Ecología Austral 32:xxx-xxx Aniversario 2022
Asociación Argentina de Ecología

Myth and reality of a global crisis for agricultural pollination

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Abstract. Mounting evidence shows that pollinators are declining as a result of widespread environmental degradation. This loss raises concerns that a global pollination crisis could threaten the human food supply by decreasing crop yield and even promote famine under a hypothetical scenario of total pollinator extinction. This catastrophic possibility has prompted intense interest from scientists, politicians and the general public. However, three lines of evidence do not support such an apocalyptic scenario. First, even though the abundance and diversity of wild pollinators are declining worldwide, the global population of managed honey-bee hives has increased by ~80% since the early 1960s. Second, agricultural production would decrease by <10% in the total absence of bees because relatively few crops are completely pollinator dependent. Lastly, despite widespread pollination deficits, current evidence is inconsistent with deceleration in yield growth with increasing pollinator dependence at a global scale, probably due to improvements in crop breeding and external agricultural subsidies. Overall, this evidence refutes simplistic claims of human starvation caused by a hypothetical total pollinator extinction. Nevertheless, pollination problems may loom. Although pollinators are responsible for a minor fraction of global agriculture production, this fraction has increased ~600% since 1961, greatly outpacing human population growth and the growth of the global population of managed honey bees. This large production increase is explained to a considerable extent by the rapid expansion of pollinator-dependent monocultures at the expense of natural and diverse agricultural habitats. By driving pollinator decline, this land-use transformation could worsen pollination deficits and promote further crop expansion given sustained market demands. Therefore, although the human food supply is not currently subject to a global pollination crisis, a spiralling positive-feedback between the impacts of agriculture expansion and pollinator decline on crop yield could accelerate precipitous biodiversity loss by promoting further habitat destruction and homogenization.

[Keywords: agriculture, cereal crops, fruit crops, honey bees, oil crops, pollination crisis, pollinator decline, pollinator dependence, root and tuber crops]

Resumen. **Mito y realidad de una crisis global de la polinización en la agricultura**. Los polinizadores están disminuyendo como consecuencia de la degradación generalizada del medio ambiente. Esta pérdida ha suscitado la preocupación de que una crisis global de polinización pueda estar amenazando nuestro suministro de alimentos vía una reducción en el rendimiento agrícola. Sin embargo, tres líneas de evidencia no apoyan tal expectativa. Primero, aunque la abundancia y la diversidad de los polinizadores silvestres están disminuyendo en todo el mundo, la población mundial de colmenas de abejas melíferas manejadas ha aumentado en un ~80% desde principios de la década de 1960. Segundo, la producción agrícola disminuiría sólo <10% en ausencia total de abejas ya que relativamente pocos cultivos dependen completamente de los polinizadores. Por último, a nivel global no parece existir una desaceleración del crecimiento en el rendimiento con el incremento en la dependencia de los polinizadores. Sin embargo, la expansión de cultivos dependientes de polinizadores puede tener un alto costo ambiental. Aunque los polinizadores son responsables de una fracción menor de la producción agrícola mundial, esta fracción ha aumentado en un ~600% desde 1961, superando el crecimiento de la población mundial de abejas melíferas manejadas. El incremento de esta fracción de la agricultura se explica en gran medida por la rápida expansión de monocultivos dependientes de polinizadores. A través de incrementar la pérdida de polinizadores silvestres, esta transformación en el uso de la tierra puede causar un incremento en los déficits de polinización y promover la expansión de cultivos dependientes de polinizadores en respuesta a demandas sostenidas del mercado. Por lo tanto, una espiral de retroalimentación positiva entre la expansión de la agricultura y un declive de los polinizadores que afecte al rendimiento de los cultivos podría acelerar la enorme pérdida de biodiversidad en curso al promover la destrucción de los hábitats naturales remanentes y la homogeneización de los paisajes agrícolas.

[Palabras clave: agricultura, cereales, frutales, abejas melíferas, oleaginosas, crisis de polinización, declive de los polinizadores, dependencia de los polinizadores, raíces y tubérculos]

Editor asociado: Pedro Blendinger
Editor junior: Facundo Palacio

Recibido: 2 de Octubre de 2021
Aceptado: 4 de Marzo de 2022

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Introduction

Human impact on Earth's natural heritage has accelerated during the last century, largely as a consequence of sustained growth of the human population and rapidly increasing per-capita consumption (Dauvergne 2008; Lenzen et al. 2012; Chaudhary and Brooks 2019). In particular, widespread habitat destruction, accelerated agricultural and urban expansion, and major species invasions are causing alarming biodiversity loss and increased biotic homogenization (IPBES 2019). This biodiversity transformation can progressively erode the nutritional, social, cultural and economic benefits that many human societies derive from natural and man-made ecosystems, named 'ecosystem services' (Díaz et al. 2006; Cardinale et al. 2012).

The ecosystem service provided by a myriad of pollinator species, mostly insects, that inhabit terrestrial ecosystems (Kremen et al. 2007; IPBES 2016; Potts et al. 2016; Rader et al. 2016) has received much recent attention due to its potential relevance for human food production and influences on other ecosystem services, such as carbon sequestration and climate regulation, via pollinators' key role in plant reproduction (IPBES 2016). Dependence on animal pollination is estimated to affect the production of about 75% of the most widely cultivated crop species, primarily those harvested for seeds and fruits that humans consume (Klein et al. 2007). However, the capacity of ecosystems to provide crop pollination is increasingly compromised by declines in abundance and diversity of many pollinating species caused by synergistic impacts of human activity, including climate change (Kerr et al. 2015; Soroye et al. 2020; Raven and Wagner 2021), habitat destruction and fragmentation (Winfree et al. 2009), agricultural expansion and industrial intensification (Aizen et al. 2019a; Raven and Wagner 2021), use of broad-spectrum pesticides (Desneux et al. 2007; Blacquière et al. 2012; Devillers and Devillers 2020) and introduction of managed pollinators that act as competitors and disease vectors for native pollinators (Stout and Morales 2009; Russo 2016; Mallinger et al. 2017; Vanbergen et al. 2018). For instance, an analysis of 54 major crops in France found that, unlike crops with limited pollinator-dependence, greater agricultural intensification failed to increase yield of highly dependent crops (Deguines et al. 2014). Consequently, increasing pollination deficits caused by declines in pollinator abundance and diversity could be threatening the yield of many fruit and seed crops (Potts et al. 2010). Extrapolation of this risk has evoked predictions of an impending pollination crisis that will compromise agricultural production and, hence, human wellbeing (Buchmann and Nabhan 1996; Allen-Wardell et al. 1998; IPBES 2016; Potts et al. 2016), and even doomsday claims in the popular media of human starvation should bees and other pollinators cease to exist (e.g., bbc.co.uk/teach/would-we-starve-without-bees/zkf292p).

Such predictions of threats to human food production by a global pollination crisis sparked opposing views based primarily on three arguments (Ghazoul 2005). First, production of the main staple food crops (e.g., wheat, corn, rice, potato, etc.) does not require pollinators, as they are self-pollinating, pollinated by wind or cultivated for vegetative organs rather than for fruits or seeds. Consequently, the core of the human diet should not be strongly affected by pollinator decline. Second, declines of wild pollinators have generally been spatially heterogeneous and so may have limited effect on global production of fruit and seed crops. Third, reduced pollination service for crops provided by wild pollinators might be replaced by pollination by managed pollinators, such as *Apis mellifera*, *Bombus terrestris*, *Megachile rotundata* and *Osmia lignaria*. As a consequence of these three features, pollinator declines may have limited impact on human food supply (Ghazoul 2005).

The original conception of the global-pollination-crisis (GPC) hypothesis (Buchmann and Nabhan 1996; Allen-Wardell et al. 1998) and contrary arguments (Ghazoul 2005) motivated a surge in related applied research during the last two decades (e.g., Biesmeijer et al. 2006; Klein et al. 2007; Aizen and Harder 2009a; Potts et al. 2010; Garibaldi et al. 2011a, 2013; Aizen et al. 2019a; Zattara and Aizen 2021). This research has addressed three main premises of the hypothesis, namely that 1) the abundance and diversity of wild and domesticated pollinators are declining globally, 2) pollinators significantly affect the yield of many crops and are therefore responsible for a large fraction of total agricultural production, and 3) declining pollinator populations are reducing the yield growth of pollinator-dependent plant species because insufficient pollination increasingly limits seed production. According to this hypothesis, evidence supporting all three premises would signal that pollinator decline will increasingly constrain agricultural production.

In a series of articles published during the last 15 years, we have addressed the three premises of the original GPC hypothesis and elaborated an expanded view that incorporates the environmental dimension of the increasing pollinator dependence of agriculture (Aizen et al. 2008, 2009; Aizen and Harder 2009a,b; Garibaldi et al. 2009, 2011a). This analysis primarily exploited the crop data submitted to the Food and Agriculture Organization of the United Nations (FAO) by member countries since 1961 (FAOSTAT 2021; hereafter, FAO dataset). Here, we present an integrated compendium of this research, updated to include current FAO data and complement it with findings of other researchers to provide a contemporary assessment of the GPC hypothesis. First, we evaluate evidence for the three premises of the GPC hypothesis (i.e., pollinator decline, agriculture dependence on pollinators and decreasing yield triggered by pollinator decline). Second, we introduce and discuss overlooked influences on a possible pollination crisis, including discrepancies between pollinator supply and demand fuelled by accelerating cultivation of pollinator-dependent crops. Finally, we present an expanded view of the GPC hypothesis that considers the positive feedback between environmental degradation, pollinator decline and agriculture expansion. The evidence we present argues that differential global expansion in pollinator-dependent agriculture could propel declines in wild pollinators.

Evidence for the premises of the pollination-crisis hypothesis

Pollinator decline

Growing evidence, mostly from western Europe and North America, shows widespread but heterogeneous declines in the abundance and diversity of many wild pollinators (Potts et al. 2010; Ollerton et al. 2011; Colla et al. 2012; Zattara and Aizen 2021). Abundance changes (declines and increases) can vary geographically within species (Aizen and Harder 2009b; Thomson 2016) and among congeneric species and taxonomic families (Biesmeijer et al. 2006; Cameron et al. 2011; Richardson et al. 2019; Zattara and Aizen 2021). Documented declines of individual pollinator species range from continued persistence at reduced abundance through local extirpation to apparent species extinction (IPBES 2016). This interspecific variability in abundance correspondingly alters regional and global pollinator diversity. For example, Zattara and Aizen (2021) considered ~2.400.000 publicly available specimen records, which were collected primarily from North America (53.8%) and Europe (21.7%), but also records from other regions (24.5%). This evidence shows that the number of bee species reported yearly worldwide has declined an average of 25% since the 1990s. However, such effects differ among pollinator groups, as illustrated by declines of bee diversity in the UK and the Netherlands during the last four decades, but not of hover-fly diversity (Biesmeijer et al. 2006). Heterogeneous abundance changes among species also tend to increase relative dominance by the few species that are thriving (Zattara and Aizen 2021). Therefore, a decline in pollinator diversity does not necessarily mean a decline in overall pollinator abundance, particularly when invasive social bees are involved (Aizen et al. 2020). Nevertheless, extant evidence supports decline and even loss of many pollinator species as part of the more general current mass decline of global biodiversity (IPBES 2019).

Environmental effects of human activity on pollinator populations (Aizen and Feinsinger 2003; Murray et al. 2009), especially those arising from crop cultivation (Ollerton et al. 2014), seem largely responsible for the observed pollinator declines. Currently, crop cultivation involves ~12% of the global land area (FAOSTAT 2021), indicating the direct extent of habitat disruption. Considerable evidence shows negative effects of habitat loss on bee diversity and abundance, even though relatively high bee diversity persists in human-modified, heterogeneous landscapes (reviewed by Winfree et al. 2009), including urban environments (e.g., Normandin et al. 2017; Buchholz et al. 2020). Furthermore, within crop fields, insect-pollinator abundance and diversity decrease with distance from natural habitat remnants or uncultivated field margins that serve as source habitats (Garibaldi et al. 2011b). In addition, even though it levelled off during the last decade, pesticide use per hectare has increased by about 70% since the early 1990s (ourworldindata.org/pesticides#pesticide-consumption), probably due to the increasing use of neonicotinoids (Hladik et al. 2018). Lethal and sublethal effects of a variety of pesticides, including neonicotinoids, can significantly depress pollinator abundance and diversity in agricultural settings (Desneux et al. 2007; Blacquière et al. 2012; Devillers and Devillers 2020). These findings imply that conventional agricultural practices over large spatial scales are an important driver of pollinator decline (Goulson et al. 2008; Potts et al. 2010, 2016). Also, bee invasions —often instigated by bee trade— can negatively affect native bees via competitive displacement or pathogen transmission (Stout and Morales 2009; Mallinger et al. 2017; Vanbergen et al. 2018). A large-scale example involves the Patagonian bumble bee, *Bombus dahlbomii*, which was extirpated from most of its range in a few generations following sequential introductions and ensuing invasions of southern South America by the European bumble bees *B. ruderatus* and *B. terrestris* (Arbetman et al. 2012; Morales et al. 2013; Aizen et al. 2019b). Finally, at even larger scales, climate change can induce the shift and contraction of species' geographical ranges, as has been recorded for several bumble-bee species (Kerr et al. 2015; Soroye et al. 2020).

A notable exception to declining bee abundance is the western honey bee, *Apis mellifera*. Humans have managed honey-bee colonies for honey for millennia and increasingly for intentional use as crop pollinators (Winston 1987). This species is native to Europe and Africa, but now is distributed in all continents, except Antarctica. As agricultural livestock or a free-roaming species it represents an important component of local pollinator faunas worldwide (Aizen and Feinsinger 2003; Hung et al. 2018). In Europe and northern Africa, wild honey bees are now rare, and managed and feral honey bees dominate pollinator communities across the Mediterranean region (Herrera 2020). In the Neotropics, the invasive African honey bee is now probably the most abundant bee species (Aizen et al. 2020; Garibaldi et al. 2021).

During the last two decades, the western honey bee has become the focus of public and media interest in pollinator decline in North America and much of western Europe, in part owing to losses of managed hives to a mysterious syndrome known as Colony Collapse Disorder (Oldroyd 2007). Public media commonly extrapolate such losses as evidence that the stock of domesticated honey bees is declining globally (e.g., ourworld.unu.edu/en/globalisation-and-agriculture-industry-exacerbating-bee-decline-says-un). However, the decline in numbers of managed honey-bee hives in the USA and some European countries (Figure 1) predates Colony Collapse Disorder (Aizen and Harder 2009a,b). Furthermore, numbers of managed

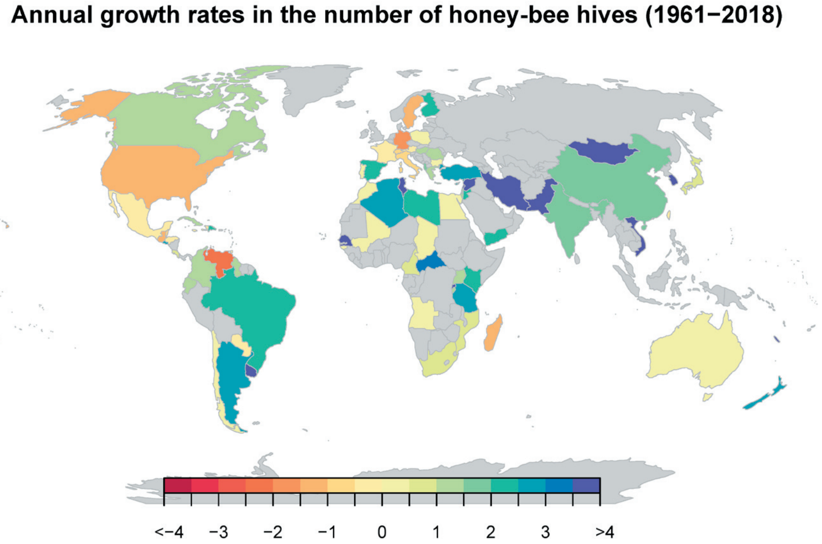


Figure 1. World map showing the annual growth rates (%/year) in number of honey-bee (*Apis mellifera*) hives between 1961 and 2018 for 76 countries that reported data to the FAO during all years (FAOSTAT 2021). The annual growth rate was estimated for each country as 100*{[e^(ln(x_{2018})-ln(x_{1961}))/57]-1},where x_{1961} and x_{2018} are the number of hives during 1961 and 2018, respectively (see also Aizen et al. 2019a).

Figura 1. Mapa mundial mostrando las tasas anuales de crecimiento (%/año) en el número de colmenas de abejas melíferas (*Apis mellifera*) entre 1961 y 2018 para 76 países que han informado datos a la FAO en forma continua durante todos los años de ese período (FAOSTAT 2021). La tasa anual de crecimiento para cada país fue estimada como 100*{[e^(ln(x_{2018})-ln(x_{1961}))/57]-1}, donde x_{1961} and x_{2018} representan el número de colmenas durante los años 1961 y 2018, respectivamente (ver también Aizen et al. 2019a).

hives have increased considerably in more countries than have experienced losses (Figure 1), resulting in ~80% global increase during the last six decades (Figure 2A). This heterogeneity apparently resulted from shifts in the global economics of honey production, with production shifting, with some exceptions (e.g., Canada, Spain, Finland), from countries with higher production costs to countries with lower production costs (Aizen and Harder 2009a,b). This change has supported increased global honey production roughly in proportion to the growth of the human population (Figure 2A). Clearly, the western honey bee as livestock is not threatened globally. Furthermore, the declines in managed hive numbers in a minority of countries, such as Germany, Sweden and Venezuela (Figure 1), likely reflect a relatively unique suite of causes not experienced by wild pollinators, including political, economic and trade factors (Aizen and Harder 2009a,b). Therefore, the honey bee is not an exemplar of pollinator decline. That said, pollination occurs locally —not globally— so that honey bees may have provided less crop pollination during recent decades in countries where numbers of managed hives have declined.

Agricultural dependence on pollinators

The second premise for pollinator decline to impact human food production significantly is that many crops require animal pollination and thus a sizable fraction of agricultural production depends on pollinators (Buchmann and Nabhan 1996; Allen-Wardell et al. 1998). This premise is supported by evidence that more than two-thirds of the leading global food crops, which account for about one third of all agricultural production, depend to some extent on pollinators to produce the seeds and fruits that humans consume (Klein et al. 2007). However, this evidence must be viewed cautiously, as pollinator dependence does not mean complete reliance on pollinators. Instead, Klein et al. (2007) recognized that dependence, as measured by the percentage

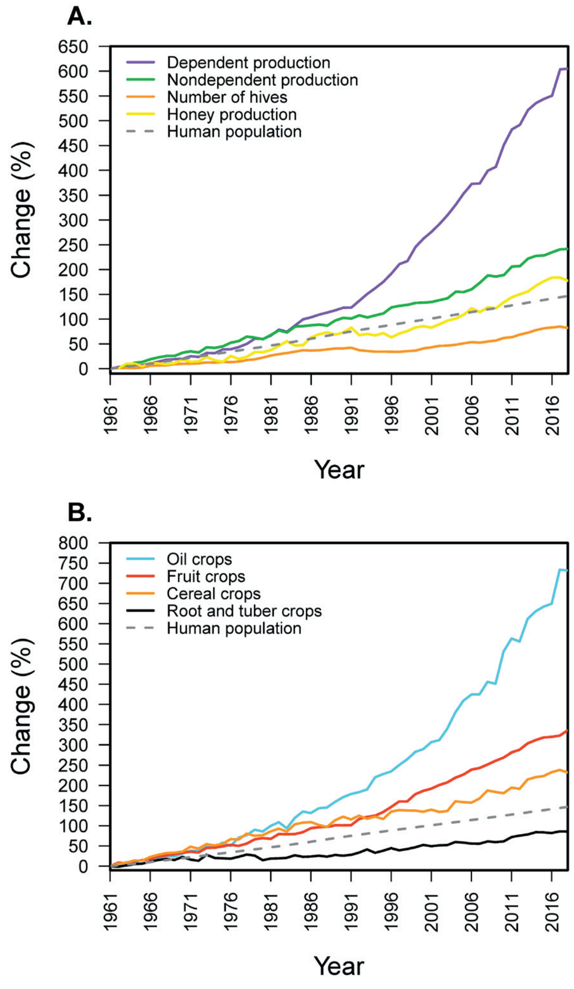


Figure 2. Global temporal trends (1961-2018) in (A) the fractions of agricultural production that depend and does not depend on pollinators (estimated following the methodology of Aizen and Harder 2009a), the number of honey-bee hives, and honey production, and (B) total production by oil, fruit, cereal and root and tuber crops (FAOSTAT 2021). The trend in the size of the human population is included in both panels as a reference. Change for each variable x from 1961 until year t is calculated as a percentage of the 1961 value. Absolute values during 1961 were: agricultural production that depended on pollinators=117.19x10^6 t; agricultural production that did not depend on pollinators=2324.41x10^6 t; number of honey-bee hives=49.17x10^6 hives; honey production=0.678x10^6 t; oil crops=132.15x10^6 t; fruit crops=199.84x10^6 t; cereal crops=876.87x10^6 t; root and tuber crops=455.31x10^6 t, and human population=3901.84x10^6 individuals.

Figura 2. Tendencias temporales (1961-2018) globales en (A) las fracciones de la producción agrícola que dependen y no dependen de los polinizadores (estimadas siguiendo la metodología de Aizen and Harder 2009a), el número de colmenas de abejas melíferas y la producción de miel, y (B) la producción total de oleaginosas, frutales, cereales y raíces y tubérculos (FAOSTAT 2021). La tendencia en el tamaño de la población humana se incluye como una referencia. El cambio en la variable x desde 1961 hasta el año t está calculada como un porcentaje del valor de 1961. Los valores absolutos para el año 1961 fueron: producción agrícola dependiente de los polinizadores=117.19x10^6 t; producción agrícola no dependiente de polinizadores=2324.41x10^6 t; número de colmenas de abejas melíferas=49.17x10^6 colmenas; producción de miel=0.678x10^6 t; oleaginosas=132.15x10^6 t; frutales=199.84x10^6 t; cereales=876.87x10^6 t; raíces y tubérculos=455.31x10^6 t, y población humana=3901.84 x10^6 personas.

of yield reduction in the absence of pollinators, ranges from 0 to 100%. For convenience, Klein et al. (2007) divided this range into five dependence categories (none [0%], little [>0 to <10%], modest [>10 to <40%], high [>40 to <90%] and essential [>90%]). Based on a sample of 134 crops cultivated partially or completely for human consumption (see Supplementary Material 1), we estimate that ~47% of crops do not depend on pollinators, ~14% are weakly dependent, ~13% are moderately dependent, ~18% are highly dependent on pollinators and pollinators are essential for only ~8% (Supplementary Material 2). Thus, among the crops that exhibit some pollinator dependence, pollinators contribute to >40% of the yield of about one quarter and only <10% of all crops would fail almost completely in the absence of pollinators.

Given these percentages, overall global agricultural production would be reduced by $\sum P_i \cdot d_i$ tonnes in the total absence of pollinators, from the current $\sum P_i$ tonnes to $\sum P_i \cdot (1-d_i)$ tonnes, where P_i is the global total production of crop i and d_i is its pollinator dependence (Aizen et al. 2009; Gallai et al. 2009; Lautenbach et al. 2012; Smith et al. 2015). We applied this equation to the 134 crops cultivated for human consumption listed in Supplementary Material 2, using the mid-values of Klein et al.'s pollinator dependence categories for d_i expressed as a fraction instead of as a percentage. The result is that global agriculture production during 2018 would have been reduced by about 794.1×10^6 tonnes in the total absence of pollinators. Although impressive, this figure represents only ~9.4% of total agriculture production. Nevertheless, the corresponding percentage for 1961 was ~4.8%, indicating increasing pollinator dependence of agriculture production during the last six decades (see also Aizen et al. 2009).

Even though complete pollinator absence would have limited impact on global agriculture production, the diversity of the human diet, which is highly influenced by income and cultural differences at the household scale, could also be impaired via a reduction in agriculture diversity (Jones 2017) caused by pollinator decline (Eilers et al. 2011; Chaplin-Kramer et al. 2014). For example, desirable foods for which animal pollination is essential include cocoa, melons and squashes (Supplementary Material 2). However, again the impact of complete pollinator loss would be relatively small, as most partially dependent crops would continue producing fruits and seeds for human consumption in proportion to their pollinator independence in the absence of pollinators. Specifically, an analysis using two quantitative diversity indices estimated <5% reduction in crop diversity in the absence of pollinators (Aizen et al. 2009).

The preceding calculations provide minimum estimates of the agricultural importance of pollinators, as animal pollination also provides other direct and indirect benefits that warrant consideration. Among the direct benefits, pollinator-dependent crops provide a disproportionate amount of dietary macro and micronutrients (Eilers et al. 2011; Chaplin-Kramer et al. 2014), which connects pollinator losses with human health through nutrition (Ellis et al. 2015; Smith et al. 2015). Among the indirect benefits, pollinators are needed for propagation via seed production of many non-dependent crops that are grown for their vegetative parts (several vegetables), in plant breeding programs and for hybrid seed production (e.g., canola, onion, sunflower) (Steffan-Dewenter 2003; Klein et al. 2007). Nevertheless, our simple analyses indicate that pollinator decline will not be a significant cause of future food limitation or reduced diet diversity at a global scale.

Yield trends of pollinator dependent crops

The GPC hypothesis predicts reduced success of pollinator-dependent plant species because insufficient pollination increasingly limits seed production as pollinator populations decline. This effect could be more significant for most fruit and seed crops, for which yield depends directly on reproductive outcomes, than for wild species, for which population abundance is often not limited by annual seed output (Turnbull et al. 2000). The pollinator-exclusion experiments used to quantify pollinator dependence (Vaissière et al. 2011) demonstrate the maximum impact expected from complete pollinator loss; but does yield of fruit and seed crops decrease proportionally with partial pollinator loss? A metanalysis of 29 crop-pollination studies revealed partial buffering against pollinator loss, as mean fruit set decreased 16% 1 km from field margins despite 34 and 27% declines in mean flower-visitor richness and visitation rate, respectively (Garibaldi et al. 2011b). Beyond the weak or moderate dependence on animal pollination of several of the crops included in that study (e.g., coffee, grapefruit, strawberry and tomato), several factors may underlie such buffering. First, pollinator species differ in their effectiveness (Hargreaves et al. 2009; King et al. 2013), so loss of ineffective pollinators should have relatively limited impact on pollination (Koski et al. 2018). Second, different pollinators can be functionally redundant (Miñarro and García. 2018), so that a reduction in pollinator diversity need not reduce pollination service (Garibaldi et al. 2011b). Third, seed production per flower varies in a decelerating manner with pollen receipt (Aizen and Harder 2007) owing to pollen-tube competition and limited ovule number or resources for seed development (Knight et al. 2005; Harder and Routley 2006; Harder et al. 2016). Therefore, if pollinators deliver sufficient pollen to support asymptotic seed production, partial pollinator loss should have a limited impact. Indeed, extremely frequent pollinator visitation can be detrimental (Aizen et al. 2014), so that partial pollinator loss could be beneficial in some cases. The buffering of plant reproduction against partial pollinator loss associated with these effects suggests that, even though crop yield can often be limited by inadequate pollination service (Garibaldi et al. 2016; Sáez et al. 2022), yield of many crops may be relatively insensitive to at least some decline in pollinator abundance.

Clear warning of an impending pollination crisis should be evident in decelerating growth of crop yield over time as pollination services decline, or even more alarmingly by a shift from positive to negative yield growth. In contrast, an initial analysis of global FAO data for 87 crops from 1961-2006 found similar linear increases in the average yield of pollinator-dependent vs. pollinator-independent crops, thus not supporting a global pollination crisis (Aizen et al. 2008). To assess whether the case for a pollination crisis had changed during the ensuing 13 years, we conducted a more detailed analysis of the relation of annual changes in yield from 1961-2018 for 128 crops (see Supplementary Material 1) classified according to the five categories of pollinator dependence (see Figure 3 for statistical methods). For crops in the essential pollinator-dependence category, annual yield growth may have declined slightly (P=0.056), whereas for those with high pollinator dependence it increased weakly (P=0.043). Overall, the slope of the relation of annual yield growth to year does not become increasingly negative (i.e., decreasing annual yield growth) with increasing pollinator dependence (Figure 3). Thus, current evidence is inconsistent with deceleration in yield growth with increasing pollinator dependence at a global scale.

Synopsis

The available evidence demonstrates that agriculture is not in the midst of a global pollination crisis. Populations of many wild pollinators are declining in concert with broader impacts of human-induced global change of climate and biodiversity. In contrast, the global abundance of managed pollinators has increased considerably during the past six decades to support the honey industry and, to a lesser extent, intentional pollination of some crops. In addition, production of the staple crops that are central to human diets does not require animal pollination. Furthermore, although many fruit and seed crops benefit from such pollination to some degree, a sizable proportion of them can yield appreciably in the absence of pollinators. Finally, despite declines of many wild pollinators, global yield growth by crops that depend highly on animal pollination has not obviously declined.

OVERLOOKED INFLUENCES ON THE POLLINATION CRISIS

The original GPC hypothesis focused on the consequences of pollinator decline for area-specific yield. Although yield is germane from the perspective of local farmers with circumscribed farms, the relevant output for satisfying global human food demand is production, which is the product of yield and cultivated area. This relation suggests that the GPC hypothesis needs to be broadened to include the implications of growing demand for agricultural produce associated with human-population growth and increasing per capita consumption, and for any related changes in cultivated area, especially that devoted to the cultivation of pollinator-dependent crops.

Discrepancies between pollinator supply and demand

A global agricultural pollination crisis will occur if human demand for products derived from pollinator-dependent crops increasingly exceeds the capacity of wild and managed pollinators to provide the necessary pollination services. Our results are consistent with this condition, as the fraction of agriculture production that can be attributed to pollinators has increased by ~600% since 1961, whereas the number of managed honey-bee hives has increased by only ~80% (Figure 2A) and natural pollination services are likely diminishing given the general

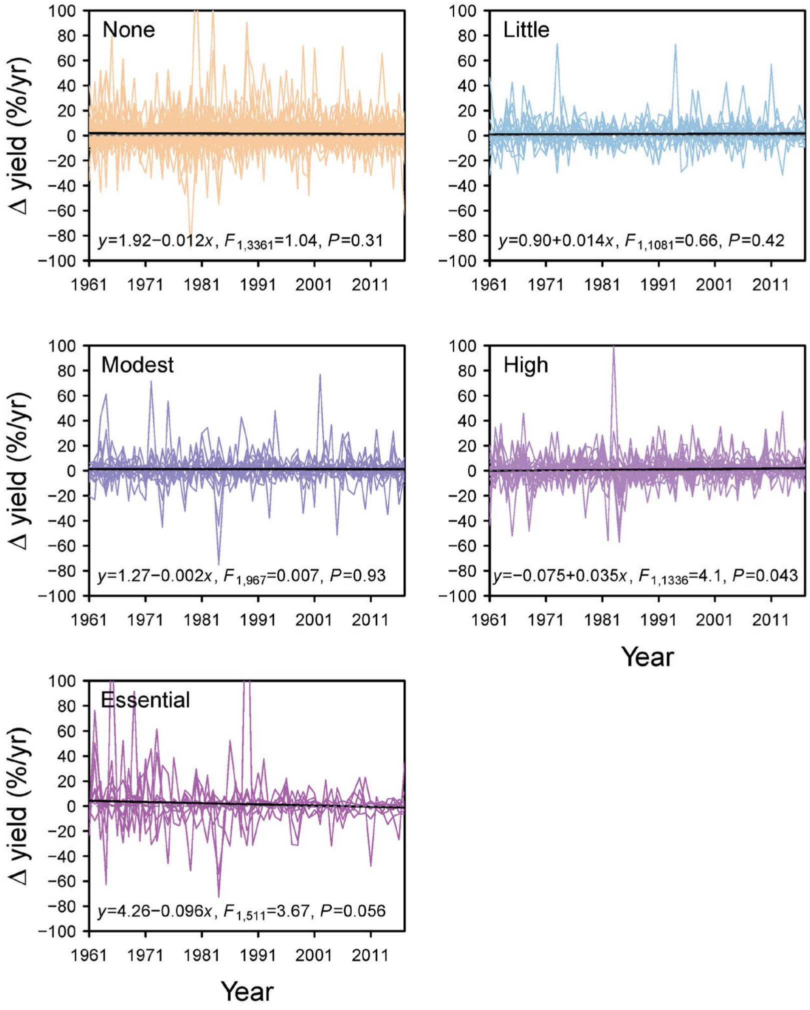


Figure 3. Global temporal trends in annual growth rates in yield between 1961 and 2018 for 128 crops with complete yield records (FAOSTAT 2021) categorized by pollinator dependence based on the percentage of yield reduction in the absence of pollinators (none [0%, n=59 crops], little [>0 and <10%, n=19], modest [>10 and <40%, n=17], high [>40 and <90%, n=24], essential [>90%, n=9]). Annual growth rates in yield were estimated using the equation in Figure 1. Rates calculated from change between consecutive years simplifies to percent change, $100^*[(x_{t+1}/x_t)-1]$, where x_t and x_{t+1} are yield values in t/ha during years t and t+1, respectively. The solid black line depicts the regression of annual yield growth rate *vs.* year (1961=year 0) for each pollinator-dependent category and the grey dashed line at 0 indicates yield constancy. The interaction between year and pollinator dependence (i.e., using the mid value for each dependence category (none [0%], little [5%], modest [25%], high [65%], essential [95%]) in a regression model that considered both predictors did not detect a temporal relation with increasing pollinator dependence ($F_{1.7292}$=0.23, P=0.64). Including 'crop' as a random effect did not improve the fit of any model. Models were implemented with the statistical software R version 4.0.2 (R Core Team 2020) using the lm function of the basic library and the lmer function of the lme4 library (version 1.1-23) (Bates et al. 2015).

Figura 3 Tendencias temporales en las tasas de crecimiento anual en el rendimiento entre los años 1961 y 2018 para 128 cultivos con registros completos (FAOSTAT 2021) categorizados por su dependencia de polinizadores en base al porcentaje de reducción en el rendimiento en ausencia de polinizadores (ninguno [0%, n=59 cultivos], poca [>0 y <10%, n=19], media [>10 y <40%, n=17], alta [>40 y <90%, n=24], esencial [>90%, n=9]). Las tasas de crecimiento anual en el rendimiento fueron estimadas usando la ecuación descripta en la Figura 1, que en el caso de calcularlas entre años consecutivos se simplifica a una estimación de cambio porcentual, $100^*[(x_{t+1}/x_t)-1]$, donde x_t and x_{t+1} son los valores de rendimiento en t/ha durante los años t y t+1, respectivamente. En cada panel, la línea sólida representa la recta de regresión de la tasa anual de crecimiento en el rendimiento *vs.* año (1961=año 0) para cada categoría de dependencia de polinizadores y la línea gris discontinua en el valor 0 indica constancia en el rendimiento. La interacción entre el año y la dependencia de polinizadores (i.e., usando el valor medio de dependencia para categoría (ninguna [0%], poca [5%], media [25%], alta [65%], esencial [95%]) en un modelo de regresión que incluyó ambas variables predictoras no evidenció ningún cambio en la relación temporal con un incremento en la dependencia por polinizadores ($F_{1.7292}$=0.23, P=0.64). La inclusión del factor 'cultivo' como un efecto aleatorio no mejoró el ajuste de ninguno de los modelos. Los modelos se implementaron con el programa estadístico R versión 4.0.2 (R Core Team 2020) usando la función lm de la biblioteca 'basic' y la función lmer de la biblioteca lme4 (versión 1.1-23) (Bates et al. 2015).

decline of wild pollinators (see subsection 'Pollinator decline'). The breakneck increase of pollinator-dependent agriculture actually underrepresents the current rate of growth in production of pollinator-dependent crops. Prior to the 1990s, the fraction of agricultural production that depended on pollinators grew at a similar rate as the large fraction of agricultural production that did not depend on pollinators (~2.5% per year), which was largely determined by growth of wind-pollinated cereal crops rather than root and tuber crops (Figure 2B). During the 1990s, the growth rate of pollinator-dependent agricultural production, but not of pollinator-nondependent production, increased abruptly to ~4.5% per year (Figure 2A) in association with increased globalisation (Aizen and Harder 2009a) and growing demands for fruit and, especially, oil crops (Figure 2B).

The results portrayed in Figure 2 reveal three obvious implications. First, the fraction of food production that does not depend on pollinators, which includes most staple crops (e.g., wheat, corn, rice, etc.) and represents >90% of total agriculture production (see subsection 'Agricultural dependence on pollinators'), grew faster than the human population (Figure 2A), indicating more food per capita now than decades ago (although food distribution remains greatly unequal). Second, the continuous growth of agriculture production during the last six decades indicates that human demand for resources, specifically agricultural production, has still not exceeded Earth's short-term capacity to provide them. Finally, the discrepancy between the rates of increase in the number of managed honey-bee hives and the fraction of agriculture production that depends on pollinators signals increasing imbalance between the demand for and supply of pollination services, which could lead to an agricultural pollination crisis if it continues unchecked.

However, relevant mitigating trends may be offsetting a potentially expanding pollination gap. First, from the plant side is the development and propagation of crop varieties that do not depend or depend less on pollinators (e.g., Sáez et al. 2019; Alsahlany et al. 2021), although a claimed pollinator independence of some of these new varieties can be overstated (Sáez et al. 2019). Second, from the pollinator side, cultural techniques have been developed for managing pollinator species other than the honey bee (Osterman et al. 2021) and non-native pollinators have been introduced to increase crop pollination, including generalist bumble bees and specialist oil-palm weevils (Goulson 2010; Corley and Tinker 2016). Of course, the direct benefits of these animal trends for agricultural pollination will likely be tempered by detrimental effects of managed and introduced pollinators on native pollinators (see subsection 'Pollinator decline'). Third, increasing demand for pollination services or absence of pollinators in some cases has motivated the use of laborious hand-pollination (Wurz et al. 2021) or the more recent development of futuristic pollinating drones (Potts et al. 2018). Nevertheless, these artificial pollination techniques are as cost-effective in practice as natural pollination and for many crops might not replace the quality and stability of the pollination services provided by diverse pollinator assemblages (see subsection 'Wild pollinators are essential for maintaining high yields'). In any event, these compensation measures could play an increasing role in crop pollination in the future, and the current implementation of at least some of them might explain the lack of evidence for declining yields of pollinator-dependent crops at a global scale (see subsection 'Yield trends of pollinator dependent crops'). However, they are likely not to be sufficient to offset fully the increasing pollination demand that could be creating an accelerated growth in pollinator-dependent agriculture.

Wild pollinators are essential for maintaining high yields

Despite the limited contribution of pollinators to overall global agricultural production (see subsection 'Agricultural dependence on pollinators'), wild pollinators are key to maintaining high yield of most pollinator-dependent crops (Rader et al. 2016) and, probably, to limiting future deficits of pollinator supply relative to demand. For example, a synthesis study of 41 crop systems in countries on all continents, except Antarctica, found that fruit set varied positively with flower visitation by wild insects for all crop systems, whereas positive effects of honey-bee visitation were evident for only 14% of the same crop systems (Garibaldi et al. 2013). Importantly, honey-bees are low-quality pollinators of some crops because of their tendency to visit many flowers from the same plant, thus promoting the transfer of self-pollen (see also Aizen et al. 2020; Sáez et al. 2022). Considered as a group, wild insects were more effective pollinators overall, with an average per-visit chance of fruit set twice that of honey bees. This study indicated that honey bees cannot generally replace the pollination services provided by wild insects (Garibaldi et al. 2013). This limitation arises, in part, because pollination efficiency depends on both pollination quantity and quality (Aizen and Harder 2007). Honey bees can be inefficient in both aspects as they often act more as pollen thieves than as pollen vectors (Hargreaves et al. 2009) and/or provide poorer-quality pollination (specifically greater self-pollination: Aizen et al. 2020; Sáez et al. 2022) than wild insects.

Furthermore, Garibaldi et al. (2013) demonstrated a positive overall relation of fruit set to pollinator diversity (see also Garibaldi et al. 2016). This favourable effect likely reflects similar benefits to those associated with a diversified portfolio of investments, including spatial and temporal complementarity in pollinator activity, enhanced probability of effective pollinator occurrence and benefits of interference competition between pollinators that promotes inter-plant movement and outcrossing (Greenleaf and Kremen 2006; Albrecht et al. 2012; Winfree et al. 2018; Senapathi et al. 2021). Together these findings illustrate that yield maximization of many pollinator-dependent crops requires the service of wild pollinators, which are generally in decline (Biesmeijer et al. 2006; Potts et al. 2010; Ollerton et al. 2014; Zattara and Aizen 2021).

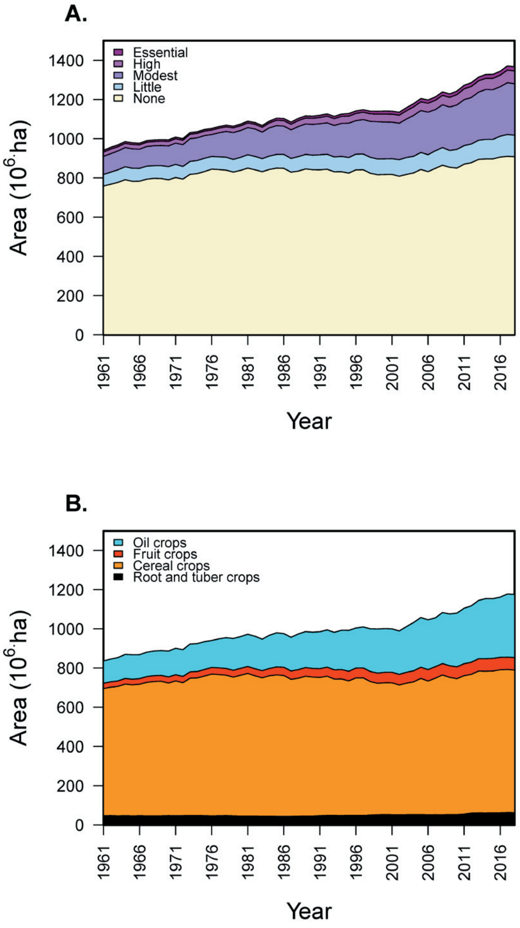


Figure 4. Global temporal trends (1961-2018) in agricultural area planted with (A) crops with different dependence on pollinators (none [0%], little [>0 and <10%], modest [>10 and <40%], high [>40 and <90%], essential [>90%]) (Klein et al. 2007), and (B) oil, fruit, cereal, and root and tuber crops (FAOSTAT 2021).

Figura 4. Tendencias temporales (1961-2018) en el área agrícola global cultivada con (A) cultivos con distinta dependencia de polinizadores (ninguna [0%], poca [>0 y <10%], media [>10 y <40%], alta [>40 y <90%], esencial [>90%]) (Klein et al. 2007), y (B) oleaginosas, frutales, cereales, y raíces y tubérculos (FAOSTAT 2021).

Rapid expansion of pollinator-dependent agriculture

Another key element of the imbalance between pollinator supply and demand is the rapid areal expansion of pollinator-dependent agriculture. Based on FAO data, the land devoted to agriculture expanded ~45% (>4x10^6 km^2) between 1961 and 2018, including area counted multiple times because of either spatial or temporal intercropping. This area expansion primarily involved increased cultivation of crops with some pollinator dependence. The area cultivated with such crops grew ~150% during this period, compared to ~20% for pollinator-independent crops (Figure 4A). Most expansion of pollinator-dependent crops involved moderately to highly dependent oil-seed crops —such as soybean, canola and oil palm— with a secondary contribution by highly dependent fruit crops, both tropical (e.g., mangoes, avocados) and temperate (e.g., blueberries, plums, cherries: Figure 4B). The area cultivated with oil and fruit crops respectively increased ~185 and ~140% since 1961, whereas that cultivated with pollinator-independent crops, such as cereals and root vegetables, expanded only ~12 and ~35%, respectively (Figure 4B) (see also Kastner et al. 2012). This differential agricultural expansion can be attributed to the higher market value of pollinator-dependent crops compared to pollinator-independent crops

(Gallai et al. 2009) and the lower yield growth of crops that depend highly on pollinators (Figure 5A) (see also Garibaldi et al. 2009). Consequently, unlike the growth in production of pollinator-independent crops, which primarily involved yield improvement, production growth of pollinator-dependent agriculture also involved rapid expansion of cultivated area, especially for fruit crops (Figures 4B and 5B). More detailed analysis reveals an additional concerning feature of the increased demand for pollinator-dependent crops, namely that it results primarily from expanded cultivation of oil crops (Figures 4B and 5B). Much of this production, as well as a substantial proportion of the production of pollinator-independent crops such as maize (Klopfenstein et al. 2013), is used for biodiesel and animal food, rather than directly to feed humans (Somerville 2007; Sharma et al. 2012; Corley and Tinker 2016). Finally, greater dependence on pollinators is also associated with more temporal variability in yield growth (Garibaldi et al. 2011a; Gleiser et al. 2021), which could also contribute to the differential expansion of pollinator-dependent agriculture to offset yield uncertainty under sustained market demand.

The global differential expansion of the area cultivated with pollinator-dependent crops belies some striking regional differences. In some countries belonging to the Global North, particularly in North America and Europe, pollinator-dependent crops are increasingly replacing pollinator-independent crops, with little expansion of total cultivated area. In contrast, in countries belonging to the Global South, particularly in South America and Southeast Asia, cultivation of pollinator-dependent crops has involved rapid expansion of total agricultural land (Figure 6). The latter expansion is associated with extensive deforestation, primarily for

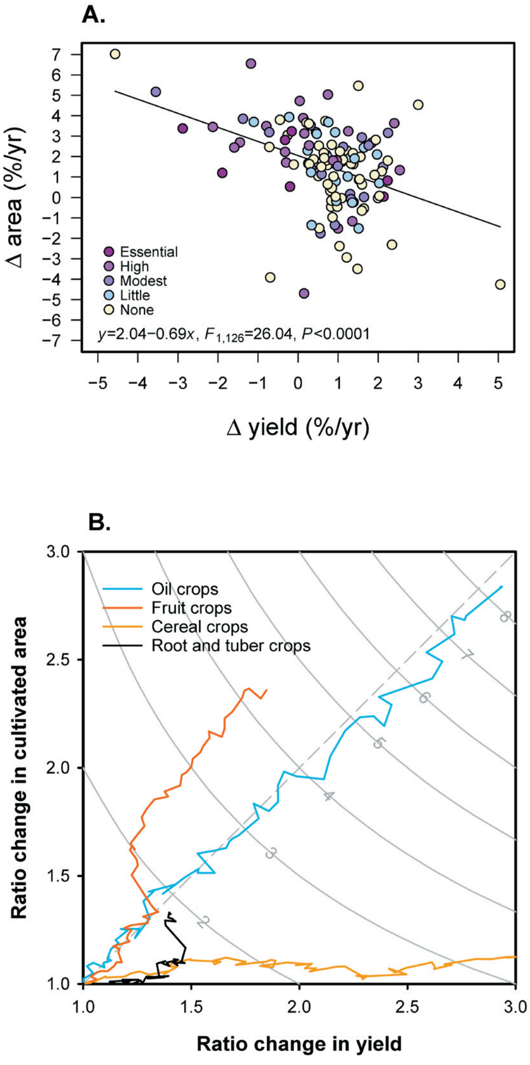
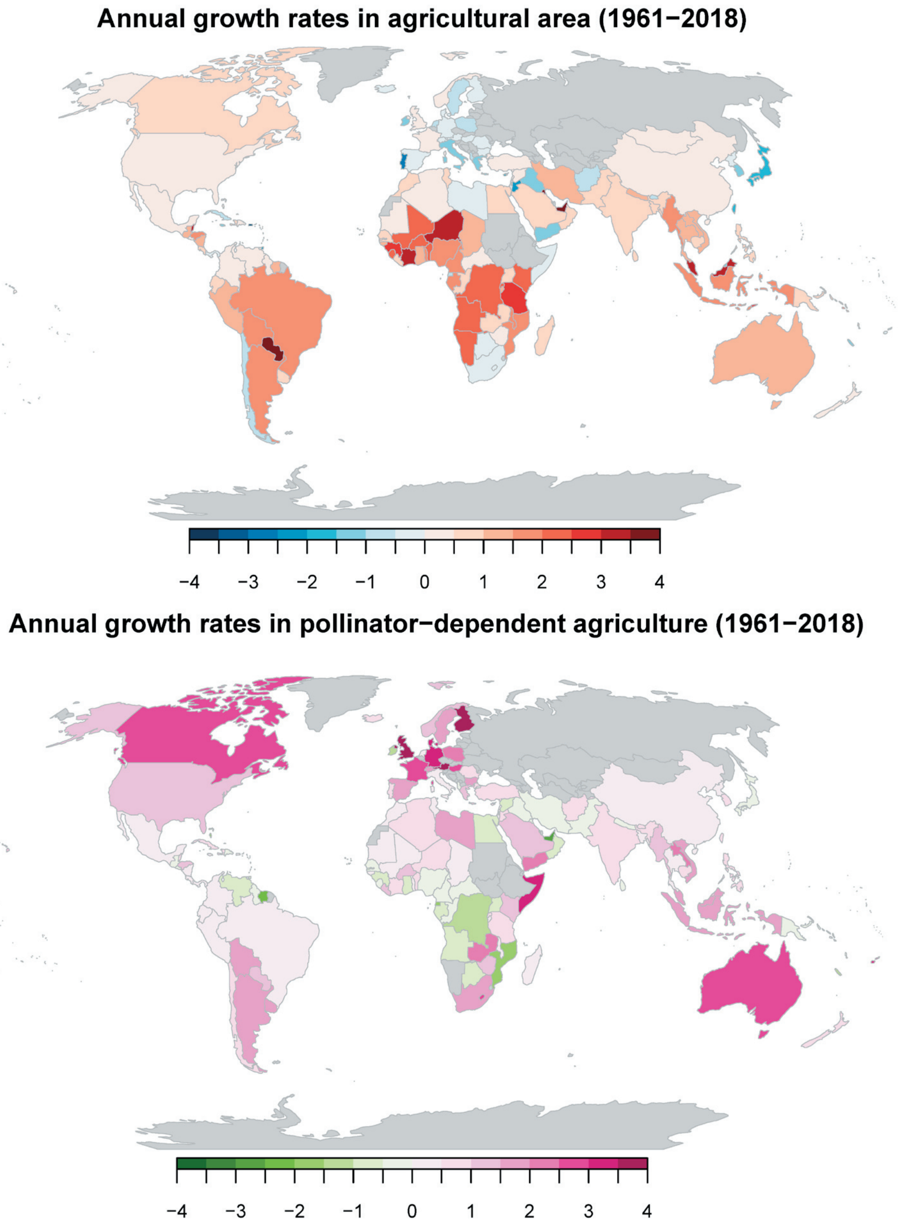


Figure 5. Relations of annual growth in global cultivated area to growth in global yield between 1961 and 2018 based on data from FAOSTAT (2021). In (A) the solid line depicts the regression of mean annual growth in cultivated area to mean annual yield growth for 128 crops categorized by pollinator dependence (none [0%, n=59 crops], little [>0 and <10%, n=19], modest [>10 and <40%, n=17], high [>40 and <90%, n=24], essential [>90%, n=9]). Adding pollinator-dependence as a categorical factor did not provide evidence that the depicted negative relation varies among pollinator dependence categories (yield growth x pollinator dependence interaction, $F_{4.118}$=0.29, P=0.88). The models were implemented using the lm function of the basic library statistical software R version 4.0.2 (R Core Team 2020). In (B) the growth trajectories depict the ratio change in cultivated area and yield for oil, fruit, cereal, and root and tuber crops based on 1961 values. The dashed gray diagonal line represents proportional change in area and yield ratios. The gray curves depict isoclines for the ratio change in total production (area x yield) as indicated by the associated number.

Figura 5. Relaciones entre la tasa anual de crecimiento en el área cultivada global y la tasa anual en el crecimiento en el rendimiento entre 1961 y 2018 en base a datos de FAOSTAT (2021). En (A) la línea sólida representa la recta de regresión de la tasa media de crecimiento en área en función de la tasa media en el crecimiento del rendimiento para 128 cultivos categorizados de acuerdo a su dependencia de polinizadores (ninguna [0%, n=59 cultivos], poca [>0 y <10%, n=19], media [>10 y <40%, n=17], alta [>40 y <90%, n=24], esencial [>90%, n=9]). La inclusión de la dependencia de polinizadores como factor categórico no proveyó evidencia de que la relación negativa graficada varía entre categorías de dependencia (interacción tasa de crecimiento en el rendimiento x dependencia de polinizadores, $F_{4.118}$=0.29, P=0.88). Los modelos fueron implementados usando la función lm de la biblioteca 'basic' del programa R versión 4.0.2 (R Core Team 2020). En (B) las trayectorias de crecimiento ilustran el cambio en el área cultivada y el rendimiento relativizados a los valores del 1961. La línea diagonal gris discontinua representa el cambio proporcional entre el área y el rendimiento. Las curvas grises representan las isoclinas de la producción relativa total (área x rendimiento relativizados) como se indica en el valor asociado a cada una de ella.

cultivation of soybean in South America (e.g., Gasparri et al. 2013; Fehlenberg et al. 2017) and oil palm in southeast Asia (e.g., Koh and Wilcove 2007; Fitzherbert et al. 2008). Therefore, the considerable expansion of agricultural land devoted to the cultivation of pollinator-dependent crops, particularly of oil-seed monocultures, is accelerating habitat destruction and increasing habitat homogenization, two important drivers of pollinator decline (Potts et al. 2010, 2016; Dicks et al. 2021).


Annual growth rates in agricultural area (1961−2018)

Annual growth rates in pollinator−dependent agriculture (1961−2018)

Figure 6. World maps showing the annual growth rates (%/year) in (A) total agricultural area and (B) proportion of agricultural area cultivated with pollinator-dependent crops between 1961 and 2018 for 162 countries that reported crop data during all years (FAOSTAT 2021). Annual growth rates were estimated as $100*\{[e\wedge(\ln((x_{2018})-(\ln(x_{1961}))/57]-1\}$, where x_{1961} and x_{2018} are total agricultural area and the proportion of that area cultivated with pollinator-dependent crops of during 1961 and 2018, respectively (see also Aizen et al. 2019a).

Figure 6. Mapas mundiales que muestran las tasas anuales de crecimiento (%/año) en (A) el área agrícola total y (B) la proporción del área agrícola cultivada con cultivos dependientes de polinizadores entre los años 1961 y 2018 pata 162 países que informaron datos a la FAO durante todos los años (FAOSTAT 2021). Las tasas anuales fueron estimadas como $100*\{[e\wedge(\ln((x_{2018})-(\ln(x_{1961}))/57]-1\}$, donde x_{1961} y x_{2018} son el área agrícola total y la proporción de área cultivada con cultivos dependientes de polinizadores durante 1961 y 2018, respectivamente (ver también Aizen et al. 2019a).

Expansion of the pollination-crisis hypothesis

A pervasive positive-feedback cycle

As described above, the growing human demand for pollinator-dependent crops is satisfied by increased use of managed and introduced pollinators, application of broad-spectrum pesticides to enhance yield and conversion of natural habitat to crop fields. To the extent that these responses degrade the conditions needed to maintain wild pollinator populations and the pollination services they provide, they could fuel a positive-feedback cycle that is the basis of an expanded pollination-crisis hypothesis.

As Figure 4 demonstrates, most agricultural expansion during the last six decades involved increased cultivation of pollinator-dependent crops, particularly oil and fruit crops (see also Lautenbach et al. 2012). Although fields cultivated with such crops provide nectar and pollen for bees and other pollinators, they do so for only a brief annual period, creating feast-famine environments that can sustain only limited pollinator abundance and diversity (Westphal et al. 2003; Nicholls and Altieri 2013). In fact, land-use change due to agricultural expansion has been identified as the main driver of terrestrial biodiversity loss (IPBES 2019), including pollinator decline (IPBES 2016; Dicks et al. 2021). Even though our analyses failed to support an impact of widespread pollinator decline on yield growth at a global scale (Figure 3) and even though crop yield can be buffered to some extent against pollinator loss (see subsection 'Yield trends of pollinator dependent crops'), there is much evidence that reduced pollinator abundance and diversity can compromise yield locally due to increasing pollination deficits (Garibaldi et al. 2011b, 2013, 2016). This evidence also suggests that the pollination deficit and decreased yield caused by declines and local extinctions of wild pollinators could not be compensated by increasing the stock of managed bees, such as the honey bee (Garibaldi et al. 2013, 2016; Sáez et al. 2022). Instead, decreased yield would be compensated, at least in part, by expanding cultivated area (Figure 5A). A simulation of the consequences of complete pollinator collapse based on 2007 data predicted that maintenance of the production of pollinator-dependent crops would require 15 and 40% expansion of total cultivated area in the Global North and South, respectively (Aizen et al. 2009). As the proportion of land cultivated with pollinator-dependent crops has increased continuously since 2007 (Figure 4), so will the expected proportion of land needed to compensate the ongoing or impending effects of pollinator decline. Therefore, the trade-off between crop yield and area growth mediated by demand for pollinator service could fuel an ongoing or future pervasive positive feedback cycle of increasing environmental degradation.

A tale of two crises

In addition to their implications for crop production, declines in the abundance and diversity of wild pollinators could affect reproduction by hundreds of thousands of wild plants (Ollerton et al. 2011); however, the pollination crisis will have different character for these two plant groups. As outlined above, pollinator declines can stimulate mitigating agricultural responses —including development and use of varieties that depend less on pollinators—, pollination supplementation by use of managed pollinators and cultivation of more land —increasing plant 'population' size—. These responses can occur relatively quickly within a season or during a few generations and so should buffer many crops against pollinator declines. In contrast, similar responses by species of wild plants, especially those with specialized pollination systems, may often require many generations of natural selection for traits that promote self-pollination or pollinator transition (Harder and Aizen 2010; Cheptou 2021). The capacity for such evolutionary changes will depend on the existence of relevant genetic variation and the magnitude of inbreeding depression. If a species' pollinators decline faster than its adaptive responses to pollen limitation and recruitment is seed limited, their populations may decline in parallel.

Concluding remarks

Current evidence documents ongoing declines and even extinction of some wild pollinators, but global food production, including of pollinator-dependent crops, has increased steadily during the last six decades owing to yield improvements and increased cultivation. This evidence contradicts apocalyptic predictions of human starvation caused by pollinator decline. Nevertheless, increased agricultural use of pesticides, intentional and inadvertent introduction of alien pollinators, and rapidly expanding cultivation of pollinator-dependent crops

—much of which is not directly used to feed humans— during recent decades are likely contributing to a largely hidden positive feedback between agriculture expansion and pollinator decline. Indeed, agricultural expansion and intensification, driven by growth of human population and per-capita demand, are fundamental drivers of habitat destruction that aggravates the ongoing biodiversity crisis (IPBES 2019). Furthermore, pollinator decline driven by agricultural expansion and other causes could degrade reproduction of the hundreds of thousands of wild flowering-plant species that require animal pollination to reproduce. Thus, even though the proposed positive feedback between agriculture expansion and pollinator decline might not currently affect crop yield globally or have any major impact on wild plant reproduction, Earth's pollination capacity could be radically impaired in coming decades as the environmental costs of agriculture expansion and intensification exceed their incremental production benefits. This possibility calls for urgent implementation of international, national and local policies concerning land conversion, the effect-spectrum and use of agricultural chemicals, trade and introduction of non-native pollinators, and development of pollinator-friendly landscapes (Nicholls and Altieri 2013; Garibaldi et al. 2014). Because of their manifold direct and indirect benefits for agriculture and nature, implementation of such policies will be key to slowing the pervasive cycle of biodiversity loss caused, in part, by agriculture expansion and intensification.

Acknowledgements. The authors acknowledge the contributions of many collaborators to the research reported here and the support of the National Fund for Scientific and Technological Research of Argentina (FONCYT) [PICT 2015-2333, PICT 2018-2145, PICT-2018-00941], Universidad Nacional de Río Negro [PI 40-B-567], and the Natural Science and Engineering Research Council of Canada [RGPIN-2018-03907].

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