pollinators. Much finer scale analysis is needed to locate specific
crop fields requiring pollination and natural and other elements in the landscape influencing pollinator behaviour. In regions that are both highly pollinator-dependent and nutritionally vulnerable, local ecological studies should be undertaken to quantify the ecosystem service provided by wild and managed pollinators and to estimate the value of natural or semi-natural habitat to maintaining that service. Research in the field of pollination services is moving toward mapping supply and demand of pollination at very small scales [49], but such research is not being undertaken in the places it is most needed to inform pollinator conservation decisions for enhanced nutritional security. The best-studied areas for understanding the magnitude of pollination services provided by nature and the consequences of their disruption to human well-being include Costa Rica, California, New Jersey, and Europe, none of which appear in the list of regions most dependent on pollination for micronutrient production. The regions where crop micronutrient production is most reliant on pollination and where malnourishment is already a problem, such as India, Africa, and parts of Southeast Asia, are also typically underserved by academic research and may lack the resources to assess the potential for wild pollinators to meet crop pollination demands. Aside from very preliminary evidence that India may already be pollinator-limited [50] and that natural and semi-natural habitats do play a role in maintaining bee diversity in Mexico, and Romania [51-52], much further study is needed in areas of high importance to nutrition.

Joining this global micronutrient pollinator-dependence screening approach with the smaller scale empirical studies on pollination services actually delivered is important for conservation planning when improving human well-being is a goal. It is a question for policy as to whether the quantity of crop production, the quality (i.e., diversity of nutrients or amount of specific nutrients) of crop production, or the monetary value of crop production derived from pollinators is most important to consider when identifying the regions of greatest concern for pollination services declines. It is clear that these different metrics lead to different conclusions about focal regions for further study, and until now human health considerations have not been driving the choice of study location. The patterns in the importance of pollination to human health should set a new research agenda, prioritizing these regions of high micronutrient dependence on
pollination for future field study to gain an understanding of the function and integrity of
pollination services where it is most critical to human health.

Conservation projects often must strike a balance between preserving biodiversity and
maintaining flows of multiple ecosystem services. Deciding which ecosystem services should be
included when weighing such trade-offs depends upon understanding the relative importance of
any particular service to human health and prosperity. While carbon sequestration and water-
related services often receive a great deal of attention in global ecosystem service assessments,
more localized services like pollination deserve special consideration in areas where nutritional
health is particularly vulnerable and micronutrient production is especially dependent upon
pollination. Highlighting such areas, as done in this study, is a first step toward better
understanding the reliance of such systems upon pollination. Future research providing a finer
scale analysis of the pollination services actually provided in such areas, especially by wild
pollinators, will inform local conservation decisions about when and where to prioritize
pollination services for improved nutrition and human health.

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References


**Figure Legends**

Figure 1. Fractional dependency of micronutrient production on pollination. This represents the proportion of production that is dependent on pollination for a) Vitamin A (in IU, RAE), b) Iron,
and c) Folate. This was calculated as the fractional pollinator dependence of each crop grown in a pixel, multiplied by the total production of that crop and the nutrient content of that crop, summed across all crops in each pixel. To aid in visibility, the upper limit of the colour bar is set to the 95th percentile value for each figure.

Figure 2. Micronutrient production, across a spectrum of pollinator-dependence, for a) Vitamin A (in IU, RAE), b) Iron, and c) Folate. Here, regions that are highly dependent on pollination, identified in Fig. 1, are further differentiated by the magnitude of their micronutrient production. Total micronutrient production, calculated as the total production of each crop (by weight) multiplied by the nutrient content of that crop, summed across all crops, is denoted by colour intensity, with brighter colours corresponding to more production. This total micronutrient production is plotted against the fractional dependency of micronutrient production on pollination (from Fig. 1), represented by the colour bar from green to red, with green representing little dependency and red representing maximal dependency. Colours are plotted such that the upper limit of the brightness scale, corresponding to 90th percentile nutrient production to aid visibility.