ENVIRONMENTAL STUDIES

Virtual pollination trade uncovers global dependence on biodiversity of developing countries

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Nations' food consumption patterns are increasingly globalized and trade dependent. Natural resources used for agriculture (e.g., water, pollinators) are hence being virtually exchanged across countries. Inspired by the virtual water concept, we, herein, propose the concept of virtual biotic pollination flow as an indicator of countries' mutual dependence on biodiversity-based ecosystem services and provide an online tool to visualize trade flow. Using information on 55 pollinator-dependent crop markets (2001–2015), we show that countries with higher development level demand high levels of biodiversity-based services to sustain their consumption patterns. Such patterns are supported by importation of virtual biotic pollination (up to 40% of national imports of pollinator-dependent crops) from developing countries, stimulating cropland expansion. Quantifying virtual pollination flow can help develop new global socioeconomic policies to meet the interconnected challenges of biodiversity loss, ecosystem health, and social justice.

INTRODUCTION

Ensuring the persistence of biodiversity and ecosystem functioning while increasing cropland productivity and human well-being is one of the main current global challenges (*1*). Agricultural systems benefit from several ecosystem services, some driven by abiotic components of the environment, e.g., water and soil (*1*), others dependent on biotic components, such as crop pollination and biocontrol (*2*, *3*). Pollination services contribute to more than 75% of worldwide crop diversity (*4*), and 35% of global crop production by volume (*4*, *5*), with demand for these crops increasing due to growing societal awareness on the importance of a healthy diet (*6*). Such biodiversity-based services are being lost at an extremely fast rate with ongoing environmental degradation (*7*), compromising cropland productivity (*3*, *4*) and affecting national economies (*8*, *9*). The ongoing decline of pollinators (*10*) is leading to reductions in crop productivity and quality worldwide (*2*, *11*), even in regions that are still rich in biodiversity (*12*). Bee management (e.g., *Apis mellifera* and *Bombus terrestris*) can help improve crop pollination, but such practices are less reliable or not appropriate for several farming systems (*11*) and can pose risks for native pollinators (*10*). While many studies have shown local socioeconomic impacts of losses of ecosystem service providers, particularly crop pollinators (*2*), it is important to also consider broader-scale impacts, e.g., on international markets that are supported by local agricultural production (*13*). Identifying societal sectors and populations that most benefit from (and affect) such ecosystem services can contribute to better recognize the shared responsibilities across regions and countries and to develop global environmental policies.

The amount of natural resources used in agricultural production, e.g., land and water, to support consumption patterns is an indicator of a country's ecological footprint (*14*, *15*). Previous studies used the concept of virtual water and land [i.e., resources used for the production of a given crop; see (*15*, *16*)] to identify how foreign demand affects ecosystems in exporting countries (*17*). Although the suitability of such concept to represent trade is debatable (*16*, *18*), the value of the concept of "virtual resource flow" (used in the past 25 years) for identification of interdependence among the world's regions is recognized in the academic and political spheres and can be used to quantify and internalize environmental costs in international governance (*16*, *19*). We, herein, extend the concept to biodiversity-based ecosystem services, applying it to the case of biotic pollination.

Similarly to water or land, crop pollination is a limited resource. A pollinator makes a certain number of visits to flowers (i.e., pollination events) during its lifetime (*20*). Therefore, although an individual pollinator can visit many plant species within a time period, when it selects which plant species to visit (e.g., crop) based on a set of morphological, phenological, and chemical clues (*20*, *21*), such pollination event is no longer available for other crops or local plant diversity (see Fig. 1). For example, mass-flowering crops can act as magnets for pollinators, potentially leading to spillover effects (i.e., increased visitation) for vegetation bordering crop fields (*22*), but at the expense of pollination further away (*23*, *24*). Therefore, even without taking into account the well-known potential negative effects of crop flower visitation on pollinator individual life span, fitness and pollination efficiency (*25*), and negative effects of crop expansion and associated loss of natural habitat on pollinator abundance and diversity due to reduction in nesting and alternative floral resources (*10*), a pollination event that leads to the production of an exported product is no longer available for wild plants and nonexported products. Here, we define virtual biotic pollination (VP) as the proportion of overall crop production resulting from the ecosystem service provided by wild pollinators (Fig. 2). VP flow is then the proportion of national crop production resulting from the

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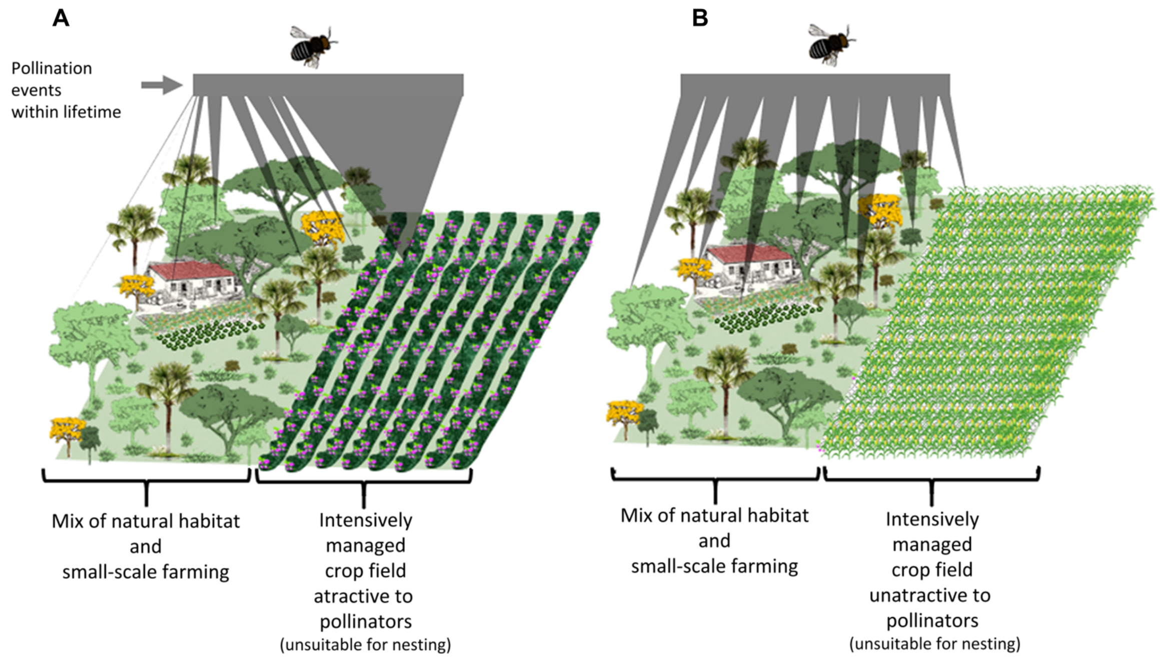

Fig. 1. Pollination events made by pollinators are a limited resource shared between flowering species within a landscape. The figure shows the distribution of pollination events made by an individual pollinator during its lifetime in two landscapes with similar amounts (50%) of natural habitat (mixed with local small-scale farming), one (**A**) with 50% of land covered by an intensively managed crop field attractive to pollinators (unsuitable for pollinator nesting and oviposition), and another (**B**) with 50% of the land covered by an intensively managed crop field unattractive to pollinators (unsuitable for pollinator nesting and oviposition). During crop flowering period, some pollinators opt to search for resources in the intensively managed crop field instead of getting such resources from other plants. This scheme ignores potential negative effects of pesticides used in intensively managed crop field on pollinator lifetime.

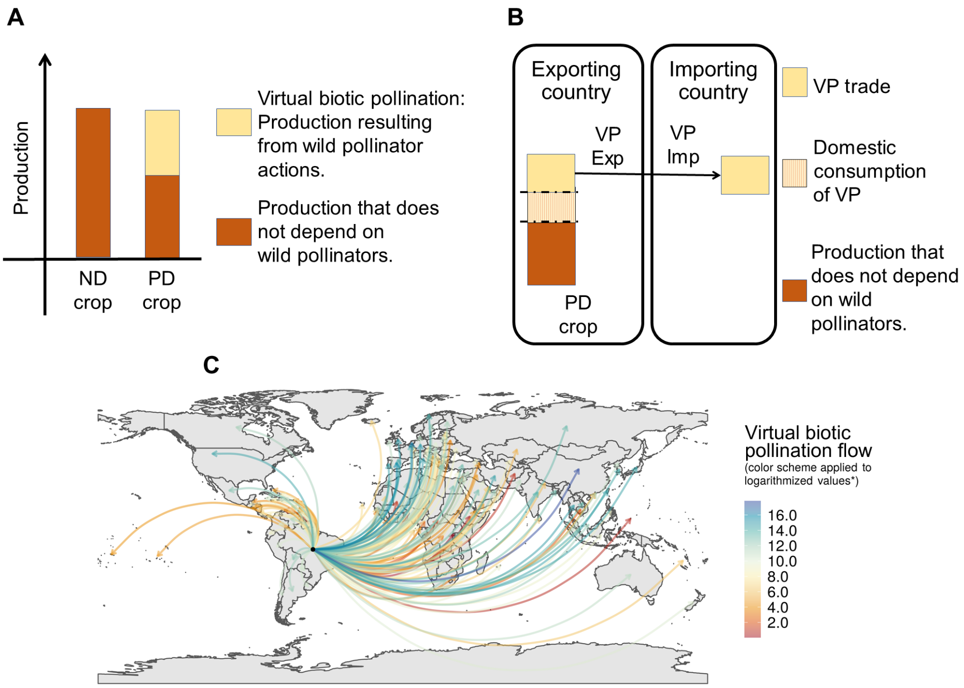

Fig. 2. Schematic representation of virtual pollination flow. (**A**) Pollinator contribution to production is based on both pollinator dependence rate and potential provision of biodiversity-based ecosystem services (i.e., percentage of cropland adjacent to vegetation areas) (ND crop, nondependent crop; PD crop, pollinator-dependent crop). (**B**) Production dependent on pollinator is produced in exporting countries and then goes to domestic consumption and trade (Exp, exportation; Imp, importation). (**C**) Example of a VP flow map (Brazilian exports, 2001–2015). Color scheme is applied to the log-transformed values of exported product (tons). Full online tool with information on all countries' exports and imports can be accessed here (https://virtual-pollination-trade.shinyapps.io/virtual-biotic-pollination-flow/).

action of pollinators that is traded between countries (Fig. 2). This concept can help identify exporting countries in which a strategic investment in biodiversity conservation is crucial for cross-scale sustainability of agriculture.

Pollinator contribution to crop production is estimated here as a function of the pollinator dependence rate of each crop (i.e., proportional yield loss in the absence of pollinators; see (*4*, *26*)] (table S1) and of pollinator access to cropland (see Materials and Methods). As pollinator abundance steeply declines with the distance from natural vegetation areas (*27*), we assumed that all cropland areas located at less than 450 m from patches of natural vegetation (see information on land use classes in table S2) were accessible to pollinators (pixel spatial resolution of 300 × 300 m; see Materials and Methods) (fig. S1) and that natural habitat patches had similar pollinator densities. An online tool with information on all countries' virtual pollination trade can be accessed in https://virtual-pollination-trade.shinyapps.io/virtual-biotic-pollination-flow/.

VP complements the analogous concepts of virtual water and soil flow. While water and soil are abiotic resources, pollination depends on biodiversity, which potentially may capture patterns not detected by virtual water and virtual soil trade. For example, production of some crops uses large quantities of water and vast soil surfaces, but no pollinators [e.g., wind-pollinated staple crops such as rice, wheat, and sugar cane; see (*17*)]; others use smaller extents of soil and less water and are highly dependent on pollinators [e.g., passion fruit, orange, (*4*)]; and finally, others require large amounts of soil surface and pollinators [e.g., sunflower (*28*), soybeans in tropical and temperate regions (*29*–*32*)]. For an example of differences, see VP flow of coffee from Brazil and oil palm from Malaysia to Europe and North America, which require quite different amounts

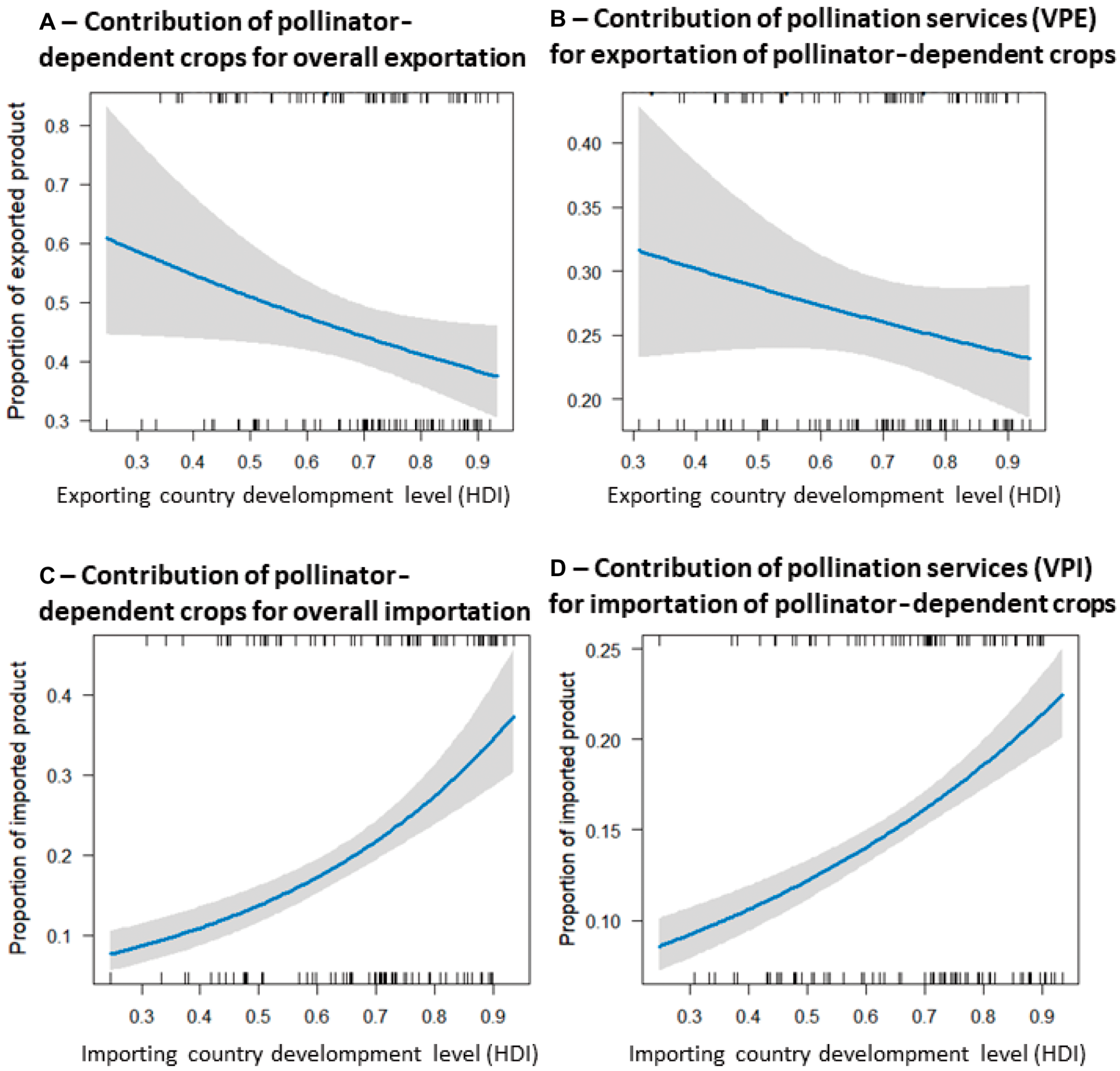

Fig. 3. Effect of country development level on trade of pollination-dependent crops. (**A** and **B**) HDI effect on the proportion of pollinator-dependent crops on overall exportation of agricultural products and on the proportion of pollination services (VPE) on overall exportation of pollinator-dependent crops, respectively. (**C** and **D**) HDI effect on the proportion of pollinator-dependent crops on overall importation and on the proportion of pollination services (VPI) on overall importation of pollinator-dependent crops, respectively. For statistical details, see table S3. Black vertical tick marks on the top and bottom of the graphs represent data density. Full online tool with information on all countries' exports and imports can be accessed here (https://virtual-pollination-trade.shinyapps.io/virtual-biotic-pollination-flow/).

of soil surfaces and virtually export similar amounts of biotic pollination to several countries (fig. S2).

We apply the concept of VP on international trade of 55 pollinator-dependent crops between 2001 and 2015 (https://virtual-pollination-trade.shinyapps.io/virtual-biotic-pollination-flow/) to test if countries' consumption patterns and human development level [here measured as Human Development Index (HDI) (*33*)] are shaping the international trade of biotic pollination services and influencing cropland expansion trends worldwide.

RESULTS AND DISCUSSION

Our results show that pollinator-dependent crops made up more than 50% of the crop products traded at international markets. At country level, the amount of product imported resulting from the activity of pollinators [i.e., VP importation (VPI)] represents up to 19.3% of nations' total crop imports and up to 40.4% of the imported amount of pollinator-dependent crops. As for exports at country level, VP exportation (VPE) contribution varied between 0.4 and 93.8% of the total amount exported and between 1.2 and 94.5% of the amount of pollinator-dependent crops. The fact that for some countries only a small portion of their pollinator-dependent crop trade was dependent on VP possibly is a result of a low proportion of cropland adjacent to naturally vegetated areas (fig. S1). However, because small fragments of natural habitat can also supply crop pollinators (*34*), it is possible that finer spatial resolution information (i.e., pixels <300 m × 300 m) on naturally vegetated areas across the globe would increase this estimate. Nevertheless, many countries could increase the pollinator contribution to exports enhancing pollination services within cropland via ecological intensification practices [e.g., implementation of flower strips and hedgerows (*35*)] that, consequently, could increase cropland productivity of many crop species (*2*, *4*).

VP flow

Our results show that the development level of countries, estimated through the HDI (*33*), strongly influences VP flow. As expected, more-developed countries export and import more than developing countries (figs. S3 and S4). Yet, in less-developed countries, importation of both pollinator-dependent crops and VP is lower than importation of nondependent crops, while exportation of these products is higher (figs. S3 and S4). Consequently, pollinator-dependent crops and pollination services contribute more to exports (and less to imports) in less-developed countries than they do in more-developed countries (Fig. 3).

More-developed countries have a greater proportion of pollination services on their imports (Fig. 3 and fig. S4). Consequently, these countries are more dependent on such services to reach their domestic consumption (Fig. 4). Because international prices of pollinator-dependent crops are on average five times higher than those of nondependent crops (*8*) [e.g., most fruits and vegetables that are components of a healthy diet, and many luxury products, such as cocoa, coffee, and almonds that depend on pollinators; see (*5*)], such differences in countries' contribution to international demand might be due to the differential purchase power of countries with high and low development levels. It is also possible that in more-developed countries, there is more investment in nondependent crops and lower land productivity to sustain pollinator-dependent crops due to less favorable climatic conditions or other environmental characteristics. Importation of less-developed countries is more dependent on staple foods (*36*), being most of such crops not dependent on pollinators (*4*), so diversified food consumption on such countries likely relies on local crop production systems (*37*, *38*).

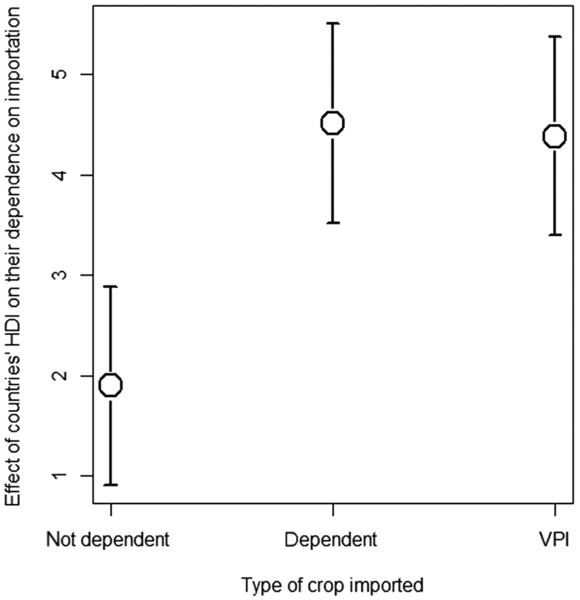

Fig. 4. Effect of country development level on dependence on importation of non–pollinator-dependent crops, pollinator-dependent crops, and virtual pollination imports (VPI). Countries' dependence is here measured by the proportion of importation on national consumption. For statistical details, see table S3.

Our results suggest that the ongoing growth in production of pollinator-dependent crops worldwide (*6*) is motivated by international demand, especially from more-developed regions. Moreover, we show that in countries where pollinators have little contribution for crop production, dependence on importation of VP for national food consumption is large (see fig. S5). In addition, the effect of development level on a country's dependence on imports is more accentuated for pollinator-dependent crops and VP than on imports of other crops (Fig. 4). Overall, these results reinforce that in richer nations, pollinator-dependent products consumed come mostly from other countries, and that estimates of countries' dependence on pollination solely based on its crop production (*9*) do not reflect their overall dependence on pollinators for maintaining food consumption patterns.

Considering that pollination services result from a direct contribution of natural habitat and that their contribution to exports of pollinator-dependent crops declines with the country's development level (Fig. 3B), our results suggest that developed countries are virtually importing pollination services from countries that sustain pollination services with natural habitat. Conservation of natural areas has opportunity costs (e.g., when a landowner is enforced to preserve natural areas by conservation policies/laws) and/or real costs for governments and farmers (e.g., when protection management is stimulated by economic instruments, such as Payment for Ecosystem Services) that could be supported by higher market price. However, as international crop price is defined regardless of environmental costs in exporting countries, the lack of economic incentives or environmental law compliance for biodiversity conservation could result in harmful practices to pollinators (e.g., intensification of conventional agriculture).

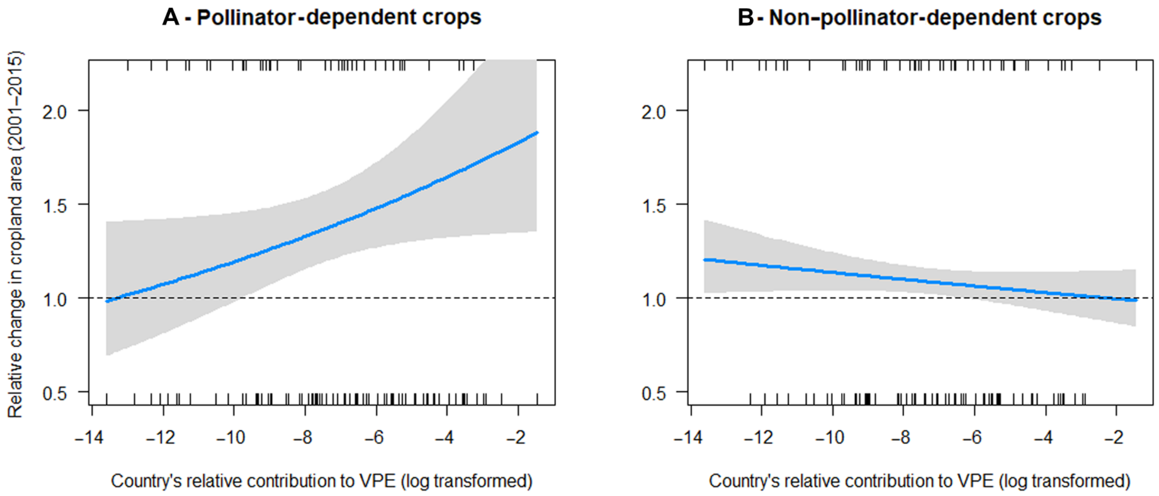

Fig. 5. Effect of virtual pollination exportation on cropland expansion. Graphs present the effect of countries' contribution to global VPE on their cropland expansion (between 2001 and 2015) of pollinator-dependent crops (**A**) and non–pollinator-dependent crops (**B**). Statistical details are presented in table S3. Black vertical tick marks on the top and bottom of the graphs represent data density. Horizontal dashed line represents no change in cropland and pollination service provision.

Pollination demand and cropland expansion

Cropland expansion is one of the main drivers of pollinator and overall biodiversity decline (*7*, *10*) and is still a common strategy to increase crop production in developing countries. Here, we show that countries that most contributed to exportation of products that directly result from the action of pollinators (VPE) have greater rates of expansion of pollinator-dependent crop areas (Fig. 5A), an effect not detected for nondependent crops (Fig. 5B), which suggests that increases in exportation are associated with replacement of other ecosystems by cropland. Such trend is likely associated with increased areas of monocultures and, consequently, greater isolation from natural habitat. Countries whose exports are most dependent on VP (those with lower HDI; Fig. 3) have the greatest declines in the proportion of cropland receiving pollination services (Fig. 6). These results suggest complex interactions and feedbacks between economy, agriculture, and environment that may threaten the sustainability of pollinator-dependent crop production in developing countries. Agricultural expansion is likely to increase isolation of croplands from natural habitat and to cause declines in pollinator-dependent crop yields, which in turn may accelerate the conversion of new natural areas to agriculture to sustain production in response to the international demand.

The increasing demand for biotic pollinator-dependent crops (*6*) can also stimulate transition from traditional small-scale diversified agricultural production systems to large-scale simplified agroecosystems [e.g., coffee (*39*)]. Together with the fact that such demand is mostly stimulated by more-developed countries (Fig. 3), our results indicate that food consumption patterns of developed countries are being supported not only by abiotic natural resources (land and water) (*15*, *17*) but also by biodiversity (pollinators) of other countries. These results highlight that both importing and exporting countries are responsible and vulnerable to the decline of biodiversity-based ecosystem services.

Making agriculture more sustainable can involve investment in precision farming (e.g., the use modern technology to support more efficient management) to increase land productivity rather than cropland expansion, or ecological intensification of farming practices to boost ecosystem services such as crop pollination [e.g., intercropping hedgerows and flower strips (*35*, *40*, *41*)]. Recent environmental protection policies have been implemented in several developed regions, e.g., ecological focus areas in the European Union's Common Agricultural Policy (CAP) (*42*) and Environmental Protection Agency Actions to Protect Pollinators in the United States (*43*). Yet, increased demand of pollinator-dependent products in such regions is being supported by wild pollinators from developing countries, where application of conservation programs is rare (*44*) and information on pollinators is scarce (*10*). Thus, to make consumption patterns more sustainable, populations and governments need to consider sustainable development practices outside their own country. Strategies that consider socioeconomic benefits of nature conservation are essential to avoid ecosystem depletion in exporting countries, which apart from supporting global food demand are dependent on their own natural resources to reduce the country's poverty and for local food security (*45*). VP flows allow for the identification of connections between trading partners, and such interdependencies may help to create new international collaborative arrangements based on sharing responsibilities for protection of the biodiversity.

International trade of agricultural products shape both virtual pollination and virtual water flows between countries. However, flow patterns are different for water and pollination and result in distinct implications for ecosystem service conservation and global governance. Exportation of virtual water from water-rich to water-poor countries can be considered an alternative to the difficult endeavor of trading real water internationally and a win-win process to improve global water use and security (*17*). In contrast, international trade is linked to a decrease in the provision of pollination services in less-developed exporting countries, threatening the sustainability of pollinator-dependent crop production and commerce. Collaborative global governance strategies that go beyond the rules of free market systems are needed to obtain synergies between virtual pollination trade and biodiversity conservation.

Economic instruments to promote biodiversity conservation, such as Payments for Ecosystem Services, are scarce and have still limited geographical scope (*46*). Furthermore, these instruments have been mostly implemented via compensation for past environmental

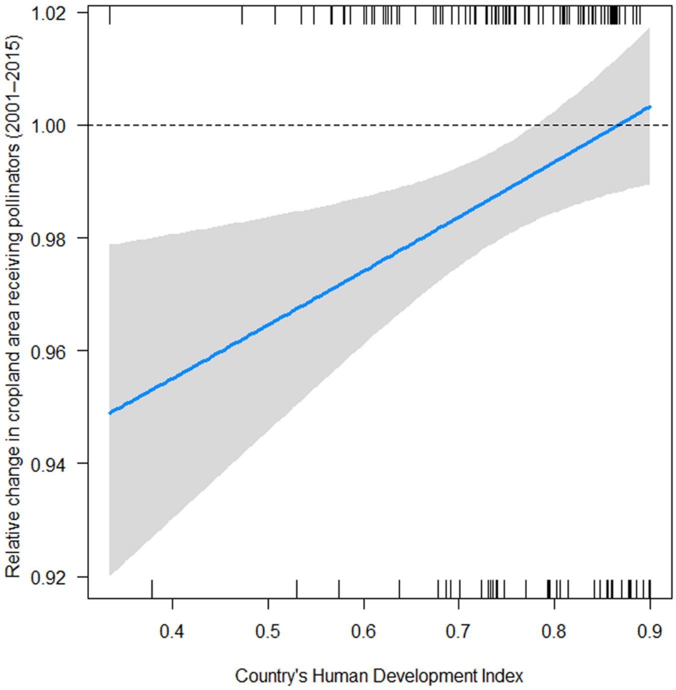

Fig. 6. Effect of development level of exporting countries on the provision of pollination services (2001–2015). Change in pollination provision was calculated between 2001 and 2015 on the basis of total area of cropland that was sufficiently near to natural vegetation (i.e., pixel center at less than 450 m) to be considered to receive pollination services (see Materials and Methods). Statistical details are presented in table S3. Black vertical tick marks on the top and bottom of the graphs represent data density. Horizontal dashed line represents no change in cropland and pollination service provision.

impacts, which have been suggested to endorse habitat destruction, especially if not accompanied by effective enforcement and sanctioning (*47*). We argue that by improving estimates of countries' dependence on the biodiversity of other nations, VP has the potential to become an important tool for international policy. Information on VP flows could contribute to more sustainable supply chains based on the trade of certified products and to internalize costs associated with ecosystem preservation (*48*). Other potential policies could involve the transfer of financial resources to developing countries for developing or importing new technologies with low impact on pollinators (*10*, *41*), lowering deforestation rates in farming regions [see Brazil's Soy Moratorium (*49*)], or rewarding farmers for the ecosystem services they generate through conditional payment or access to specific credit lines (*47*).

Concluding remarks

By taking international trade into account, our analysis of VP flow shows that socioeconomic benefits of biodiversity-based ecosystem services (pollination) are distributed globally across country boundaries and are socially and economically asymmetric. Further improvements and applications of this tool may involve more detailed economic evaluations of virtual pollination flow, also taking into account market values, implementation, and opportunity costs associated with pollinator-friendly practices. As different crops are pollinated by different pollinator species (*50*), improvements may also involve evaluations of the contribution of particular ecosystems or specific functional groups of pollinators to exportation. Nevertheless, it is clear that quantifying virtual pollination flow can help develop new global socioeconomic policies. The recognition of the mutual dependence of countries on biotic pollination can help develop strategies to protect biodiversity in agricultural systems linked to export markets, involving shared responsibility, economic rewards, and/or biodiversity conservation enforcement across regions.

MATERIALS AND METHODS

We used information on cropland areas, trade, and crop production of 55 pollinator-dependent crops and 45 nondependent crops at country level between 2001 and 2015 taken from the Food and Agriculture Organization of the United Nations (FAO) (*51*), one of the most comprehensive and available global dataset (tables S1 and S2). Information on cropland area and production per crop species and country was gathered from the FAO Crops dataset (http://fao.org/faostat/en/#data/QC), and trade information was gathered from the FAO Detailed Trade Matrix (http://fao.org/faostat/en/#data/TM), a dataset including trade information for exporting countries and their respective trading partners. We gathered information from 235 world nations. Regional data were available for China (i.e., mainland, Hong Kong, Macao, and Taiwan), so they were aggregated to account for data at the national level. As calculations based on trade and consumption in countries that are very small can be very sensitive to lack of precision in trade information, we excluded such countries (i.e., those with agricultural areas lower than 100.000 ha) from the analyses. We also excluded countries that had no information on the variables used in our analyses: *HDI*, population, cropland area, trade (exportations or importation), and crop production. Seven countries were also excluded because most pollinator-dependent crop information (>70%) was available for groups of crops (and, hence, it was not possible to assess its pollination dependence). Three countries were removed because of detected inconsistency in dataset, i.e., exportation crop volume higher than national agricultural production (Costa Rica) and discontinuity of data due to unification or separation of regions (Sudan and South Sudan). After applying the selection criteria, we ended up with 119 countries for statistical analysis. For each of these countries, we calculated cropland area and production in 2001 and 2005 for pollinator-dependent (all with pollinator dependence rate larger than zero; see below) and non–pollinator-dependent crops.

Pollinator dependence rates (*D*)

A crop was considered as pollinator dependent when its yield (i.e., part of the plant used for consumption) can be increased by pollinators at some level, and as nondependent crop when its yield is not known to be influenced by pollinators, even if dependent on pollinators for plant reproduction (e.g., seed production of carrot and onion). Information on the contribution of crop pollination to individual crop species [i.e., pollinator dependence rate, which is typically estimated by comparing the difference in yield with and without exposure to flower visitors (*52*)] was extracted from previous works (see details on sources in table S1). Although pollination dependence varies across different cultivars and breeding types (*28*), due to lack of information at variety level, we assumed that pollination dependence level was similar across cultivars of a single crop species. It is, however, important to highlight that information on pollinator contribution is not available for several crops and that many aggregated classes of crops that may include pollinator-dependent crops were not considered pollinator dependent. Therefore, we are underestimating the value of the contribution of wild pollinators to crop production.

Pollination service provision

Pollinator contribution to crop production varies across regions, depending not only on plant's dependence rate but also on landscape characteristics that regulate pollinator availability. A large number of studies from multiple crops all over the world have shown that pollinator density and diversity steeply decline with the distance from natural vegetation areas [see (*27*)]. Hypothetically, a crop species can have the same production in two countries with different contributions of pollinators. For example, for a given crop with 25% pollinator dependence rate and a maximum productivity of 1 ton/ha, in a region with high provision of pollination service, pollinators produce ca. 0.25 ton (i.e., 25%), while in regions with absence of such service, farmers would have to increase cropland area or intensify the productivity to produce the same 1 ton. Here, we assume that cropland areas in proximity to natural or seminatural vegetation areas [up to 600 m; see (*27*)] benefit from pollination service provision, while isolated areas only receive an insignificant portion of such service that do not result in any benefit (more than 600-m away) and applied a correction in our analyses based on a metric of pollination service provision to agricultural areas: the proportion of cropland area adjacent to vegetated areas in a given country.

The analyses were carried out using the land use cover maps from the Climate Change Initiative of Land Cover (CCI-LC) product of the European Space Agency at 300-m spatial resolution on an annual basis from 2001 to 2015 (*53*) with 22 general land use cover classes: (1) cropland (rainfed); (2) cropland (irrigated or postflooding); (3) mosaic cropland (>50%)/natural vegetation (tree, shrub, and herbaceous cover) (<50%); (4) mosaic cropland (<50%)/natural vegetation (tree, shrub, and herbaceous cover) (>50%); (5) tree cover, broadleaved, evergreen, and closed to open (>15%); (6) tree cover, broadleaved, deciduous, and closed to open (>15%); (7) tree cover, needle leaved, evergreen, and closed to open (>15%); (8) tree cover, needle leaved, deciduous, and closed to open (>15%); (9) tree cover and mixed leaf type (broadleaved and needle leaved); (10) mosaic tree and shrub (>50%)/herbaceous cover (<50%); (11) mosaic herbaceous cover (>50%)/tree and shrub (<50%); (12) shrubland; (13) grassland; (14) lichens and mosses; (15) sparse vegetation (tree, shrub, and herbaceous cover) (<15%); (16) tree cover, flooded, fresh, or brackish water; (17) tree cover, flooded, and saline water; (18) shrub or herbaceous cover, flooded, and fresh/saline/brackish water; (19) urban areas; (20) bare areas, (21) water bodies, and (22) permanent snow and ice. The classes 1 to 4 were classified as cropland areas, and classes 5 to 18 as natural areas. Class 3 was assumed to have 75% of cropland, and class 4 was assumed to have 25% of cropland area. All analyses on the extraction of "crop area" pixels that are near (i.e., centroid equal or less than 450 m) to "natural area" pixels (we used a buffer of 2 pixels) were done in the Google Earth Engine platform (*54*).

For many crops, pollinator abundance (and flower visitation) can decline to less than half of its maximum potential within a few hundred meters from natural habitat (~500 m) (*12*, *27*). Therefore, for each country, we used landscape information to estimate the percentage of cropland pixels that is near (i.e., pixel center at less than 450 m) to natural vegetation areas. It is important to highlight that, given the limited spatial resolution of global country-level data on landscape, our analyses are not able to consider pollination services from small patches of natural habitat (i.e., <300 × 300 m), margins with ruderal vegetation, and low-intensity management gardens (*34*). Therefore, the calculation using the information on adjacent natural areas described above will lead to further underestimation of wild pollinators' contribution to crop production.

Calculating virtual pollination flow

VP is here defined as the proportion of overall crop production resulting from the action of pollinators (Fig. 2). We estimate the contribution of pollinators to crop production assuming that pollinator-dependent crop yield is higher where pollinators are more likely to be present, i.e., cropland areas next to natural areas. National production (NP_{ij})(t) of a given crop i in a given country j results from production in cropland that receives pollination services (NP_{ij}) and cropland that does not receive pollination services ($Cnpoll_{ij}$) (Eq. 1). The pixel productivity (y_{ij}) (t/pixel), which depends on the crop's pollinator-dependence rate (D_i), can be estimated as the ratio between national production (NP_{ij}) and the sum of cropland receiving ($Cpoll_j$) or not receiving ($Cnpoll_j$) pollination services weighted by its relative productivity levels (Eq. 2)

$$\mathrm{NP}_{ij} = \mathrm{Cnpoll}_j * (1 - D_i) * y_{ij} + \mathrm{Cpoll}_j * y_{ij} \tag{1}$$

$$y_{ij} = \frac{\mathrm{NP}_{ij}}{[\mathrm{Cnpoll}_j * (1 - D_i) + \mathrm{Cpoll}_j]} \tag{2}$$

Overall production due to biotic pollination (PB_j) (t/year) in a given country j can be estimated by multiplying the crop yield of each crop i obtained from cropland area that receives pollination services (y_{ij}) (t/pixel) by the dependence rate (D_i) and by the number of pixels receiving pollination services (p_j), (Fig. 2A). Overall crop production due to biotic pollination (PB) was calculated using information extracted from the FAO over 2001–2015 (*51*). For statistical analysis, we used the average of PB during this period

$$PB_j = y_j * p_j * D_i \tag{3}$$

To assess the VP flow (exportation and importation), similarly to VP production, the same procedure was applied for the fraction of each crop that was exported (VPE) and imported (VPI). For trade of oil crops in which information was provided as oil amount, we used information of oil content (or oil extraction rate) to convert the oil volume into tons of raw products (table S1). For statistical analysis, we used yearly average data for both virtual pollinator exportation and importation over 2001–2015.

A country's dependence on importation is defined here as the proportion of domestic consumption of a given product that is imported. To assess countries' dependences on importation of VP, domestic consumption of such services in a given country j (C_j) (ton/year) was calculated as a sum of its crop production dependent on biotic pollination (PB_j) (ton/year) and its net values of international trade of VP ($VPE_j - VPI_j$) (ton/year) (Eq. 4). Thus, domestic consumption also can be considered as the pollination footprint of countries. The dependence of a given country j on international trade of VP indicates, then, the level of domestic consumption of such service that is met by importation. Thus, dependence of a given country j (DVP_j) was calculated by the ratio between VPI (VPI_j) (ton/year) and domestic consumption (C_j) (ton/year) (Eq. 5). These estimates were also calculated for consumption of pollinator-dependent crops, nondependent crops, and overall crops (dependent and nondependent crops). Calculations of consumption and dependence were done using annual average of crop production and trade (importation and exportation) at country level over 2001 and 2015

$$C_j = \mathrm{PB}_j + \mathrm{VPI}_j - \mathrm{VPE}_j \tag{4}$$

$$\mathrm{DVP}_j = \frac{\mathrm{VPI}_j}{C_j} \tag{5}$$

The calculations of all variables associated to VP and statistical analysis were carried out using R (*55*). Online flow map of VP flow between all countries from 2001 to 2015 were built using R (https://virtual-pollination-trade.shinyapps.io/virtual-biotic-pollination-flow/).

Country development level

To account for countries' development level, we used the HDI, a widely used indicator in academic and political scopes that encompass three key dimensions of human development: living standard, knowledge, and health. Information on HDI was gathered from the United Nations Development Programme (*33*). The development level of a given country *j* ($\mathrm{HDI_j}$) was calculated by the annual average of its HDI between 2001 and 2015.

Statistical analyses

All statistical analyses were carried out with R (*55*) and the R package "lme4" (*56*).

To verify whether VP flow is affected by country's development level (*HDI*), we first focused on exportation. We used generalized linear models (GLMs) assuming a gamma error distribution and considered two types of exportation: (i) the contribution of pollinator-dependent crops for the country's overall exports (i.e., proportion made by pollinator-dependent crops) and (ii) the contribution of VPE for country's exportation of pollinator-dependent crops (i.e., VPE/total pollinator-dependent exports). The interaction between *HDI* and *type of export* was included as a fixed term. To account for any variation caused by the country's production area on international market flow, we used *average cropland area* as a control explanatory variable. To better understand the patterns detected in such analyses, we evaluated how *HDI* and *countries' land area* affect the relative contribution of each country to global exports (country value/global value) of nondependent crops, pollinator-dependent crops, and VPE. Such comparison between pollinator-dependent versus nondependent products is important to detect if trends are merely a reflection of the general exportation pattern.

We then repeated the analyses for importation, using two response variables: (i) the contribution of pollinator-dependent crops to overall imports and (ii) the contribution of biotic pollination services to imports of pollinator-dependent crops (i.e., VPI/total pollinator-dependent crops imported). We used a GLM (gamma distribution with log link function). As a country's population will have a strong influence on food demand, we used the *average population size* over 2001–2015 as a control explanatory variable (table S2). Similarly to what was done for exportation, to better understand the patterns detected in such analyses, we evaluated how the relative contribution of each country to global importations (country value/global value) of nondependent crops, pollinator-dependent crops, and VPI was affected by *HDI* and *population size*.

To check whether more-developed countries had a greater dependence on importation to reach their domestic consumption of VP, we used GLM with countries' dependence on VPI (*DVP*) as response variable and countries development level (*HDI*), country's cropland area, and population size as explanatory variables (table S2). To compare with the general pattern of countries dependence, we also assessed the nations' dependence on imports of pollinator-dependent and nondependent crops. Population size and cropland area were log transformed to normalize residuals.

To check whether countries that are not so dependent on pollinators for production do depend on pollinators for consumption (via importation), we also evaluated how the dependence on pollinators for production was related (gamma error distribution, log link function) with the dependence of overall consumption on importation of biotic pollination (*VPI*).

To verify whether countries that most contributed to VP flow are also those that have greatest rates of expansion of pollinator-dependent cropland, we analyzed the effect of foreign pollinator demand (i.e., *VPE*) on cropland expansion (i.e. relative change in cropland area between 2001 and 2015) using GLMs assuming gamma error distribution (log link function). For comparison, we repeated the process with nondependent crops.

We also assess the effect of development level of exporting countries on the change of provision of pollination services through time (2001–2015). Change in pollination provision was calculated between 2001 and 2015, and all croplands near to natural vegetation (i.e., pixel central at less than 450 m) were considered to receive pollination services. For all analyses related with cropland expansion, Uruguay was a very influential point due to the fast expansion of soybean fields between 2001 and 2015. Therefore, we repeated all analyses with and without this country to ensure that the overall patterns were maintained (we report the results based on the full dataset).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/11/eabe6636/DC1

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