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International food trade benefits biodiversity and food security in low-income countries

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To achieve the United Nations Sustainable Development Goals related to food security and biodiversity, understanding their interrelationships is essential. By examining datasets comprising 189 food items across 157 countries during 2000–2018, we found that high-income countries exported more food to low-income countries than they imported. Many low-income countries, especially those with biodiversity hotspots, increasingly acted as net importers, suggesting that imports from high-income countries can benefit biodiversity in low-income countries. Because low-income countries without hotspots have rapidly raised their amounts of food exports to hotspot countries, such exports might help further reduce negative impacts on biodiversity. The increasing complexity of food trade among countries with and without biodiversity hotspots requires innovative approaches to minimize the negative impacts of global food production and trade on biodiversity in countries worldwide.

As the world pursues the ambitious United Nations (UN) Sustainable Development Goals (SDGs), including food security and biodiversity, it is important to understand their interrelationships[1–3]. The 17 SDGs were adopted by the UN General Assembly in 2015 to maintain the sustainability and prosperity of the planet[1]. Quantitative information on the connections among SDGs is needed to assess whether and how the multiple SDGs can be achieved simultaneously[2,4,5]. Furthermore, as the UN aims to achieve SDGs everywhere, it is crucial to evaluate how SDGs in one place are affected by other places through telecouplings (environmental and socio-economic interactions across distant systems, such as international trade)[6–8]. Increasing food availability (a key component of food security) while sustaining biodiversity is important for global sustainability[9–13]. Thus, identifying the relationships between global food production, trade and biodiversity is essential to simultaneously achieve both SDGs 2 (food security) and 15 (biodiversity)[1,2,12].

With continuous population and income growth[11,14] as well as uneven distribution of food supply and demand, international food trade is essential for ensuring food availability[15], improving nutrient access[16] and meeting rising food demands[9,17]. Many countries depend on food imports to meet their growing demands[18–20], but rapid increases of international food trade can lead to displaced environmental impacts[11,21,22]. Producing food for exports causes changes in land use and land cover[13,19,23] and exerts pressure on biodiversity in exporting countries[20,21,23–25].

Biodiversity is also distributed unevenly across space[26]. The impact of international food trade on biodiversity is therefore highly dependent on the origins of food production[10,19,20]. It is widely recognized that importing food from tropical, low-income countries to high-income countries is worsening biodiversity in low-income countries according to studies at the national, continental and global scales[20,21,23]. However, little is known about the biodiversity implications of food exports from high-income countries to low-income countries, despite the fact that some high-income countries have biodiversity hotspots (areas with high concentrations of biodiversity in many types of habitats, such as forests and grasslands[27,28]), while some low-income countries do not have biodiversity hotspots. Failing to recognize hotspot countries with high income and non-hotspot countries with low income may lead to biased results about the impacts of food trade on biodiversity worldwide. Thus, understanding food trade among countries with and without biodiversity hotspots is crucial for uncovering the implications of international food trade for global biodiversity.

To address the fundamental knowledge gaps, we divided 157 countries with relevant data into three categories regarding their biodiversity: high-hotspot, low-hotspot and non-hotspot countries. Specifically, we identified 64 high-hotspot countries (countries where biodiversity hotspots account for more than 50% of terrestrial lands), 50 low-hotspot countries (biodiversity hotspots < 50%) and 43 non-hotspot countries (countries with no biodiversity hotspots) (Extended Data Fig. 1 and Supplementary Table 1). We also classified the countries in each category as low-income (including low, low-middle and upper-middle income) and high-income according to the World Bank's income classification[29]. On the basis of the framework of telecoupling[30–32], these classifications help with analysing food trade among countries with different concentrations of biodiversity and levels of economic development. Our food dataset contains relevant annual information for 189 food items, including 145 crops, from 2000 to 2018 (Supplementary Table 2).

Results

Food trade between high- and low-income countries. Our results indicate that high-income countries were net food exporters, while low-income countries were net food importers during 2000–2018 (Figs. 1 and 2 and Extended Data Fig. 2). Among the exports from high-income countries to low-income countries, almost all (97.1%) went to hotspot countries. Specifically, hotspot countries with low income received 97.7% of the exports from high-income hotspot countries to low-income countries (Fig. 2 and Supplementary Table 3). Of exports from high-hotspot countries with high income to low-income countries, 33.2% and 54.7% went to high- and low-hotspot countries with low income, respectively.

Over half of exports (57.0%) from low-income countries went to other low-income countries rather than to high-income countries (Fig. 2 and Supplementary Table 3). Of these, the destinations of

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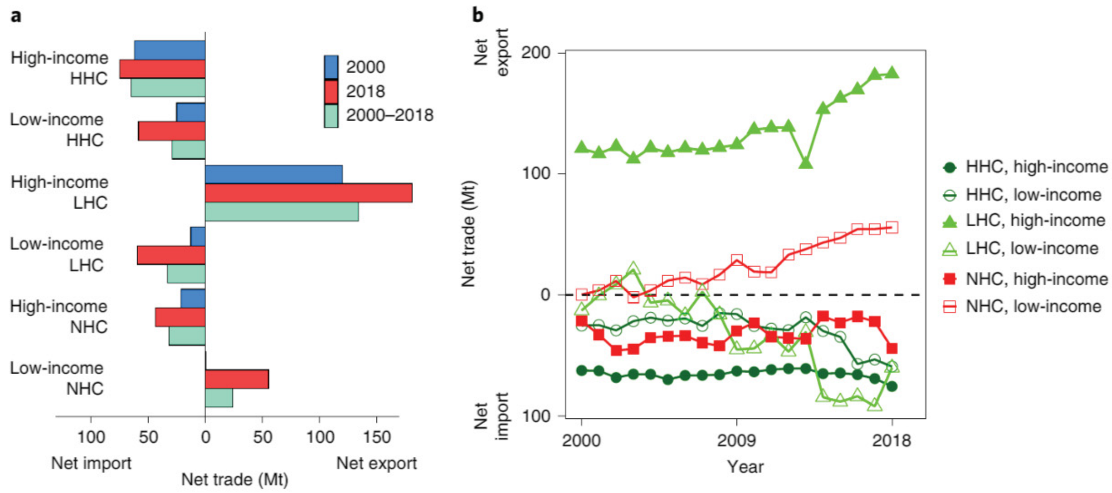

Fig. 1 | Quantity of net food trade between high-hotspot countries, low-hotspot countries and non-hotspot countries with high and low income. **a**, Blue indicates net food trade in 2000, red indicates net food trade in 2018 and cyan indicates average net annual food trade from 2000 to 2018. The net amounts of food trade in each group did not linearly increase or decrease over time. The net amounts of food trade in 2000 and 2018 were lower or higher than those in other mid-years. **b**, The amounts of net food trade between high- and low-income countries in high-hotspot countries (HHC), low-hotspot countries (LHC) and non-hotspot countries (NHC) from 2000 to 2018. Non-hotspot countries are indicated by red, high-hotspot countries by dark green and low-hotspot countries by light green.

59.0% and 43.3% of exports from hotspot and non-hotspot countries with low income were other low-income countries. In other words, high-income countries received less than half of the exports from low-income hotspot countries and more than half of the exports from low-income non-hotspot countries. These results were complemented by the different population sizes between high- and low-income countries. In our analyses, the number of low-income countries ($n=110$) was 2.3 times higher than that of high-income countries ($n=47$). Low-income countries had 81.7% of the total population, while high-income countries had 18.3% (Fig. 3 and Supplementary Table 4).

The role of major net exporters. Low-hotspot countries with high income (for example, the United States and France) were the main contributors to international food trade as net exporters. Over the period 2000–2018, low-hotspot countries with high income accounted for 34.5% of total global exports (Extended Data Fig. 2). Among the exports from low-hotspot countries with high income, 56.9% were destined for low-income countries. Specifically, the United States and France accounted for 76.6% (158.2 Mt yr^{-1} during 2000–2018) of food exported from low-hotspot countries with high income (206.6 Mt yr^{-1}). Within France, non-hotspot areas accounted for 94% of the total harvested areas with 95.5% of the total crop production, while hotspot areas in southern France accounted for only 6% of harvested areas with 4.5% of the total crop production in 2010 (Extended Data Fig. 3). In the United States, crop production per capita in hotspot areas (5,265 kg per capita in 2010; 95% confidence interval (CI), 4,235.7–6,294.4) had only 29% of the country's average (18,166 kg per capita; 95% CI, 16,647.2–19,685.4) (Supplementary Data 1). In contrast, in low-hotspot countries with high income, Saudi Arabia and Israel were net importers, and their hotspot areas accounted for 28.2% and 77.9% of the total harvested areas in 2010, respectively. Hotspot areas in Saudi Arabia (368.9 kg per capita; 95% CI, 32.1–705.6) and Israel (933.1 kg per capita; 95% CI, 67.8–1,798.4) also had 14.5% and 2.3% lower per capita crop production than the country averages (422.5 kg per capita; 95% CI, 138.6–706.4; and 955 kg per capita; 95% CI, 76.3–1,833.8), respectively.

Additionally, non-hotspot countries with low income (for example, Ukraine and Romania) played an increasingly important role as net food exporters (with an average net food export of 24.4 Mt yr^{-1} during 2000–2018) (Figs. 1 and 2). They exported 3.2% (6.3 Mt) of their food production in 2000 but 18.7% (68.8 Mt) in 2018 (Supplementary Table 4). Such exports freed much area for production in hotspot countries. For instance, high-hotspot countries with high income saved agricultural areas of 30,362 km^2 (33.1% of the territory of Portugal) in 2018 (Supplementary Table 5). High-hotspot countries with low income saved agricultural areas of 6,054 km^2 (55.9% of the territory of Jamaica) in 2000 and increased this to 99,246 km^2 (approximately the territory of Cuba) in 2018 (Supplementary Table 5). In non-hotspot countries with low income, Ukraine rapidly increased the amount of food exported from 2.1 Mt in 2000 to 45.9 Mt in 2018, and this country also had high crop production per capita (Fig. 3). Ukraine had 4,154.9 kg per capita (95% CI, 3,858.6–4,451.1) of crop production in 2010 (Supplementary Data 1).

Non-hotspot countries with low income had lower agricultural intensification than other types of countries, which suggests that food imports from non-hotspot countries with low income further reduce biodiversity threats from food production in hotspot countries (Fig. 4). Fertilizer use per unit of agricultural land in non-hotspot countries with low income (1.2 t km^{-2}) was 77.0% lower than in low-hotspot countries with low income (5.4 t km^{-2}) and 73.8% lower than in high-hotspot countries with low income (4.8 t km^{-2}) in 2018 (Fig. 4a). Pesticide use per unit in non-hotspot countries with low income (0.010 t km^{-2}) was 92.1% lower than in low-hotspot countries with low income (0.131 t km^{-2}) and 85.4% lower than in high-hotspot countries with low income (0.072 t km^{-2}) in 2018 (Fig. 4b). In 2017, freshwater withdrawal (3,964 m^3 km^{-2}) for agricultural production in non-hotspot countries with low income was 94.8% lower than in low-hotspot countries with low income (75,648 m^3 km^{-2}) and 96.7% lower than in high-hotspot countries with low income (119,643 m^3 km^{-2}) (Fig. 4c). While agricultural areas in non-hotspot countries with low income increased by 1.5% from 2000 to 2018, agricultural areas in low-hotspot countries with low income and high-hotspot countries with low income increased by 0.3% and 5.4%, respectively (Fig. 4d).

High-hotspot countries as net importers. High-hotspot countries with low income were net food importers (29.0 Mt yr^{-1} of average net annual food imported) from 2000 to 2018 (Fig. 1 and Extended Data

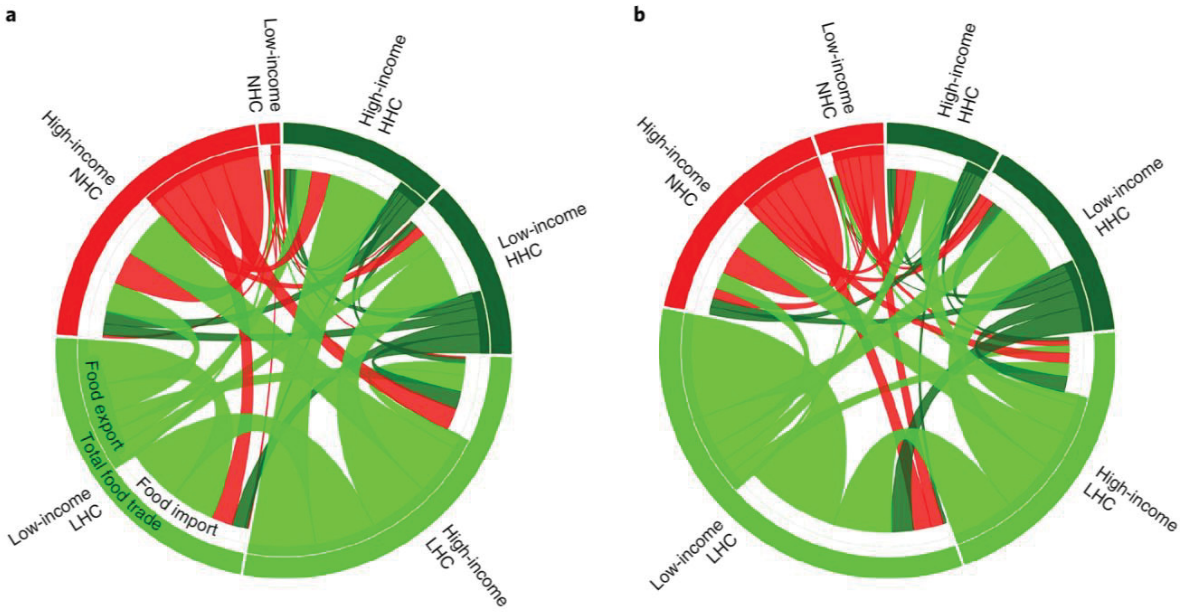

Fig. 2 | Annual food flows (Mt). a,b, Food flows between high-hotspot countries, low-hotspot countries and non-hotspot countries with high and low income in 2000 (**a**) and 2018 (**b**). Non-hotspot countries are marked by red, high-hotspot countries by dark green and low-hotspot countries by light green. The arc length of an outer circle indicates the sum of food exported and imported in each group. The arc length of a middle circle refers to the quantity of food exports. The inner arc length shows the quantity of food imports. The raw data are from the UN Food and Agriculture Organization (FAO)[52].

Fig. 2). For instance, Mexico, Vietnam and Morocco were major net importers from 2000 to 2018. Moreover, Vietnam alone increased the amount of food imported from 1.2 Mt in 2000 to 23.2 Mt in 2018. Vietnam had 1,292.5 kg per capita (95% CI, 1,188–1,397.1) of crop production in 2010, whereas Malaysia, a net exporter, had 7,871 kg per capita (95% CI, 5,532.6–10,209.4) (Extended Data Fig. 3 and Supplementary Data 1). Such imports are particularly important for reducing agricultural impacts on biodiversity in high-hotspot countries because 78.1% of high-hotspot countries had over 90% of their terrestrial area as biodiversity hotspots, and approximately 95% of high-hotspot countries' harvested area was located in biodiversity hotspots (Extended Data Figs. 3 and 4). Over the same period, high-hotspot countries with low income accounted for 51.6% (98.3 Mt yr^{-1} during 2000–2018) of the total food imports among all high-hotspot countries (190.4 Mt yr^{-1}) (Supplementary Table 3). The amount of food imported from low- and non-hotspot countries to high-hotspot countries with low income was equal to the output of roughly 19.1% of the annual agricultural area (848,573 km^2, approximately the sum of the territory of Thailand and Malaysia) in high-hotspot countries with low income (Supplementary Table 5).

Imports to high-hotspot countries with high income (65.3 Mt yr^{-1} of average net annual food imported during 2000–2018) can also help further reduce negative impacts on biodiversity because agricultural intensification in high-hotspot countries with high income was higher than in other types of countries, except for fertilizer use in non-hotspot countries with high income (Fig. 4). For example, fertilizer use per unit of agricultural land in high-hotspot countries with high income (7.1 t km^{-2}) was 48.4% higher than in high-hotspot countries with low income (4.8 t km^{-2}) in 2018 (Fig. 4a). Pesticide use per unit in high-hotspot countries with high income (0.258 t km^{-2}) was 260.4% higher than in high-hotspot countries with low income (0.072 t km^{-2}) in 2018 (Fig. 4b). In 2017, freshwater withdrawal (178,061 $m^3 km^{-2}$) for agricultural production in high-hotspot countries with high income was 48.8% higher than in high-hotspot countries with low income (119,643 $m^3 km^{-2}$) (Fig. 4c). Food imports may therefore decrease biodiversity threats in high-hotspot countries with high income, as, without food imports, more agricultural land in these countries would be used or intensified for domestic food production. The amount of food imported from low-hotspot and non-hotspot countries to high-hotspot countries with high income saved approximately 17.7% of annual agricultural area (150,534 km^2, approximately half of the territory of Italy) in high-hotspot countries with high income (Supplementary Table 5).

Since our hotspot classification did not capture the different role of each country's net trade (export–import) within the same hotspot group, we calculated the amounts of net food trade and land saved at a country level as well as per capita crop production and harvested areas at a hotspot level (Supplementary Data 1 and Extended Data Fig. 3). This country-level calculation helped identify which high-hotspot countries were the principal beneficiaries of international food trade (for example, Mexico and Vietnam). Additionally, although high-hotspot countries acted as net importers from 2000 to 2018, Indonesia and Malaysia increasingly played important roles as net exporters, partly because of the expansion of oil palm for high-income countries[33].

Linkages between hotspot areas and international food trade. Panel data analyses for three different periods (2000–2008, 2009–2018 and 2000–2018) identified changes in the role of biodiversity hotspots for global food trade flows over time. The percentage of biodiversity hotspots out of the total land area was positively associated with the quantity of both food exports and imports from 2000 to 2008, but this variable became insignificant from 2009 to 2018 (Supplementary Table 6). This result indicates that, from 2000 to 2008, countries with higher percentages of biodiversity hotspot areas tended to have more food exports and imports, but this relationship weakened over the period 2009–2018. Our results thus showed that low- and non-hotspot countries played an increasingly important role in international food trade.

Our panel data analyses also included environmental and socio-economic factors to avoid spurious effects. The results indicate that countries with larger agricultural areas tended to produce more food for both domestic consumption and exports, whereas countries with smaller agricultural areas tended to import more food. This

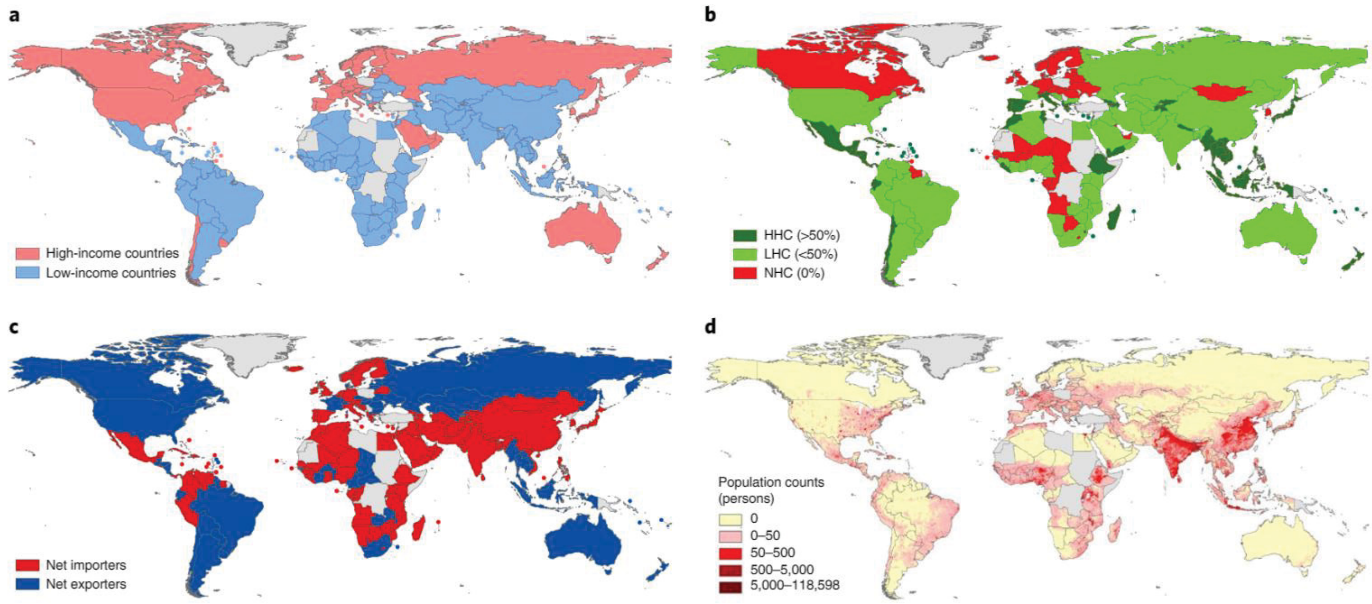

Fig. 3 | Spatial distributions of income, hotspots, net trade (export–import) and population. a, High- and low-income countries. **b**, High-, low- and non-hotspot countries. **c**, Net exporting and importing countries. **d**, Population.

result may indicate that food importers with smaller agricultural areas displaced agricultural land use to food exporters. For instance, high-hotspot countries with high income had the smallest agricultural areas among the six types of countries (Fig. 4d) and would have saved 173,126 km^2 of agricultural area (approximately 47.5% of the territory of Japan) per year during 2000–2018 as net food importers, accounting for roughly 20.3% of their annual agricultural area (Supplementary Table 5). In addition, the average dietary energy supply adequacy had a positive association with the quantity of food imported. Countries that had a higher average dietary energy supply imported more food from abroad to meet increases in per capita caloric and protein demands[34]. Per capita gross domestic product (GDP) and population size both drove significant correlated results with food production and trade (Supplementary Table 6).

Alternative classification of hotspot countries

Our hotspot classification used the ratio of biodiversity hotspot areas to total land areas, but a few low-hotspot countries with large total land areas had relatively small harvested areas. Harvested areas generate direct impacts on biodiversity through agricultural production. Thus, generally speaking, the smaller the harvested areas, the smaller the impacts on biodiversity. To account for this phenomenon, we also used an alternative way to classify countries on the basis of the proportion of hotspot areas in harvested areas instead of total land areas (Supplementary Data 1). The alternative classification changed nine low-income countries from low-hotspot to high-hotspot countries (Supplementary Table 1). These countries acted as both net exporters (for example, Brazil and Paraguay) and net importers (for example, Algeria, Iran and Colombia). In this alternative classification, high-hotspot countries with low income changed from net importers (29.0 Mt yr^{-1} of average net annual food imported) to net exporters (7.4 Mt yr^{-1} of average net annual food exported) from 2000 to 2018 (Extended Data Fig. 5). Brazil alone led this conversion with rapid increases in food exports from 18.1 Mt in 2000 to 127.6 Mt in 2018 (Supplementary Data 1), partly because of the rapid expansion of soybean production for China and European countries[35]. Without Brazil in this alternative classification, high-hotspot countries with low income acted as net importers (49.1 Mt yr^{-1} of average net annual food imported) from 2000 to 2018 (Supplementary Data 1).

In the alternative classification, the amount of net food exported in high-hotspot countries with low income (7.4 Mt yr^{-1}) was 94.7% lower than that in low-hotspot countries with high income (138.5 Mt yr^{-1}) and 69.6% lower than that in non-hotspot countries with low income (24.4 Mt yr^{-1}) (Extended Data Fig. 5). Due to food imports from low- and non-hotspot countries, high-hotspot countries with low income increased the amount of land saved by 27.4%, from 848,573 km^2 in our original classification to 1,168,885 km^2 in the alternative classification from 2000 to 2018 (Supplementary Table 7). This increase was because some net importers (for example, Alegria, Iran and Colombia) were also classified as high-hotspot countries (Supplementary Data 1). We also performed an alternative model that included the percentage of biodiversity hotspots in harvested areas instead of total land areas (Supplementary Table 8). The results also confirmed that low- and non-hotspot countries had an increasingly important role in international food trade, although Brazil changed the status of high-hotspot countries with low income from net importers to net exporters in the alternative classification. Low-hotspot countries with low income maintained the status of net importers (69.6 Mt yr^{-1} of average net annual food imported) from 2000 to 2018. Particularly, China, Egypt and Bangladesh played increasingly important roles as net importers during this period.

Conclusion and discussion

Our research indicates that the impact of international food trade flows on biodiversity hotspots is more complex than reported in previous studies. By differentiating countries as high-, low- and non-hotspot countries, we were able to directly link the food flows among low-income and high-income countries with different proportions of biodiversity hotspot areas in those countries. In addition to the large proportion of net food exported from low-hotspot countries with high income, non-hotspot countries with low income increasingly acted as net exporters by raising the proportion of food production for exports in international food trade. In the context of land sharing and land sparing[36], such exports from low- and non-hotspot countries spare agricultural land for biodiversity in high-hotspot countries. Our findings suggest that it is time to rethink international food trade by creating more innovative approaches to minimize the negative impacts of global food

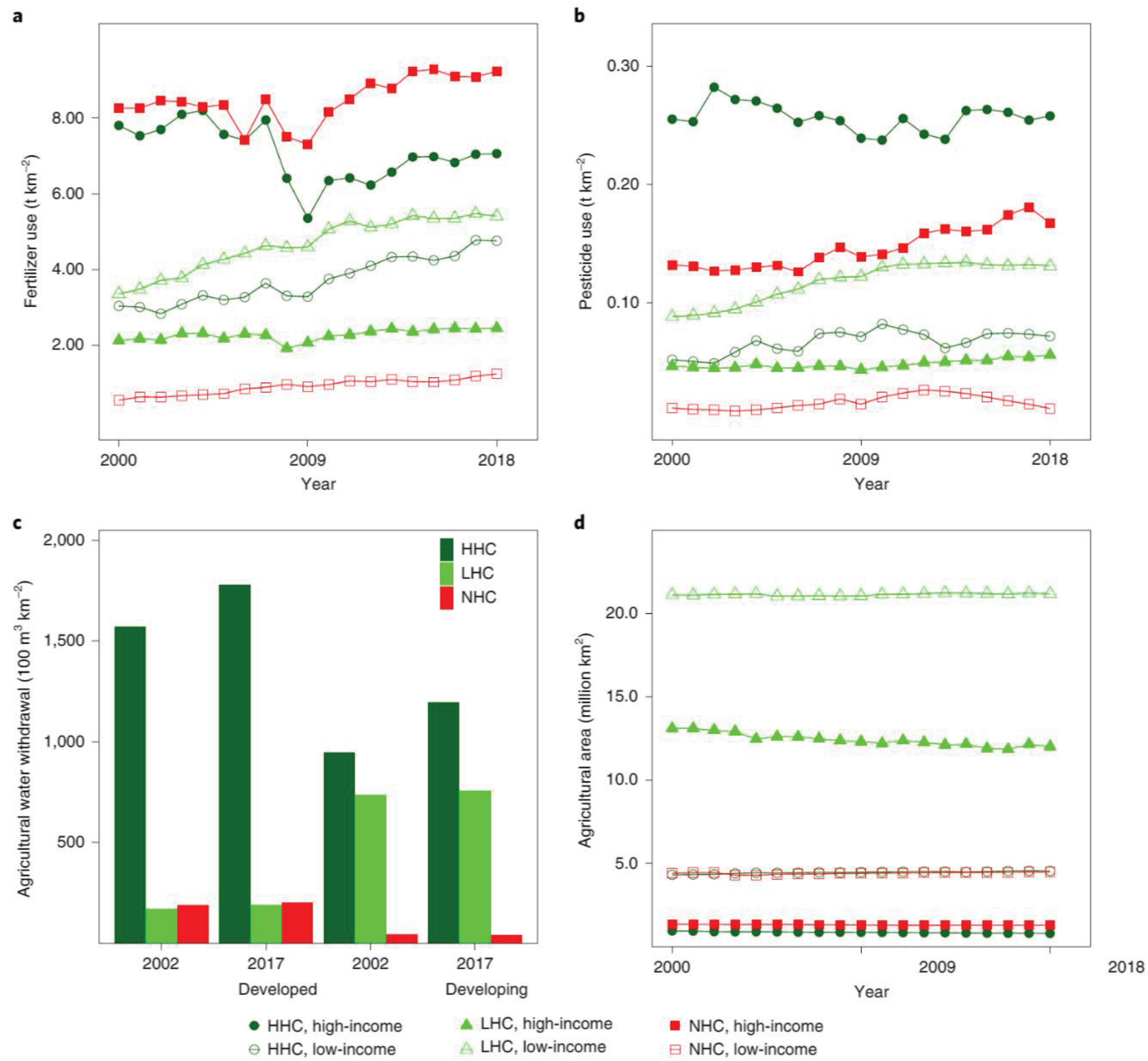

Fig. 4 | Changes in agricultural intensification and agricultural area in high-hotspot countries, low-hotspot countries and non-hotspot countries, with each group subdivided into high- and low-income countries. a, Fertilizer use (t km^{-2}). **b**, Pesticide use (t km^{-2}). **c**, Agricultural water withdrawal (m^3 km^{-2}). **d**, Agricultural area (km^2). The raw data are from UN FAO[52].

production and trade on biodiversity in both high- and low-income countries, especially high-hotspot countries.

We note that exporting food from low-income countries with biodiversity hotspots to high- and other low-income countries can still damage biodiversity in those exporting countries. The palm oil problems in Indonesia and Malaysia provide an example of high-income countries contributing to biodiversity loss in low-income countries with high hotspots[33]. In Brazil's Atlantic and Cerrado hotspots, soybean expansion for exports to high- and low-income countries threatens their exceptional biodiversity substantially[35].

Biodiversity hotspots did not include some grasslands, which have low numbers of species across large geographical ranges[37]. For example, the substantial grain exports from the United States and Ukraine come at the expense of such grasslands[37–39]. The large degree of land conversion may threaten grassland species in non-hotspot areas of the United States, Ukraine and other net exporting countries.

To address these issues in the future, species-specific analyses are needed within national boundaries because threats from agricultural activities vary among species and across space[20,26]. Worldwide, identifying species-specific relationships with international food trade items would be possible through the analysis of high-resolution data[12,20,25]. Future research efforts are needed to accurately determine causal relationships among global food production and trade and biodiversity on the basis of high-resolution subnational and local data over time[10,12,20,25] and to identify the impacts of food production for export in specific locations[40,41]. The approaches and findings in this paper provide a foundation for further work incorporating data with higher resolutions to quantify the biodiversity impacts of telecouplings[31,42,43].

With increasing attention to food security and biodiversity (for example, global assessment of biodiversity and ecosystem services[44] and the upcoming meeting of the Conference of the Parties to the Convention on Biological Diversity[45]), new international initiatives and agreements are necessary to reduce threats to biodiversity from food production and trade[26,46,47]. Food prices should incorporate the biodiversity cost of production[48], and the earnings from such price hikes could be used to mitigate impacts on biodiversity[49]. Both food importing and exporting countries working together to implement new policies and technologies can lower negative impacts on biodiversity while increasing food security. They can also help operationalize the post-2020 global biodiversity framework and achieve the UN's SDGs (for example, Goal 2—food security and Goal 15—biodiversity) across multiple scales worldwide.

Methods

Biodiversity hotspot and non-hotspot countries. We divided all 157 countries with available data into 114 hotspot countries and 43 non-hotspot countries (Fig. 3 and Supplementary Table 1) on the basis of the relevant biodiversity hotspot information[27,28]. Hotspot countries are those that contain at least part of a recognized global biodiversity hotspot[27,28,50]. Biodiversity hotspots are areas with not only a high degree of species richness (they hold ≥0.5% of the world's plants as endemics) but also a high degree of vulnerability (they have lost ≥70% of their primary, native vegetation) to human disturbance[27,28]. Biodiversity hotspots include many types of habitats such as forests and grasslands (Extended Data Fig. 1). In contrast, non-hotspot countries do not include any part of a global biodiversity hotspot. Because hotspot countries vary substantially in terms of biodiversity hotspot areas (Extended Data Fig. 4), we classified hotspot countries into 64 high-hotspot countries and 50 low-hotspot countries, in which biodiversity hotspots account for more or less than 50% of terrestrial lands, respectively. Additionally, many biodiversity hotspots are located in agricultural land; we thus used an alternative hotspot classification based on the proportion of biodiversity hotspots in harvested areas. In this alternative classification, 114 hotspot countries were divided into 73 high-hotspot countries and 41 low-hotspot countries (Supplementary Table 1).

High-hotspot countries, low-hotspot countries and non-hotspot countries have a number of other differences. For example, in high-hotspot countries with high and low income, 88.2% and 96.7% of harvested areas were located in biodiversity hotspots, respectively, whereas in low-hotspot countries with high and low income, only 16.4% and 19.7% of the total harvested areas were located in biodiversity hotspots, respectively. Since non-hotspot countries have no hotspots, agricultural areas in non-hotspot countries were of course not located in any biodiversity hotspots. Per capita GDP of non-hotspot countries with high income in 2018 ($38,385 in 2010-constant USD) was roughly 38.9% and 29.9% higher than that of high-hotspot countries with high income ($27,635) and low-hotspot countries with high income ($29,559), respectively. Low-income countries had similar per capita GDP across high-hotspot ($4,383 in 2010-constant USD), low-hotspot ($3,899) and non-hotspot countries ($4,327). High-hotspot countries with high income had the lowest population growth rates (5.1%) during 2000–2018, followed by non-hotspot countries with high income (11.5%) and low-hotspot countries with high income (13.7%). Population size in high-hotspot countries with low income, low-hotspot countries with low income and non-hotspot countries with low income increased by 29.5%, 25.9% and 30.5% during 2000–2018, respectively. In addition, land area in low-hotspot countries with high income in 2018 (36,495,165 km^2) was 15.1 times and 3.2 times as large as that of high-hotspot countries with high income (2,413,139 km^2) and non-hotspot countries with high income (11,516,626 km^2), respectively. Land area in low-hotspot countries with low income in 2018 (47,155,016 km^2) was 4.2 times and 4.6 times larger than that of high-hotspot countries with low income (11,152,907 km^2) and non-hotspot countries with low income (10,330,225 km^2), respectively.

Data collection. The datasets were obtained from the UN FAO, the UN Data and the World Bank[29,51,52]. Our databases consisted of agricultural, environmental and socio-economic data. We selected the period from 2000 to 2018 because of data availability. The agricultural datasets were obtained from the UN FAO[52] and included information about food production, food trade matrices, agricultural areas, agricultural intensification (fertilizer application, pesticide use and water withdrawal) and average dietary energy supply adequacy (a percentage of the average dietary energy requirement). We included 189 food items that are raw, processed or prepared from crops and livestock (Supplementary Table 2). The basic food trade unit in this research was the physical volume (metric tonne) of food produced, imported and exported. This unit was chosen for two reasons. First, the number of countries in the volume dataset was much higher than in the monetary dataset. Second, using the volume of food trade is more appropriate for showing the extent to which food trade is linked with each agricultural area because the monetary value varies with price fluctuations. Socio-economic data such as population and per capita GDP came from the World Bank[29].

Aggregate analysis. In the aggregate analysis, we divided the data collected from the individual countries into three groups of countries (high-hotspot countries, low-hotspot countries and non-hotspot countries), which were further divided into high- and low-income countries. We calculated agricultural intensification and agricultural area change from 2000 to 2018. By using agricultural intensification and land use datasets, we calculated agricultural intensification uses per agricultural area (fertilizer application, pesticide use and water withdrawal) in each country. Then, with the weights of each country's agricultural land size, we averaged these intensification values in each group using R v.4.0.5[53]. We also calculated food trade flows among high-hotspot countries, low-hotspot countries and non-hotspot countries in each individual year from 2000 to 2018 as well as annual averages over the same period. In the FAO food trade matrix dataset[52], we used food import matrix data. Food export matrix datasets were used to fill in the data gaps in the food import data. In addition, we used an origin-tracing algorithm to reduce data uncertainty regarding re-exports[22,54]. For example, some countries such as the Netherlands import food products from exporting countries and re-export them to other importing countries. The origin-tracing algorithm by Kastner et al.[54] has a basic assumption that food consumption in each country proportionally originates from their domestic production and from other countries. The origin of food imported can be examined using the bilateral food trade data. This algorithm assigns re-export volumes from intermediate countries to the original exporting country of production[22,54].

We also estimated the amount of land saved due to food imports on the basis of yield and quantity of those imports over 189 food items[55]. Each year, we divided the total amount of food production by the total food production area to calculate each country's average food yield due to the limitation of the data on the yield and production area for each food item. To estimate the amount of land saved from importing food each year, we divided the quantity of food imports (t) by yield ($t\,km^{-2}$) in each country. We then aggregated the amount of land saved by food imports for high- and low-income countries in high-hotspot countries, low-hotspot countries and non-hotspot countries. We note that this calculation simplified the amounts of land saved for domestic food production due to imports, and thus this result could not identify species-specific relationships with food production and trade.

Panel data analysis. To uncover factors affecting food production for domestic supply, food exports and food imports, we performed panel data analyses in R v.4.0.5[53]. Panel data analysis allows control for variables in different entities (for example, countries) over time[56]. We selected the random-effects model because agricultural, socio-economic and environmental differences across countries have some influence on the quantity of food production and trade. The random-effects model assumes that each entity has its own error term that is random and not correlated with independent variables in the model[56]. An advantage of the random-effects model over fixed effects is that time-invariant variables can be included as independent variables. We used the same value of biodiversity hotspots in our panel data analyses because of the lack of time-series data for biodiversity hotspots.

Since food production has two important purposes—domestic supply and export—we included the quantities of food production for domestic supply and export separately. This separation is essential for identifying responsible parties. For example, although the impact of food production on biodiversity is probably the same irrespective of whether the produced food is consumed locally or exported, the percentages of food exported out of food produced differed among countries. Exporting countries may shift some responsibility for biodiversity loss caused by food production for exports to importing countries.

To identify the changes in significant factors for food production and trade over time, we constructed random-effects models for three different periods (2000–2008, 2009–2018 and 2000–2018) (Supplementary Table 6). The three random-effects models had 157 countries and included 9, 10 and 19 temporal points in each panel, respectively. We estimated the amounts of food production for domestic supply, food exports and food imports as a function of agricultural factors (average dietary energy supply adequacy and total agricultural area), socio-economic factors (per capita GDP and total population) and environmental factors (ratio of biodiversity hotspots to total land areas). In an alternative model, we included the proportion of biodiversity hotspots in harvested areas instead of total land areas (Supplementary Table 8). We performed log transformation on all dependent and independent variables, as the log–log transformation allows us to interpret coefficients as an elasticity[57].

We performed the Breusch–Pagan Lagrange multiplier test to choose between a random-effects model and a simple ordinary least squares model[56]. The Lagrange multiplier test concluded that there are significant differences across countries (existence of panel effects) and that our random-effects models were more suitable. The random-effects model allows us to include time-invariant variables that preclude fixed effects. We also tested for heteroscedasticity using the Breusch–Pagan test. Since heteroscedasticity was detected in all random-effects models, we controlled for heteroscedasticity using a robust covariance matrix estimation (also known as a sandwich estimator)[56]. We identified multicollinearity problems using variance inflation factors (VIFs). A VIF of 10 indicates a severe multicollinearity problem[58]. All VIF results in our models were less than 3.8.

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

Data availability

All data analysed during the current study are available from the corresponding author on reasonable request. The data that support the findings of this study are available within the paper, its Supplementary Information and Supplementary Data 1.

Code availability

The codes to perform our panel data analyses can be found at https://github.com/mingonchung/foodtrade-hotspot.

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Author contributions

M.G.C. analysed the model and drafted the manuscript. M.G.C. and J.L. conceived of the study, revised the manuscript and reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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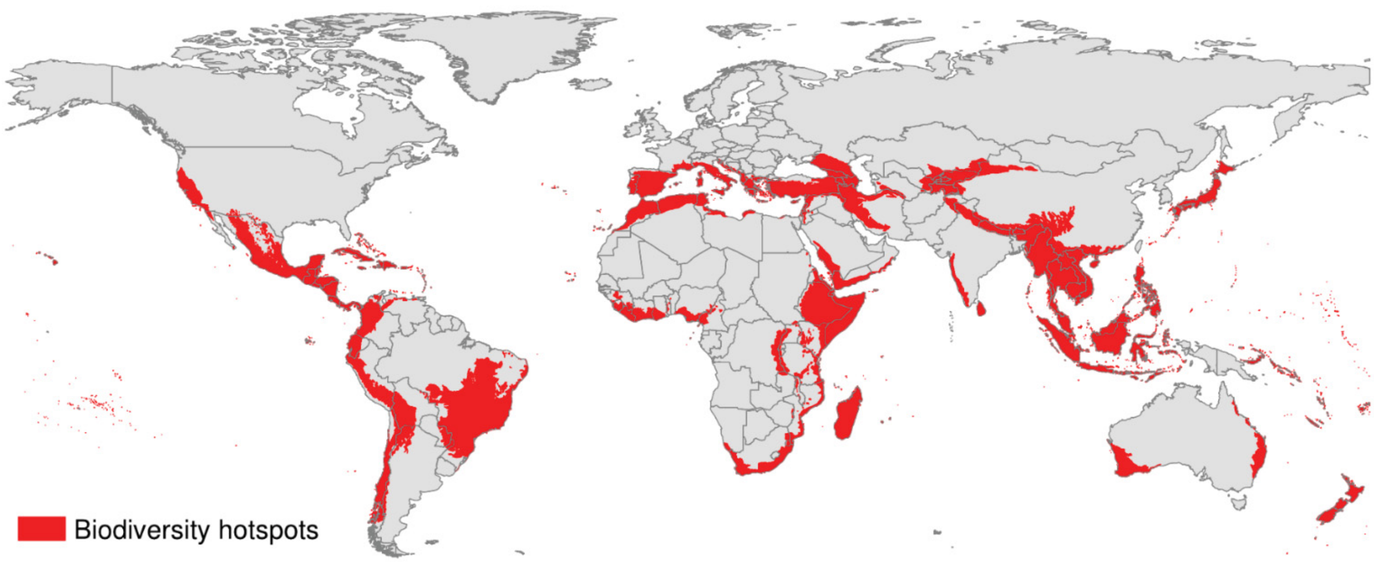
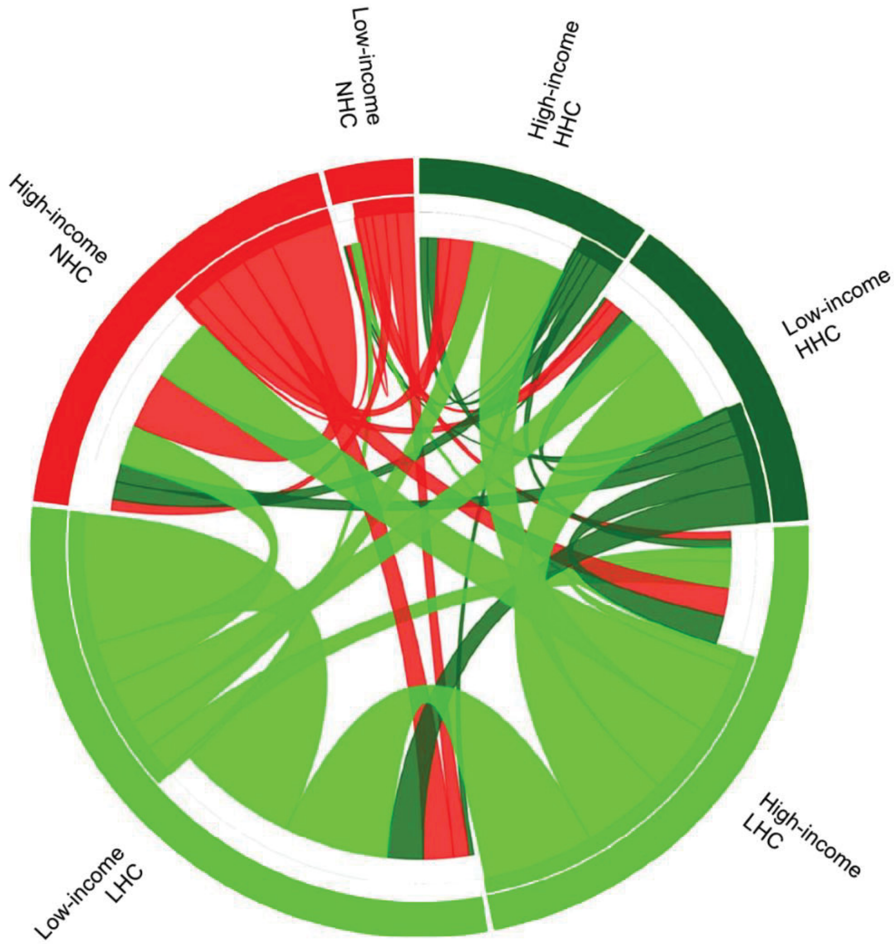
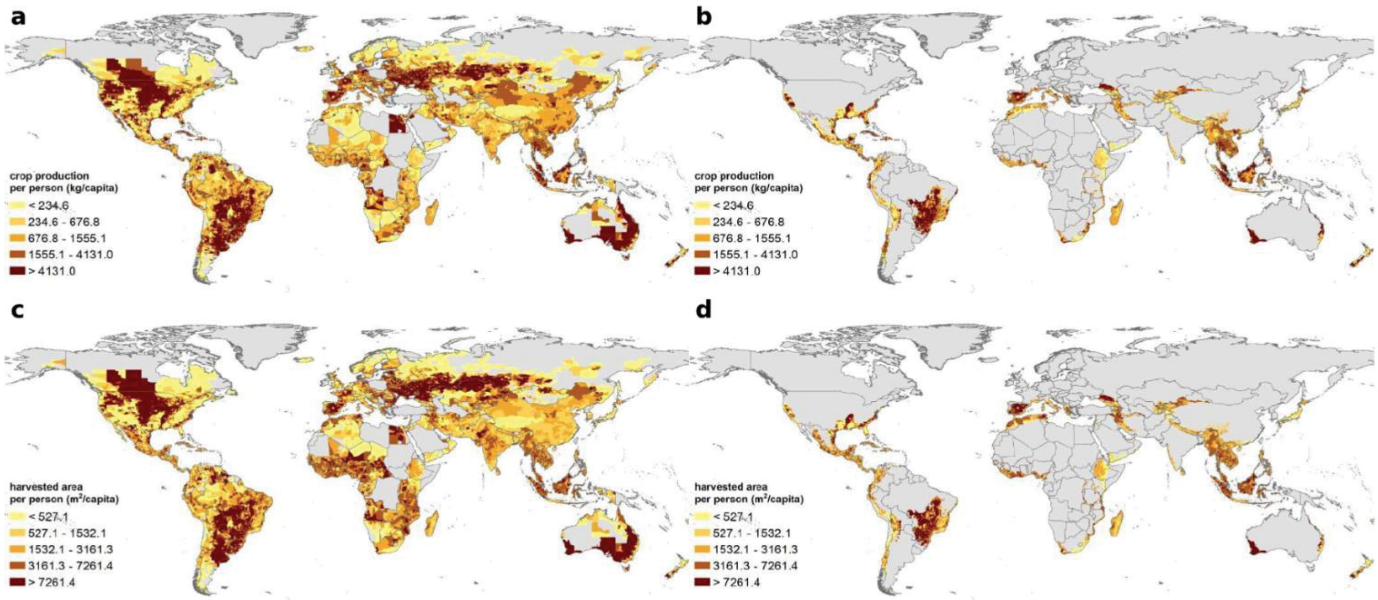


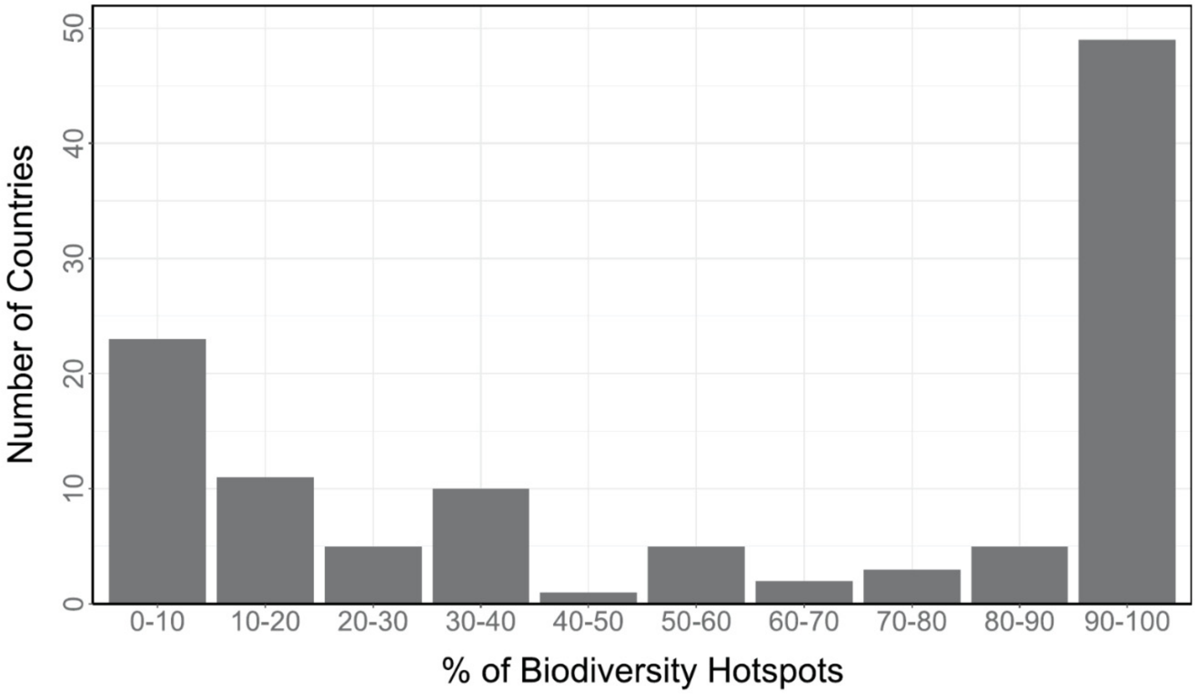
Extended Data Fig. 1 | Spatial distribution of biodiversity hotspots. Raw data from Myers et al.[27] and Hoffman et al.[28].



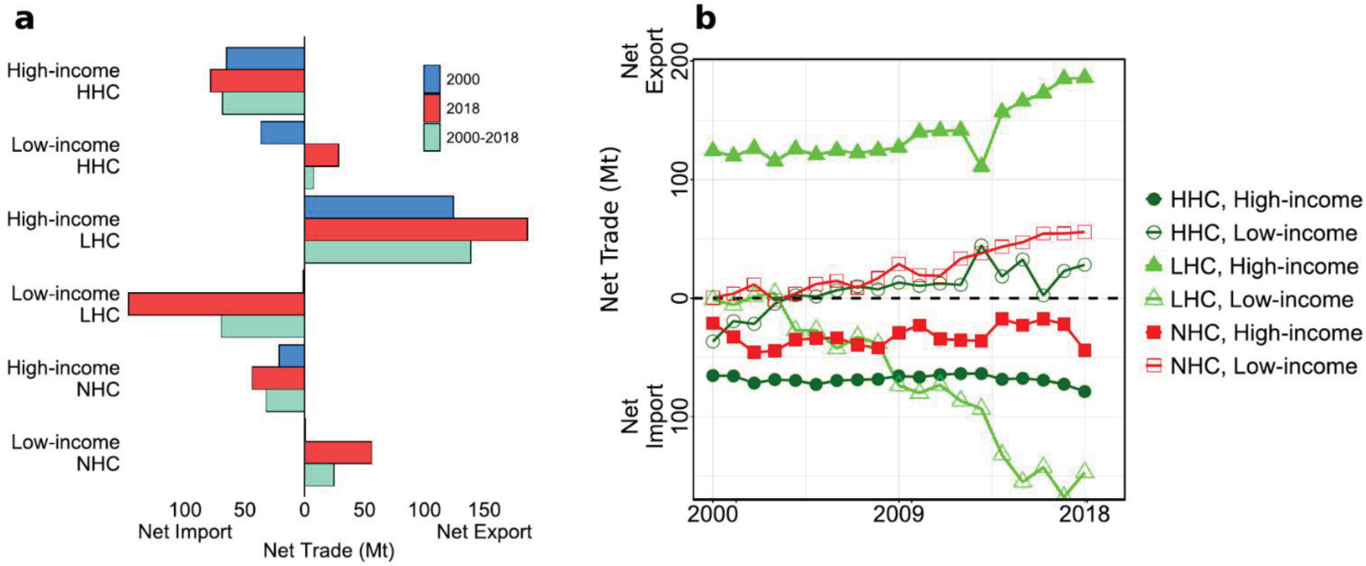
Extended Data Fig. 2 | Average annual food flows (Mt/year) from 2000 to 2018. Food flows between high-hotspot countries (HHC), low-hotspot countries (LHC), and non-hotspot countries (NHC) with high- and low-income. Non-hotspot countries are marked by red, high-hotspot countries by dark green, and low-hotspot countries by light green. The arc length of an outer circle indicates the sum of food exported and imported in each group. The arc length of a middle circle refers to the quantity of food exports. The inner arc length shows the quantity of food imports. Raw data from UN FAO[52].



Extended Data Fig. 3 | Spatial distribution of per capita crop production (kg/capita) and per capita harvested areas (m^2/capita) in 2010. (**a**) county-level of crop production, (**b**) hotspot-level of crop production, (**c**) county-level of harvested area, and (**d**) hotspot-level of harvested area.



Extended Data Fig. 4 | Number of countries with different percentages of biodiversity hotspots (land area with biodiversity hotspots out of total terrestrial land area). Raw data from Myers et al.[27] and Hoffman et al.[28].



Extended Data Fig. 5 | Quantity of net food trade between high-hotspot countries (HHC), low-hotspot countries (LHC), and non-hotspot countries (NHC) with high and low income. The group of high-, low-, and non-hotspot countries were classified with the proportion of biodiversity hotspots in harvested areas: (**a**) Blue indicates net food trade (export-import) in 2000, red indicates net food trade in 2018, and cyan indicates average net annual food trade from 2000–2018. The net amounts of food trade in each group are not linearly increased or decreased over time. The net amounts of food trade in 2000 and 2018 can be lower or higher than those in other mid-years. (**b**) The amounts of net food trade between high-income and low-income countries in high-hotspot countries (HHC), low-hotspot countries (LHC), and non-hotspot countries (NHC) from 2000–2018. Non-hotspot countries are indicated by red, high-hotspot countries by dark green, and low-hotspot countries by light green.