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Food plants in Brazil: origin, economic value of pollination and pollinator shortage risk

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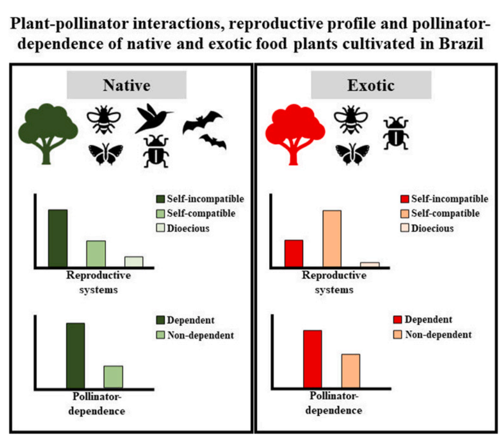
HIGHLIGHTS

- *Apis mellifera* interacts extensively with native and exotic crops, while vertebrates exclusively pollinate native crops
- 71.4% of native food crops have essential pollinator dependence, contrasting the 30.2% of exotic
- 81.5% of the total agricultural area in Brazil is cultivated with exotic food crops, of which 46% is soybean
- For native crops, pollinator shortage risk is mainly concentrated in the Northeast and Southeast Brazilian regions
- Considering the Brazilian biomes, the Atlantic forest is at higher risk of pollinator shortage

GRAPHICAL ABSTRACT



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ABSTRACT

Pollination is a key ecosystem service of critical importance for food production. However, globally, several regions are already experiencing pollinator shortage as pollinators are declining. Here, we investigate the origin, pollinator dependence and economic value of 199 food crops cultivated in Brazil to understand to which extent (1) Brazilian agriculture is vulnerable to pollinator shortage, and (2) Brazilian society has already achieved a comprehensive perspective about crop dependence. We used Brazil as a case study as it is a megadiverse tropical country and the 3rd largest world crop producer and exporter, with most of the crops depending on pollinators. Our findings revealed that over half (53.7%) of the food crops in Brazil are native, with the North region of Brazil housing the higher diversity of native crops, in contrast with the South and Southeast regions. Additionally, considering the reproductive systems, among native food crops, 65.6% exhibit self-incompatibility or dioecy (i.e.,

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requiring obligatory cross-pollination), whereas 30.6% of exotic food crops display this trait. Overall, Brazilian municipalities produce more exotic crops than native ones, with almost 4/5 of the total agricultural area of the country dedicated to the cultivation of exotic crops, which are generally self-compatible commodities that rely low to modestly on pollinators. Regarding the biomes, we observe that this pattern is followed by most of them, but for the Caatinga dry forest, where native crops dependent on pollinators predominate. However, when soybean is removed from the analysis, the areas devoted to exotic crops always decreased, even being equal to native crops in the Atlantic forest. Our results also indicate that considering the pollinator shortage, some Brazilian biomes may be at risk of losing >20% of their yields, mainly in the Caatinga dry forest and the Atlantic forest. Therefore, in this paper, we are discussing that the expansion of monocultures in Brazil's agricultural lands may have several impacts on the provision of pollination services, food production and, then, on food security not only for the Brazilian population, as Brazil is the 3rd largest world agricultural producer and exporter.

1. Introduction

Pollination is a key ecological function for maintaining biological communities worldwide and it also represents an essential ecosystem service for human well-being, with approximately 90% of all flowering plants pollinated by biotic vectors (Ollerton et al., 2011) and one-third of the main global crops we consume are dependent on animal pollination, mainly bees (Klein et al., 2007). In general, pollinators play an important role in the production of many food crops that humans consume, having a large and strong contribution to world agricultural production and human food security (Giannini et al., 2015; Dicks et al., 2016; IPBES, 2016; BPBES, 2019; Porto et al., 2021), with estimated global values of the service of agricultural pollination ranging from US $195 to approximately US$387 billion annually (sensu Porto et al., 2020). Additionally, biotic pollination contributes to improving the quantity and quality of fruits and seeds produced (Klein et al., 2007; Aizen et al., 2009; Junqueira and Augusto, 2017; Nicholson and Ricketts, 2019). Therefore, compromising the pollination process in these crops can result in low economic yields in agricultural fields, due primarily to reduce fruit production, which is a key component of agricultural production (Garibaldi et al., 2013).

Although pollination represents such importance, the ecosystem service provided by this ecological process is at risk (IPBES, 2019), mainly due to intense practices that are not nature-friendly, since modern society still does not understand the importance of pollination for human food production, health, and well-being (Oliveira et al., 2020). In this way, agricultural expansion and the intensive use of pesticides are considered one of the main drivers of pollinator decline (Dicks et al., 2016; IPBES, 2016). These impacts on the pollinator community result in direct effects on the pollination service and, consequently, reduce the productivity of crops and could also negatively affect the global economy (IPBES, 2016). The expansion of agricultural areas is followed by reductions in vegetation cover (Foley et al., 2005) and in the provision of ecosystem services due to the reduction in the global stock of pollinators (Potts et al., 2010). In this sense, agricultural expansion can constrain the stability of essential crop yields for human food security (Schmidhuber and Tubiello, 2007). Generally, crop expansion has been strongly associated with commodity cultivation, mainly those that have modest dependence on pollinators, such as soybean (Aizen et al., 2019).

Modern agriculture has been developing through the productivity of a few crops, instead of increasing the biological diversity of agricultural production worldwide (Aizen et al., 2019). In this context, the expansion of local agricultural practices and the inclusion of new cultures of native and wild plants can have a potential role in diversifying food production and ensuring human food security (e.g., Gahukar, 2014; Shelef et al., 2017; Singh et al., 2019). Therefore, popularizing and learning to use native plants as sources of nutrition, considering the environmental issues involved, can be a nature-based solution to guarantee food sovereignty and biocultural diversity (Jacob et al., 2020; Medeiros et al., 2021). Since the dawn of civilization, human beings have learned to domesticate plants and use them for livelihood, such as for food purposes (Purugganan and Fuller, 2009). However, after being domesticated and with the advance of industrial agriculture, many crops expanded and are currently cultivated in regions that are not their areas of origin (Drewnowski and Popkin, 1997), such as wheat, soybeans, sugarcane, and corn, which are crops produced on a large scale worldwide (FAO, 2016). Therefore, the expansion of agricultural frontiers destined for the cultivation of these monocultures results in several ecological costs, such as loss of habitats, reduction of biodiversity, intensification of climate change, and unbridled use of pesticides, which affect not only biodiversity but also human health (Horrigan et al., 2002; Massy, 2017).

Brazil is the 3rd largest world agricultural producer and exporter (Schneider et al., 2021), with approximately 60 % of the crops depending to some extent on pollinators to set fruits and seeds (Giannini et al., 2015). Brazil is also the most biologically megadiverse country (BPBES, 2019), but the diversity of many potential crop pollinators is neglected, with many plant-pollinator interactions not included in the conservation agenda for agricultural stability, also the pollinators of major commercially important crops remain unknown (Lopes et al., 2021). In addition, as a pattern observed for tropical countries, Brazil has played as a leading exporter in the international food trade, producing exotic commodities on a high scale to supply the demands of industrialized and developed countries, like China and the United States (Chaudhary and Kastner, 2016). Currently, Brazil is the largest producer of soybean worldwide (FAOSTAT, 2021), reinforcing the consequences of the intense exportation of commodities to rich countries, which have severe impacts on biodiversity. In addition, even though Brazil appears as one of the largest agricultural producers and exporters worldwide, nowadays >125 million Brazilians are facing some level of food insecurity (PENSSAN/VIGISAN, 2022; Oliveira et al., 2023), and over 60 million are under conditions of moderate or severe food insecurity, which makes the nation reentry in the world hunger map (FAO et al., 2022; Oliveira et al., 2023).

In this context, our main goal was to examine the role played by exotic vs. native food plants in the different biomes of Brazil, their associated pollinator community, their biotic pollination dependence and economic contribution. Moreover, we aim to unravel areas that are at high risk of experiencing a pollination crisis in Brazil. We specifically aimed to answer four questions: (i) Do native and exotic crops differ in terms of pollinator richness that they depend on? (ii) What are the differences in pollinator dependence between native and exotic crops across the biomes of Brazil? (iii) What are the differences in cropland area between exotic and native crops across the six biomes of Brazil? and (iv) how is pollinator shortage risk of native and exotic crops spatially distributed across the biomes of Brazil? To do this, we collected information about the production, pollination dependence and pollinator identity for 107 native and 92 exotic crops across 5572 counties of Brazil and calculated the risk of pollinator shortage for all counties based on two main aspects: (i) percentage of production dependent on pollinators; and (ii) remaining native vegetation in the county and surrounding areas. Our hypotheses are (1) native crops will depend more on a richer pollinator community than exotic crops, (2) cropland area cultivated with exotic crops will be higher than native, mainly due to monoculture, (3) native crops will be at higher risk of pollinator shortage than exotics.

2. Methods

2.1. Dataset survey of crop species cultivated in Brazil

A list of 199 food crop species cultivated in Brazil was retrieved from the Brazilian Thematic Report on Pollination, Pollinators and Food Production (BPBES/REBIPP, 2019) (Table 1). We then identified from this plant survey what species are native or exotic to Brazil, according to the Flora do Brasil (n.d.) website. We then retrieved information about the identity of the pollinators that pollinate these crops for 104 out of the 199 species from the BPBES/REBIPP (2019) database. The pollinators were classified into three main groups based on taxonomic information: (i) bees, (ii) other insects, and (iii) vertebrates. Regarding cropland area, we surveyed the Brazilian Institute of Geography and Statistics (IBGE, 2021) database for the harvested area and economic yields of the crops for 5572 counties across the six main biomes of Brazil in 2021: (i) Amazon, (ii) Cerrado, (iii) Caatinga dry forest, (iv) Pantanal, (v) the Atlantic forest, and (vi) the Pampa. We were able to compile data for the harvested area and economic yield for 52 species out of the 199 initial species list using the IBGE (2021) database.

2.2. Reproductive systems and Pollinator dependence

We surveyed the reproductive systems of the crop species, based on field observations, and published and referenced data. The reproductive systems were classified into three categories: (1) self-incompatible, (2) self-compatible, and (3) obligatory cross-pollination [self-incompatible + dioecious] (sensu Girão et al., 2007; Lopes et al., 2009). In addition, we applied some well-accepted standards of relative dependence on pollinators in the world (Klein et al., 2007; BPBES, 2019) for classifying the crops (Table 1). Then, we classified the crops into five categories of pollinator dependence based on yield reduction into two classes, *(a) non-dependent*: no differences in yields under conditions with and without animal-mediated pollination, and *(b) pollinator-dependent*: (1) little [>0% and ≤ 10%], (2) modest [>10% and ≤ 40%], (3) high [>40% and ≤ 90%], and (4) essential [>90%]. In total, we grouped information on the dependence on pollinators for 164 of the 199 crop species based on Klein et al. (2007) and BPBES (2019) databases, of which for 22 species we extrapolated missing information of pollinator dependence based on information from other species of the same genera. Additionally, for 26 crops we used available information on the reproductive system or pollination system as variables to predict the dependence on pollinators as follows: crops with obligatory cross-pollination reproductive system (self-incompatibility or dioecy) were classified as essentially dependent on pollinators, and crops that are pollinated only by wind were classified as non-dependent.

2.3. Economic value of pollination

We calculated the economic value of pollination (EVP) for 52 crops out of 199 species, given that these were the ones for which cropland area and monetary earnings were available (Table 1). These were calculated by adapting the equation proposed by Gallai and Vaissière (2009), following Porto et al. (2020):

$$\text{EVP} = \sum_{i=1}^{I}\sum_{x=1}^{X} (PVix \text{ x } Di)$$

where PV*ix* is the production value available in the IBGE database that represents the price of the crop (*i*) production paid to producers (*x*), and D_i is the category of pollinator dependence of the crop (*i*) in a way that crops that are essentially dependent on pollination received a *i* value of 1, greatly dependent received a *i* value of 0.75, modestly dependent received a *i* value of 0.5, little dependent received a *i* value of 0.25, and non-dependent received a *i* value of 0.

2.4. Pollinator shortage risk index

We calculated pollinator shortage risk using a multiplicative approach between two variables: (i) the inverse of the proportion of remaining native vegetation in the county and in a 30 km buffer from its geographical limits, and (ii) the proportion of production dependent on pollination. The first metric that was aggregated into the pollinator shortage risk was the inverse of the proportion of natural vegetation remaining in each county. The proportion of natural vegetation was retrieved using a compilation of cloudless Landsat classified satellite images from the MapBiomas database of 2021, which classifies these satellite images based on 30 different classes from native vegetation, to farming, non-vegetated areas and water (Souza Jr. et al., 2020). We retrieved the proportion of native vegetation considered a 30 km buffer from the geographical limits of each county because the surrounding vegetation may be a source of pollinators, and 30 km is the maximum reported dispersal distance for bees in Brazil (Borges et al., 2020), and a reasonable amount for other less-dominant non-migratory pollinator taxa (Bernard and Fenton, 2006; Hadley and Betts, 2009; Marini-Filho and Martins, 2010; Reis et al., 2012; Penz et al., 2015). Then, we inverted this proportion of natural vegetation subtracting it by 1 and then multiplying this result by −1 (i.e., *Inverse of proportion of natural vegetation = (Proportion of natural vegetation-1) * (−1)*). In this way, higher values of this metric represent counties with a low proportion of remaining natural vegetation.

The second metric that was further aggregated in the pollinator shortage risk index was the proportion of the production in a county that depended on pollination. After classifying the crops into the categories of pollinator dependence, we calculated the amount of agricultural yield that depended on pollination for each crop of a county. Then, we summed the production that depended on pollination of all crops produced in a county and divided it by the total production of the county to retrieve the proportion of production in a county that depended on pollination for yield. After calculating this proportion of production dependent on pollination, we multiplied it with the inverse of the proportion of natural vegetation in a county to retrieve the pollinator shortage risk of each county (i.e., *pollinator shortage risk = inverse of the proportion of natural vegetation in a county * proportion of the production dependent on biotic pollination in a county*). We chose to calculate this index using a multiplicative approach so that small values have a higher importance in the index, in this way, if a county has high natural vegetation around it but a low dependence on pollinators, for example, then the final values of pollinator shortage risk are going to be low. The final pollinator shortage risk index ranged from 0 to 0.86, and higher values represent areas where pollinator dependence is high and the proportion of native vegetation is low.

2.5. Statistical analysis

To access our first question and test for differences in pollinator diversity between native and exotic crops and between the three different groups of pollinators, we conducted a two-way Analysis of Variance (ANOVA) (Legendre and Legendre, 2012). In this analysis, the pollinator richness of each crop was considered as a response variable, while the three different pollinator groups (i.e., bees, other insects, and vertebrates), the crop origin (i.e., native and exotic), and the interaction between these two variables were considered as predictors (i.e., *pollinator richness ~ pollinator group + crop origin + pollinator group: crop origin*). We further constructed a plant-pollinator network to visually represent the associations between pollinators and the crop species. Moreover, to identify differences in the crop richness of each county between native and exotic crops and across the six biomes of Brazil, we conducted a two-way ANOVA. In this analysis, the biomes, the crop origin (i.e., native or exotic), the biomes and the interaction between these last two categorical variables were considered as predictors of crop richness (i.e., the number of plant species cultivated in each county of

Table 1
List of orders, families, crop species, common name, origin (i.e., if the species are native or exotic to Brazil), categories of pollinator-dependence and the Economic Value of Pollination (EVP). A dash (−) in the Common name column indicates that the English name is not widespread. [1]"Data deficient" in this column indicates a lack of information on the pollinator dependency of the respective crop; [2]"Data deficient" in this column indicates a lack of information on cropland area for the respective crop; [a]Pollinator dependence retrieved from BPBES (2019), [b]Data from this study, and [c]Pollinator dependence retrieved from Klein et al. (2007).

Taxa	Common name (Brazilian Portuguese/English)	Origin	Pollinator dependence[1]	EVP[2]
Apiales				
Apiaceae				
Daucus carota L.	Cenoura/carrot	Exotic	Non-dependent[a]	Data deficient
Aquifoliales				
Aquifoliaceae				
Ilex paraguariensis A.St.-Hil.	Erva-mate/ Yerba mate	Native	Great[a]	$100,693,944.75
Araucariales				
Araucariaceae				
Araucaria angustifolia (Bertol.) Kuntze	Pinhão/Brazilian pine	Native	Non-dependent[a]	Data deficient
Arecales				
Arecaceae				
Acrocomia aculeata (Jacq.) Lodd. ex R.Keith	Macaúba/macaw palm	Native	Great[a]	Data deficient
Astrocaryum vulgare Mart.	Tucumã/(−)	Native	Data deficient	Data deficient
Attalea phalerata Mart. ex Spreng.	Ouricuri/(−)	Native	Essential[b]	Data deficient
Attalea speciosa Mart.	Babaçu/babassu palm	Native	Essential[b]	Data deficient
Bactris gasipaes Kunth	Pupunha/peach palm	Native	Data deficient	Data deficient
Bactris glaucescens Drude	Palmito tucum/(−)	Native	Data deficient	Data deficient
Butia paraguayensis (Barb.Rodr.) L.H.Bailey	Butiá do cerrado/(−)	Native	Data deficient	Data deficient
Cocos nucifera L.	Côco/coconut	Exotic	Modest[c]	$120,504,139.00
Elaeis guineensis Jacq.	Dendê/oil palm	Exotic	Little[a]	$47,572,727.13
Elaeis oleifera (Kunth) Cortes	Cauiaê/American oil palm	Native	Little[b]	Data deficient
Euterpe edulis Mart.	Palmito/palm tree	Native	Great[a]	$44,042,105.63
Euterpe oleracea Mart.	Açaí/assai	Native	Great[b]	$738,132,278.63
Euterpe precatoria Mart.	Açaí da mata/(−)	Native	Great[b]	Data deficient
Mauritia flexuosa L.f.	Buriti/(−)	Native	Essential[a]	Data deficient
Oenocarpus distichus Mart.	Bacaba de azeite/white bacaba	Native	Data deficient	Data deficient
Oenocarpus mapora H.Karst.	Bacabi/bamboo palm	Native	Data deficient	Data deficient
Asparagales				
Amaryllidaceae				
Allium cepa L.	Cebola/onion	Exotic	Great[a]	$346,488,308.25
Allium sativum L.	Alho/garlic	Exotic	Non-dependent[a]	$0.00
Asparagaceae				
Asparagus officinalis L.	Aspargo/asparagus	Exotic	Non-dependent[a]	Data deficient
Orchidaceae				
Vanilla bahiana Hoehne	Baunilha/vanilla	Native	Great[a]	Data deficient
Asterales				
Asteraceae				
Cichorium sp.	Chicória/chicory	Exotic	Non-dependent[a]	Data deficient
Cynara cardunculus L.	Alcachofra/artichoke	Exotic	Non-dependent[a]	Data deficient
Helianthus annuus L.	Girassol/sunflower	Exotic	Great[a]	$19,445,779.50
Lactuca sativa L.	Alface/lettuce	Exotic	Non-dependent[a]	Data deficient
Brassicales				
Brassicaceae				
Brassica napus L.	Canola/rapeseed	Exotic	Non-dependent[a]	Data deficient
Brassica rapa L.	Nabo/ Turnip	Exotic	Great[a]	Data deficient
Brassica chinensis	Brócolis, couve-flor/broccoli, cauliflower	Exotic	Non-dependent[a]	Data deficient
Brassica oleraceae	Repolho/cabbage	Exotic	Non-dependent[a]	Data deficient
Crambe hispanica subsp. *abyssinica* (Hochst. ex R.E.Fr.) Prina	Cambre/(−)	Exotic	Data deficient	Data deficient
Caricaceae				
Carica papaya A.St.-Hil.	Mamão/papaya	Native	Little[c]	$65,279,861.50
Jacaratia spinosa (Aubl.) A.DC.	Jacaratiá/(−)	Native	Essential[b]	Data deficient
Moringaceae				
Moringa oleifera Lam.	Moringa/drumstick tree	Exotic	Data deficient	Data deficient
Caryophyllales				
Cactaceae				
Selenicereus undatus (Haw.) D.R.Hunt	Pitaia/pitaya	Exotic	Data deficient	Data deficient
Cucurbitales				
Cucurbitaceae				
Citrullus lanatus (Thunb.) Matsum. & Nakai	Melancia/watermelon	Exotic	Essential[a]	$342,190,922.50
Cucumis anguria L.	Maxixe/maroon cucumber	Exotic	Essential[b]	Data deficient
Cucumis melo L.	Melão/melonseed	Exotic	Essential[a]	$116,555,400.50
Cucumis sativus L.	Pepino/cucumber	Exotic	Great[a]	Data deficient
Cucurbita maxima Duchesne	Abóbora/pumpkin	Exotic	Essential[a]	Data deficient
Cucurbita pepo L.	Abobrinha/zucchine	Exotic	Essential[c]	Data deficient
Momordica charantia L.	Melão de são joão/(−)	Exotic	Modest[a]	Data deficient
Sicyos edulis Jacq.	Chuchu/chayote	Exotic	Data deficient	Data deficient
Dioscoreales				
Dioscoreaceae				
Dioscorea sp.	Inhame/yam	Native	Non-dependent[a]	Data deficient
Ericales				

(*continued on next page*)

Table 1 (*continued*)

Taxa	Common name (Brazilian Portuguese/English)	Origin	Pollinator dependence[1]	EVP[2]
Ebenaceae				
Diospyros kaki L.f.	Caqui/persimmon	Exotic	Little[c]	$17,764,732.13
Ericaceae				
Vaccinium corymbosum L.	Mirtilo/blueberry	Exotic	Great[c]	Data deficient
Lecythidaceae				
Bertholletia excelsa Bonpl.	Castanha do Pará/Brazil nut	Native	Essential[a]	Data deficient
Sapotaceae				
Pouteria caimito (Ruiz & Pav.) Radlk.	Abiu/(−)	Native	Data deficient	Data deficient
Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	Quixabá/(−)	Native	Essential[a]	Data deficient
Theaceae				
Camellia sinensis (L.) Kuntze	Chá-da-índia/tea plant	Exotic	Non-dependent[a]	$0.00
Fabales				
Fabaceae				
Adesmia exilis Clos	Babosinha do campo/(−)	Exotic	Essential[a]	Data deficient
Arachis hypogaea L.	Amendoim/peanut	Native	Little[c]	$122,600,289.00
Cajanus cajan (L.) Huth	Feijão gandu/pigeon pea	Exotic	Little[c]	Data deficient
Dipteryx alata Vogel	Baru/(−)	Native	Essential[a]	Data deficient
Glycine max (L.) Merr.	Soja/soybean	Exotic	Modest[c]	$31,697,095,465.00
Glycine wightii	Soja perene/perennial soybean	Exotic	Modest[b]	Data deficient
Hymenaea stigonocarpa Mart. ex Hayne	Jatobá do cerrado/(−)	Native	Essential[b]	Data deficient
Medicago sativa L.	Alfafa/lucerne	Exotic	Data deficient	Data deficient
Phaseolus sp.	Feijão/bean	Native	Little[a]	$558,794,403.13
Phaseolus vulgaris L.	Feijão/common bean	Native	Little[c]	Data deficient
Pisum sativum L.	Ervilha/pea	Exotic	Data deficient	Data deficient
Vicia faba L.	Fava/broad bean	Exotic	Modest[c]	$5,719,985.25
Vigna unguiculata (L.) Walp.	Feijão de corda/cow peas	Exotic	Non-dependent[a]	Data deficient
Fagales				
Juglandaceae				
Carya illinoinensis (Wangenh.) K.Koch	Noz pecã/pecan	Exotic	Data deficient	Data deficient
Juglans regia L.	Noz-inglesa/English walnut	Exotic	Data deficient	Data deficient
Gentianales				
Apocynaceae				
Hancornia speciosa Gomes	Mangaba/(−)	Native	Essential[a]	Data deficient
Rubiaceae				
Coffea arabica L.	Café-arábica/coffee	Exotic	Modest[a]	$2,489,024,994.75
Coffea canephora Pierre ex A.Froehner	Café-canephora/robusta coffee	Exotic	Modest[c]	$747,635,675.50
Cordiera macrophylla (K.Schum.) Kuntze	Marmelada-de-bezerro/(−)	Native	Essential[b]	Data deficient
Lamiales				
Lamiaceae				
Ocimum basilicum L.	Manjericão/basil	Native	Data deficient	Data deficient
Ocimum carnosum (Spreng.) Link & Otto ex Benth.	Alfavaca/(−)	Native	Data deficient	Data deficient
Oleaceae				
Olea europaea L.	Azeitona/olive	Exotic	Non-dependent[c]	$0.00
Pedaliaceae				
Sesamum indicum L.	Gergelim/sesame	Exotic	Little[a]	Data deficient
Plantaginaceae				
Plantago sp.	Erva-de-orelha/(−)	Native	Data deficient	Data deficient
Verbenaceae				
Lippia alba (Mill.) N.E.Br. ex Britton & P.Wilson	Erva-cidreira/(−)	Native	Data deficient	Data deficient
Laurales				
Lauraceae				
Persea americana Mill	Abacate/avocado	Exotic	Great[a]	$98,833,565.25
Magnoliales				
Annonaceae				
Annona aurantiaca Barb.Rodr.	Araticum de cabo verde/(−)	Native	Essential[b]	Data deficient
Annona cherimola Mill.	Cherimóia/cherimoya	Exotic	Essential[a]	Data deficient
Annona coriacea Mart.	Araticum liso/(−)	Native	Essential[a]	Data deficient
Annona cornifolia A.St.-Hil.	Caritu cuí/(−)	Native	Essential[b]	Data deficient
Annona crassiflora Mart.	Araticum/(−)	Native	Essential[a]	Data deficient
Annona montana Macfad	Guanabana/mountain soursop	Native	Essential[b]	Data deficient
Annona muricata L.	Graviola/soursop	Native	Little[a]	Data deficient
Annona squamosa L.	Pinha/sugar apple	Exotic	Essential[a]	Data deficient
Annona tomentosa R.E.Fr.	Araticum marolo/(−)	Native	Essential[b]	Data deficient
Xylopia brasiliensis Spreng.	Pindaíba/(−)	Native	Data deficient	Data deficient
Malpighiales				
Caryocaraceae				
Caryocar brasiliense A.St.-Hil.	Pequi/pekea nut	Native	Essential[a]	Data deficient
Caryocar villosum (Aubl.) Pers.	Piquiá/(−)	Native	Essential[b]	Data deficient
Clusiaceae				
Platonia insignis Mart.	Bacuri/(−)	Native	Essential[b]	Data deficient
Euphorbiaceae				
Jatropha curcas L.	Pinhão manso/Barbados nut	Native	Essential[a]	Data deficient
Manihot esculenta Crantz	Mandioca/cassava	Native	Non-dependent[a]	$0.00
Ricinus communis L.	Mamona/castor bean	Exotic	Great[a]	$14,568,196.13
Malpighiaceae				

(*continued on next page*)

Table 1 (*continued*)

Taxa	Common name (Brazilian Portuguese/English)	Origin	Pollinator dependence[1]	EVP[2]
Byrsonima coccolobifolia Kunth	Moressuma/(−)	Native	Essential[b]	Data deficient
Byrsonima crassifolia (L.) Kunth	Murici/Nance	Native	Essential[a]	Data deficient
Byrsonima gardneriana A.Juss.	Murici pitanga/(−)	Native	Essential[b]	Data deficient
Malpighia emarginata DC.	Acerola/(−)	Exotic	Essential[a]	Data deficient
Passifloraceae				
Passiflora alata Curtis	Maracujá-doce/sweet passionfruit	Native	Essential[b]	Data deficient
Passiflora cincinnata Mast.	Maracujá-do-mato/(−)	Native	Essential[b]	Data deficient
Passiflora coccinea Aubl.	Maracujá-poranga/(−)	Native	Essential[b]	Data deficient
Passiflora edulis Sims	Maracujá-amarelo/passionfruit	Native	Essential[a]	$284,549,580.00
Passiflora giberti N.E.Br.	Maracujá-de-veado/(−)	Native	Essential[b]	Data deficient
Passiflora nitida Kunth	Maracujá-suspiro/(−)	Native	Essential[b]	Data deficient
Malvales				
Bixaceae				
Bixa orellana L.	Urucum/annatto	Native	Modest[a]	$6,452,524.75
Malvaceae				
Abelmoschus esculentu (L.) Moench	Quiabo/okra	Exotic	Data deficient	Data deficient
Corchorus capsularis L.	Juta/jute	Exotic	Data deficient	Data deficient
Malva L.	Malva/(−)	Exotic	Data deficient	Data deficient
Theobroma cacao L.	Cacau/Cacao	Native	Essential[c]	$737,067,369.50
Theobroma grandiflorum (Willd. ex Spreng.) K.Schum.	Cupuaçu/(−)	Native	Essential[a]	Data deficient
Theobroma speciosum Willd. ex Spreng.	Cacauí/(−)	Native	Essential[b]	Data deficient
Myrtales				
Lythraceae				
Punica granatum L.	Romã/pomegranate	Exotic	Data deficient	Data deficient
Melastomataceae				
Mouriri guianensis Triana	Muriri/(−)	Native	Data deficient	Data deficient
Myrtaceae				
Blepharocalyx salicifolius (Kunth) O.Berg	Murta/(−)	Native	Essential[a]	Data deficient
Campomanesia adamantium (Cambess.) O.Berg	Guavira/(−)	Native	Great[a]	Data deficient
Campomanesia guazumifolia (Cambess.) O.Berg	Sete-capotes/(−)	Native	Essential[b]	Data deficient
Campomanesia phaea (O.Berg) Landrum	Cambuci/(−)	Native	Essential[a]	Data deficient
Campomanesia pubescens (Mart. ex DC.) O.Berg	Guabiroba/(−)	Native	Essential[a]	Data deficient
Campomanesia velutina (Cambess.) O.Berg	Guabiroba-veludo/(−)	Native	Essential[b]	Data deficient
Campomanesia xanthocarpa (Mart.) O.Berg	Guabiroba-amarela/(−)	Native	Essential[b]	Data deficient
Eugenia dysenterica DC.	Cagaita/(−)	Native	Great[a]	Data deficient
Eugenia pitanga (O.Berg) Nied.	Pitanga-peba/(−)	Native	Essential[b]	Data deficient
Eugenia pyriformis Cambess.	Uvaia/(−)	Native	Essential[b]	Data deficient
Eugenia selloi B.D.Jacks	Pitangatuba/(−)	Native	Essential[a]	Data deficient
Eugenia sp.	Pitanga-silvestre/(−)	Native	Essential[b]	Data deficient
Eugenia speciosa Cambess.	Laranjinha do mato/(−)	Native	Essential[b]	Data deficient
Eugenia stipitata McVaugh	Araçá-boi/(−)	Native	Essential[b]	Data deficient
Eugenia uniflora Nied.	Pitanga/(−)	Native	Essential[a]	Data deficient
Feijoa sellowiana (O.Berg) O.Berg	Goiaba-serrana/(−)	Native	Data deficient	Data deficient
Myrcia linearifolia Cambess.	Araçazinho/(−)	Native	Essential[b]	Data deficient
Myrcia splendens (Sw.) DC.	Baicamim/(−)	Native	Essential[b]	Data deficient
Myrciaria dubia (Kunth) McVaugh	Camu-camu/(−)	Native	Data deficient	Data deficient
Myrciaria floribunda (H.West ex Willd.) O.Berg	Cambuíva/(−)	Native	Data deficient	Data deficient
Myrciaria glomerata O.Berg	Cabeludinha/(−)	Native	Data deficient	Data deficient
Plinia cauliflora (Mart.) Kausel	Jabuticaba/Brazilian grape	Native	Non-dependent[a]	Data deficient
Plinia coronata (Mattos) Mattos	Jabuticaba-de-coroa/(−)	Native	Non-dependent[b]	Data deficient
Plinia peruviana (Poir.) Govaerts	Jabuticaba-sabará/(−)	Native	Non-dependent[b]	Data deficient
Psidium acutangulum DC.	Araçá-pera/(−)	Native	Great[b]	Data deficient
Psidium cattleyanum Sabine	Araçá-rosa/(−)	Native	Great[b]	Data deficient
Psidium firmum O.Berg	Araçá-do-cerrado/(−)	Native	Great[a]	Data deficient
Psidium grandifolium Mart. ex DC.	Araçá-cinzento/(−)	Native	Great[b]	Data deficient
Psidium guajava L.	Goiaba/Guava	Native	Great[a]	$135,390,328.50
Siphoneugena densiflora O.Berg	Cambuí-azul/(−)	Native	Essential[b]	Data deficient
Syzygium aromaticum (L.) Merr. & L.M.Perry	Cravo-da-índia/clove	Exotic	Non-dependent[a]	Data deficient
Syzygium cumini (L.) Skeels	Jambolão/(−)	Exotic	Data deficient	Data deficient
Syzygium malaccense (L.) Merr. & L.M.Perry	Jambo/(−)	Exotic	Great[a]	Data deficient
Oxalidales				
Oxalidaceae				
Averrhoa carambola L.	Carambola/star fruit	Exotic	Essential[b]	Data deficient
Piperales				
Piperaceae				
Piper nigrum L.	Pimenta-do-reino/black pepper	Exotic	Non-dependent[c]	$0.00
Piper retrofractum Vahl	Pimenta-longa/javanese long pepper	Exotic	Non-dependent[b]	Data deficient
Poales				
Bromeliaceae				
Ananas ananassoides (Baker) L.B.Sm.	Abacaxi do cerrado/(−)	Native	Non-dependent[a]	Data deficient
Ananas comosus (L.) Merr.	Abacaxi/pineapple	Native	Non-dependent[c]	$0.00
Poaceae				
Avena sativa L.	Aveia/oat	Exotic	Non-dependent[c]	$0.00
Hordeum vulgare L.	Cevada/barley	Exotic	Non-dependent[c]	$0.00
Oryza sp.	Arroz/rice	Exotic	Non-dependent[c]	$0.00

(*continued on next page*)

Table 1 (*continued*)

Taxa	Common name (Brazilian Portuguese/English)	Origin	Pollinator dependence[1]	EVP[2]
Saccharum officinarum L.	Cana-de-açúcar/sugar cane	Native	Non-dependent[c]	$0.00
Secale cereale L.	Centeio/rye	Exotic	Non-dependent[c]	$0.00
Sorghum bicolor (L.) Moench	Sorgo/millet	Exotic	Data deficient	Data deficient
Triticosecale rimpaui (M.Graebn.) Wittm. ex A.W.Hill	Triticale/triticale	Exotic	Non-dependent[a]	$0.00
Triticum sp.	Trigo/wheat	Exotic	Non-dependent[c]	$0.00
Zea mays L.	Milho/corn	Exotic	Non-dependent[c]	$0.00
Proteales				
Proteaceae				
Macadamia integrifolia Maiden & Betche	Macadâmia/macadamia	Exotic	Data deficient	Data deficient
Rosales				
Moraceae				
Ficus carica L.	Figo/fig	Exotic	Modest[c]	$12,756,000.25
Rhamnaceae				
Ziziphus joazeiro	Juá/(−)	Native	Essential[a]	Data deficient
Rosaceae				
Cydonia oblonga Mill.	Marmelo/quince	Exotic	Data deficient	Data deficient
Fragaria x ananassa	Morango/strawberry	Exotic	Modest[c]	Data deficient
Malus domestica (Suckow) Borkh	Maçã/apple	Exotic	Essential[a]	$434,131,029.50
Prunus armeniaca L.	Damasco/apricot	Exotic	Great[a]	Data deficient
Prunus cerasus L.	Cereja/cherry	Exotic	Great[a]	Data deficient
Prunus persica (L.) Batsch	Pêssego/peach	Exotic	Great[a]	$71,744,953.88
Prunus sp.	Ameixa/plum	Exotic	Great[a]	Data deficient
Pyrus pyrifolia (Burm.f.) Nakai	Pêra/pear	Exotic	Essential[a]	$7,389,949.00
Rubus sp.	Amora/blackberry	Native	Modest[a]	Data deficient
Sapindales				
Anacardiaceae				
Anacardium occidentale L.	Cajú/cashew	Native	Essential[a]	$88,480,532.00
Mangifera indica L.	Manga/mango	Exotic	Non-dependent[a]	$0.00
Schinus terebinthifolia Raddi	Aroeira vermelha/(−)	Native	Essential[b]	Data deficient
Spondias mombin L.	Cajá/mombin	Native	Essential[a]	Data deficient
Spondias purpurea L.	Ceriguela/red mombin	Exotic	Essential[b]	Data deficient
Spondias tuberosa Arruda	Umbu/Brazil plum	Native	Essential[a]	Data deficient
Rutaceae				
Citrus aurantiifolia (Christm.) Swingle	Lima/lime	Exotic	Data deficient	Data deficient
Citrus limonum L.	Limão/lemon	Exotic	Little[c]	$69,334,706.00
Citrus reticulata Blanco	Tangerina/tangerine	Exotic	Essential[a]	$252,056,287.00
Citrus sinensis (L.) Osbeck	Laranja/Orange	Exotic	Modest[a]	$1,162,600,937.75
Sapindaceae				
Litchi chinensis Sonn.	Lichia/Litchi	Exotic	Data deficient	Data deficient
Paullinia cupana Kunth	Guaraná/(−)	Native	Great[a]	$5,545,383.38
Talisia esculenta (A.St.-Hil., A.Juss. & Cambess.) Radlk.	Pitomba/(−)	Native	Essential[b]	Data deficient
Solanales				
Convolvulaceae				
Ipomoea batatas (L.) Lam.	Batata-doce/sweet potato	Exotic	Non-dependent[a]	$0.00
Solanaceae				
Capsicum annuum L.	Pimentão/bell pepper	Exotic	Modest[a]	Data deficient
Capsicum chinense Jacq.	Pimenta-malagueta/Chile pepper	Native	Great[a]	Data deficient
Capsicum frutescens L.	Pimenta-malagueta-silvestre/(−)	Native	Modest[a]	Data deficient
Capsicum sp1.	Pimenta/pepper	Exotic	Little[c]	Data deficient
Capsicum sp2.	Pimenta-doce/sweet pepper	Exotic	Non-dependent[b]	Data deficient
Solanum lycopersicum L.	Tomate/tomato	Exotic	Little[a]	$300,457,410.75
Solanum melongena L.	Beringela/eggplant	Exotic	Great[a]	Data deficient
Solanum paniculatum Mart.	Jurubeba/(−)	Native	Essential[a]	Data deficient
*Solanum sessiliflorum*Dunal	Cubiu/(−)	Native	Essential[b]	Data deficient
Solanum tuberosum L.	Batata-inglesa/potato	Exotic	Non-dependent[a]	$0.00
Vitales				
Vitaceae				
Vitis labrusca	Uva/grape	Exotic	Little[a]	$197,857,870.88
Zingiberales				
Musaceae				
Musa sp.	Banana/banana	Exotic	Non-dependent[a]	$0.00
Zingiberaceae				
Zingiber officinale Roscoe	Gengibre/ginger	Exotic	Non-dependent[a]	Data deficient

Brazil).

Moreover, to investigate our second, third and fourth questions related to cropland area, pollinator dependence and pollinator shortage risk, we constructed three different two-way ANOVAs (Legendre and Legendre, 2012). In these ANOVAs, the predictor variables were always the same three: (i) the six biomes of Brazil, (ii) the crop origin, and (iii) the interaction between these last two. We added a third level in the "crop origin" categorical variable in our analysis. Besides *native* and *exotic* crops, we also calculated crop area, pollinator dependence and pollinator shortage risk for *exotic crops without soybean* to investigate how soybean, the crop that occupies most of the cultivated areas in Brazil (FAO, 2016), influences the patterns we found. The response variable was different for each of these three ANOVAs. For the first ANOVA, the crop area in each Brazilian county was the response variable (i.e., the final model is *crop area* ~ *biomes* + *crop origin* + *biomes*:*crop origin*). In the second ANOVA, we calculated the proportion of the agricultural yield that depends on pollination for each of the 5572 counties of Brazil and used this variable as a response variable, as this proportion does not depend on county area (i.e., the final model is *proportion of production dependent on pollination ~ biomes + crop origin + biomes*: *crop origin*). In the last ANOVA, the pollinator shortage risk index was the response variable (i.e., the final model is *pollinator shortage risk index ~ biomes + crop origin + biomes*: *crop origin*). Whenever we identified a statistically significant difference in any ANOVA throughout this study (i.e., using a significance level of 0.05), we conducted a post-hoc Tukey test to check the pairwise differences between levels (Legendre and Legendre, 2012).

We constructed maps for crop richness, crop area, pollinator dependence and pollinator shortage risk of native and exotic crops across all counties of Brazil to represent the spatial distribution of these response variables. All data treatment and analysis were conducted in the R language (R Development Core Team, 2020) and all graphical visualizations of the results were constructed using the *ggplot2* package (Wickham, 2011).

3. Results

3.1. Pollinator and crop diversity

From the 199 food plant species that are cultivated in Brazil, we were able to retrieve information regarding their respective pollinator for 104 species of plants. Overall, we retrieved that 202 bee species, 91 species of other insects and 18 vertebrate species are responsible for the pollination of 68 native and 36 exotic crops that had information regarding their pollinators. We found no differences in pollinator richness between native and exotic crops ($F = 0.13$, $P = 0.72$; Appendix S1, Table S1), even after considering the different taxonomic groups ($F = 2.4$, $P = 0.09$; Appendix S1, Fig. S1). Bees and other insects can pollinate native crops as much as exotic ones, with *Apis mellifera* being, by far, the bee species with the greatest number of interactions with native and exotic crops, followed by *Trigona spinipes*, *Xylocopa frontalis* and *Bombus morio* (Fig. 1). However, we found that vertebrate species pollinate only native crops, not exotic ones (Fig. 1).

We found that counties that cultivate more species of native crops are situated in the North of Brazil, especially in the Amazon (Fig. 2A-C). Whereas counties that cultivate more species of exotic crops are situated in the South and Southeast of Brazil, especially in the Pampa (Figure 2BG). Across the biomes, we found that crop richness was different between biomes and these differences depend on crop origin ($F = 205.05$, $P < 0.001$; Appendix S2). Within the biomes, we found that the richness of exotic crops always surpassed the richness of native crops in all Brazilian biomes (Fig. 2C-H).

3.2. Reproductive systems, Pollinator dependence and Economic value of pollination

In terms of the reproductive systems, we observed that most of the cultivated crops in Brazil are self-compatible (52.0%), with 39.9% of the crops being self-incompatible and only 8.1% being obligatory cross-pollinated. Regarding the origin of the crops (Fig. 3A), we observe that, in contrast to what was observed at the country level excluding the crop's origin, most of the native crops are self-incompatible (54.0%), followed by self-compatible (34.4%) and obligatory cross-pollination (11.6%). On the other hand, the most representative reproductive system in exotic crops was self-compatibility (69.4%), followed by self-incompatibility (25.8%) and obligatory cross-pollination (4.8%; Fig. 3A).

We were able to retrieve data regarding pollination dependence for 82.4% out of the 199 crop species, of which 77.4% are dependent on pollinators at some level (Appendix S3). Considering the origin, we observe that 90% of the native crops that we were able to retrieve pollinator dependence information depend on pollinators to some extent, contrasting with 62.16% of the exotic crops (Appendix S3; Fig. 3B). Regarding the categories of pollinator dependence, we observe that for native crops, 62.2% are essentially dependent on pollinators, 17.7% are greatly dependent, 3.3% are modestly dependent, and 6.7% are little dependent (Table 1; Fig. 3B). Considering the exotic crops cultivated in Brazil, we verify that 18.9% are essentially dependent on pollinators, 16.2% are greatly dependent, 16.2% are modestly dependent, and 10.8% are little dependent (Table 1; Fig. 3B). Nevertheless,

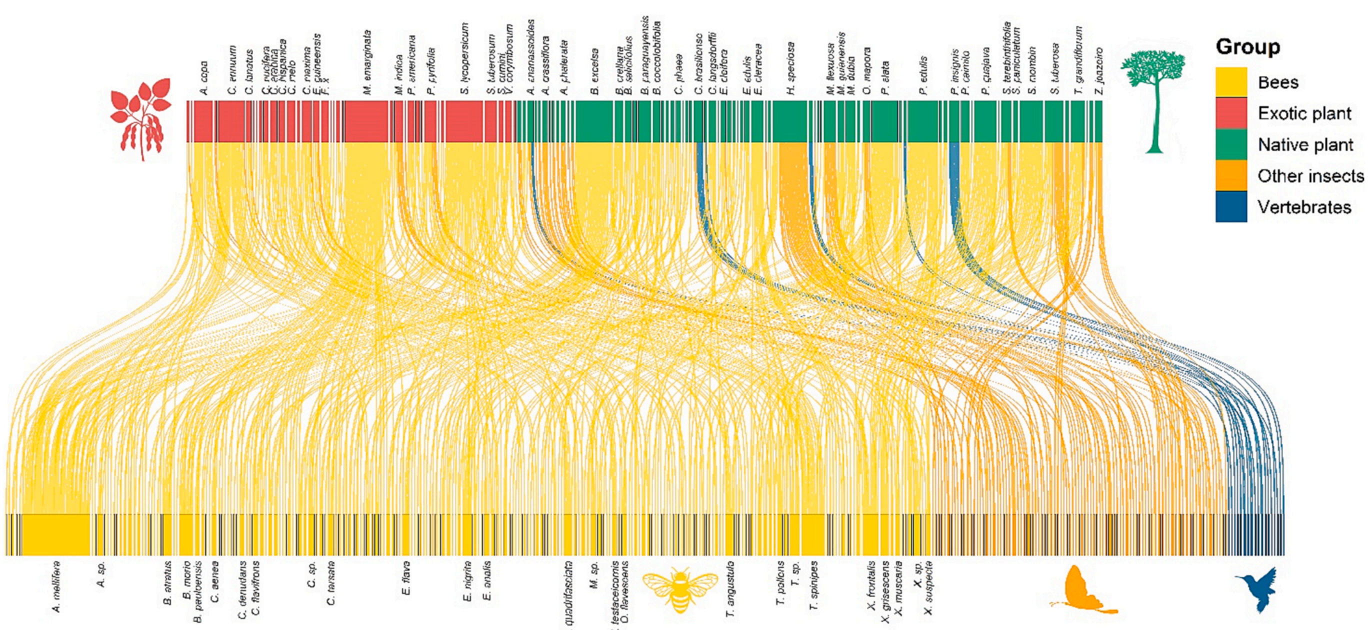

Fig. 1. Plant-pollinator network comprising 202 bees, 91 other insects and 18 vertebrate species that pollinate the 68 native and 36 exotic crops evaluated in this study across Brazil. Top row comprises plant species, which are colored according to crop origin (i.e., reds are exotic and greens are native), while bottom row represents the pollinator species colored according to major taxonomic groups (i.e., yellows are bees, oranges are other insects and blues are vertebrates). Lines represent which pollinator species pollinate each crop species. The size of bars in the top and bottom rows represent the number of interactions in which a specific species is involved, with bars larger than the 75% quantile distribution being identified by the species name.

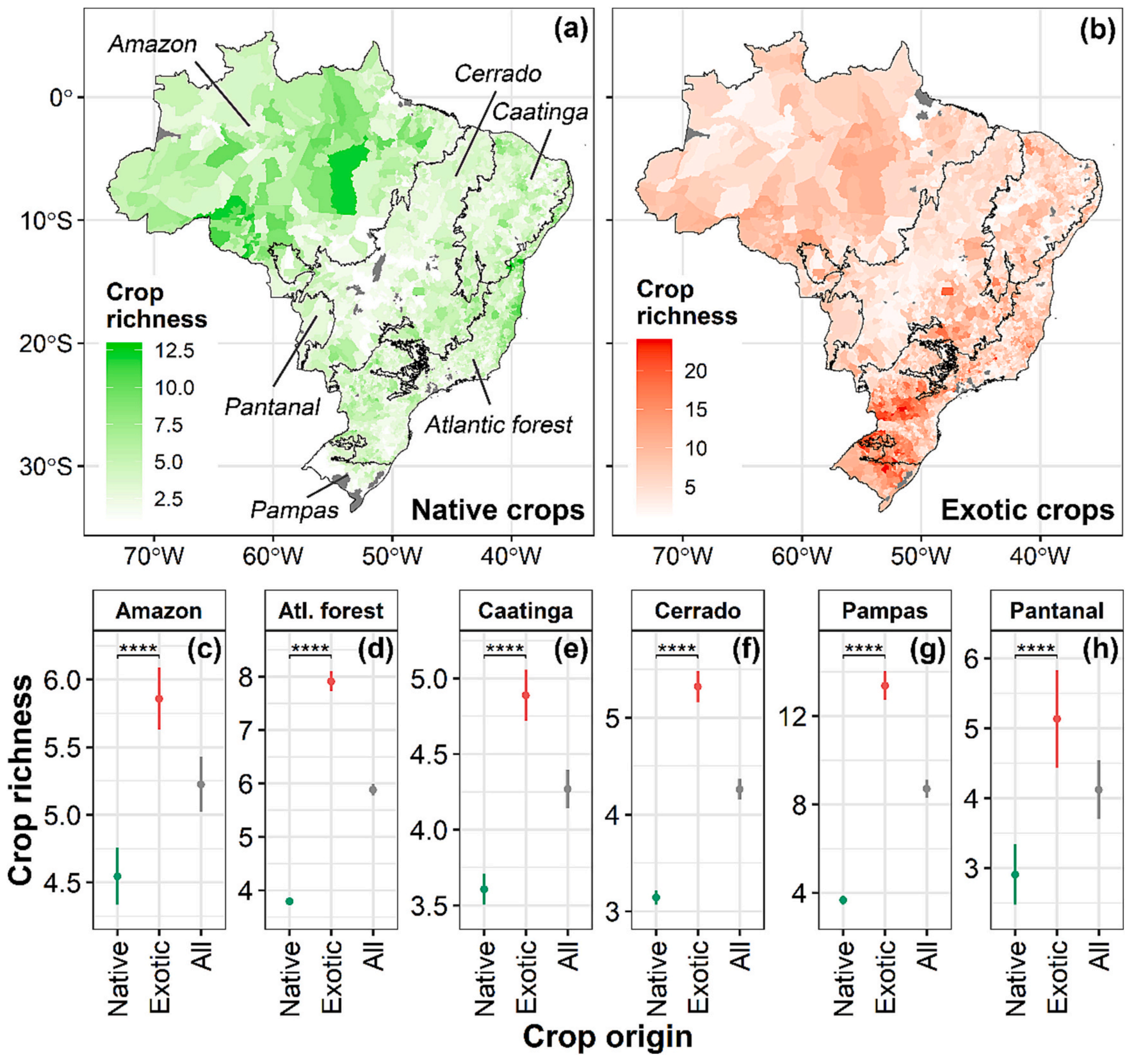

Fig. 2. Graphical representations of the crop richness across Brazil for (a) native and (b) exotic crops. Panels from c to h represent the difference in richness of native and exotic crops within each biome of Brazil. Points in the middle of bars in plots c to h represent the mean richness, while the bars represent its 95% possible confidence interval. Lines above bars in panels c to h represent the pairwise comparisons between crop origin within each biome. In this way, if a comparison is represented by a "****", then their values of crop richness are statistically different ($p < 0.0001$), as returned by the post-hoc Tukey test. For the results of the pairwise comparisons between biomes, see Appendix S2.

although there are more native crops dependent on pollinators than exotics, we observe that still have a lack of knowledge in terms of the crop pollination of the native crops in Brazil, mainly those that are native food species. This is evidenced by the remaining 35 crops without data available for dependence on pollinators, of which 48.5% (17) are native crops.

Native crops present both extremes of pollination dependence, with some counties in the North and Northeast of Brazil presenting 100% of their croplands dependent on pollination (Fig. 4A), and others in the North and Central Brazil presenting nearly 0% of pollinator dependence (Fig. 4A). As for exotic crops, we evidenced that pollination dependence is evenly distributed across the extension of Brazil, with most counties presenting at least 25% of pollinator dependence for their exotic croplands, on average, especially in South and Central Brazil (Fig. 4B). However, when we removed soybean from our analysis, we found that exotic crops cultivated in counties of the North and Southeast of Brazil have a higher pollinator dependence than other regions (Fig. 4C). We found differences in the percentage of the croplands that depend on pollination between the six biomes of Brazil, especially when considering its interaction with crop origin ($F = 112.21$, $P < 0.001$; Appendix S3). Within Brazil's biomes, we evidenced that exotic croplands depend more on biotic pollination than native crops (Fig. 4D, E, G, H and I), except in the Caatinga dry forest (Fig. 4F). However, after the removal of soybean from this analysis, the pollinator dependence of exotic croplands became statistically equal to the pollinator dependence of native croplands in the Amazon (Fig. 4D), Atlantic forest (Fig. 4E), Pantanal (Fig. 4I), and even lower in the Pampa (Fig. 4H).

Considering only the 52 crops from which we were able to retrieve cropland area, we estimate that pollination contributes to US$ 41,458,757,637 out of the total earnings of US$ 131,352,000,000, which corresponds to one-third of the agriculture earnings of Brazil in 2021. When we take into consideration the origins of the crops, we estimate that pollination contributed to earnings of US$ 2,887,028,601 for native crops and US$ 38,571,729,036 for exotic crops. The five crops for which the economic value of pollination is greater are soybean (US$ 31,697,095,465; exotic crop), coffee (i.e., *Coffea arabica* and *C. canephora*; US$ 3,236,660,670; exotic crop), orange (US$ 1,162,600,938; exotic crop), açaí (US$ 738,132,279; native crop), and cacao (US$ 737,067,370; native crop), respectively, which together account for 90% of the total economic value of pollination in Brazilian croplands.

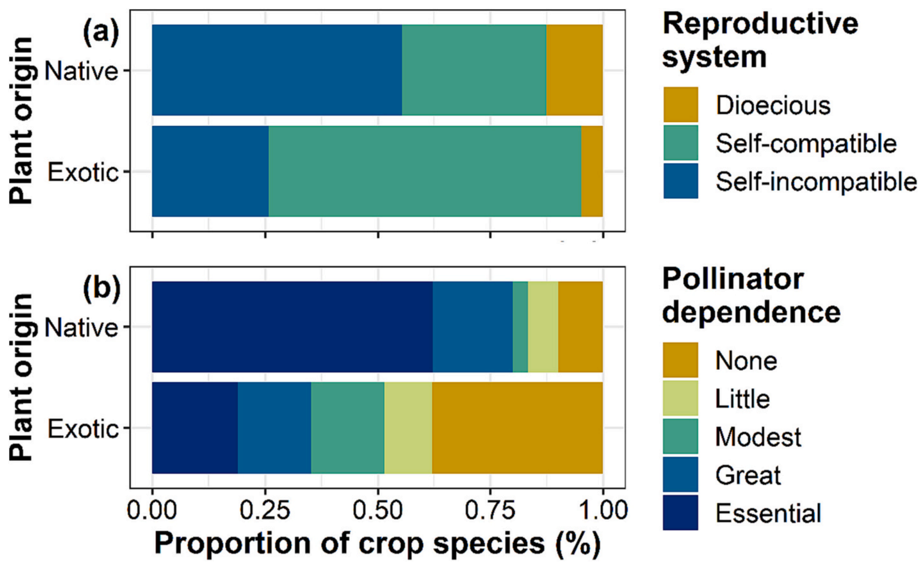

Fig. 3. Proportion of crop species in each (a) reproductive system and (b) pollinator dependence categories, considering the crop origin (i.e., native and exotic).

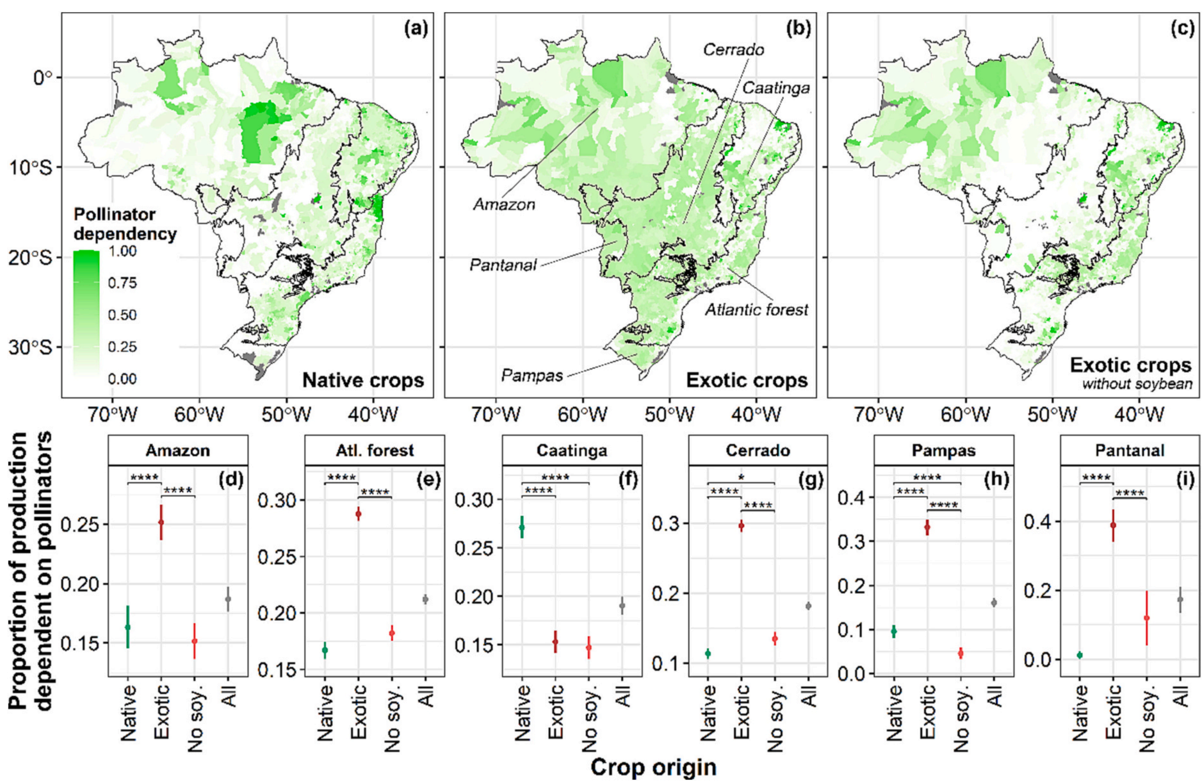

Fig. 4. Maps representing the spatial distribution of pollinator dependence of (a) native croplands, (b) exotic croplands, and (c) exotic croplands without soybean across the counties of Brazil. Panels from d to i represent the differences in pollinator dependence between native and exotic croplands (also after removing soybean, under "*No soy.*") within each of the major biomes of Brazil. Points in the middle of bars in plot (b) represent the mean area, while the bars represent its 95% possible confidence interval. Lines above bars in panels c to h represent the pairwise comparisons between crop origin within each biome. In this way, "****" is $p < 0.0001$, "***" is $p < 0.001$, and "*" is $p < 0.05$ as returned by the post-hoc Tukey test. If no lines are shown above a pair of bars, then they do not differ in crop area (i.e., $p > 0.05$). For the results of the pairwise comparisons between biomes, see Appendix S3.

3.3. Cropland area

We observed that 81.27% of the harvested area in Brazil is cultivated with exotic food crops, and only 18.73% with native crops (Fig. 5A). Only soybean occupies 46.79% of the total area of croplands in Brazil. When we removed soybean crops from the analysis, we evidenced that 35.2% of the remaining crop area is devoted to the cultivation of native crops, whereas 64.8% is devoted to other exotic crops (Fig. 5B). However, there is still a great lack of information on agricultural areas in Brazil, with 68.12% of the food crops without data for the harvested or cultivated area, of which 34.04% are exotic and 65.96% are native.

The area devoted to the cultivation of crops in Brazil differed across the six Brazilian biomes, with remarkable differences in the area devoted to native and exotic crops ($F = 31.28$, $P < 0.001$; Appendix S4).

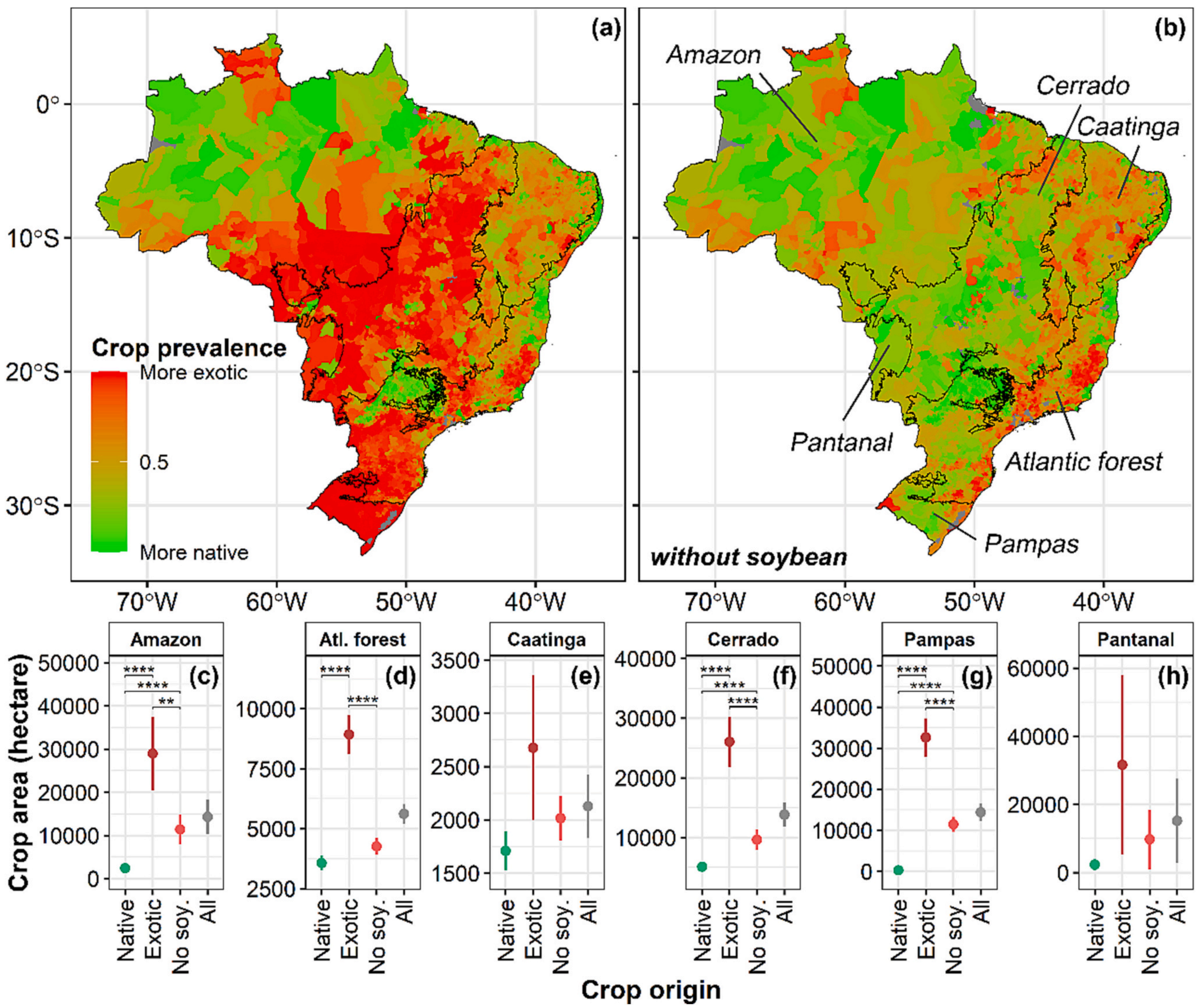

Fig. 5. Graphical representations of the prevalence of native and exotic crops across all counties of Brazil (a) considering soybean and (b) after removing soybean from our analysis. Panels from c to h represent the differences in area (in hectares) devoted to the cultivation of native and exotic crops (also after removing soybean, under "*No soy.*") within the six major biomes of Brazil. Points in the middle of bars in plot (b) represent the mean area, while the bars represent its 95% possible confidence interval. Lines above bars in panels c to h represent the pairwise comparisons between crop origin within each biome. In this way, "****" is $p < 0.0001$ and "***" is $p < 0.001$, as returned by the post-hoc Tukey test. If no lines are shown above a pair of bars, then they do not differ in crop area (i.e., $p > 0.05$). For the results of the pairwise comparisons between biomes, see Appendix S4.

The Pampa region presents the largest area devoted exclusively to the cultivation of exotic crops (Fig. 5G), followed by the Pantanal (Fig. 5H), Amazon (Fig. 5C), Cerrado (Fig. 5F), Atlantic forest (Fig. 5D), and the Caatinga dry forest (Fig. 5E). Moreover, the Cerrado has the largest cropland area devoted to native crops (Fig. 5F), followed by the Atlantic forest (Fig. 5D), the Amazon (Fig. 5C), the Pantanal (Fig. 5H), the Caatinga dry forest (Fig. 5E) and the Pampa (Fig. 5G; Appendix S4). Within each biome, the area devoted to the cultivation of exotic crops was higher than the area for the cultivation of native crops (Fig. 5C, D, F and G), except for the Caatinga dry forest (Fig. 5E) and the Pantanal (Fig. 5H). Once we removed soybean from our analysis, we evidenced that the area devoted to the cultivation of exotic crops decreased in all biomes, becoming essentially equal to the crop area devoted to the cultivation of native crops in the Atlantic forest (Fig. 5D).

3.4. Pollinator shortage risk

We calculated pollinator shortage risk for the 52 crops in which cropland area was available and found that pollination risk is unevenly distributed across Brazil. For native crops, pollinator shortage risk is mainly concentrated in the Northeast and the Southeast of Brazil, but also in some counties in the North (Fig. 6A). Whereas for exotic crops, pollinator shortage is higher in South, Southeast and Central Brazil (Fig. 6B). After the removal of soybean from this analysis, we evidenced that the pollinator shortage risk of the remaining exotic crops is higher in the Southeast of Brazil, with many areas of overlap where the pollinator risk of native crops is also high (Fig. 6C). We found that pollinator shortage risk differs across the six biomes of Brazil, especially when we considered its interaction with crop origin ($F = 94.12$, $P < 0.001$; Appendix S5). Pollinator shortage risk is higher in exotic crops than native ones in all biomes but the Caatinga dry forest (Fig. 6F). The Atlantic forest is at a higher risk of pollinator shortage than other Brazilian biomes (mean pollinator shortage risk of 0.16 ± 0.14 SD), followed by the Pampa (0.14 ± 0.12), the Cerrado (0.12 ± 0.14), the Pantanal (0.10 ± 0.12), the Caatinga dry forest (0.09 ± 0.10), and the Amazon (0.08 ± 0.09), respectively. When we removed soybean from the analysis, we evidenced that the pollinator shortage risk became equal to the pollinator shortage risk of native crops in the Amazon (Fig. 6D) and Pantanal

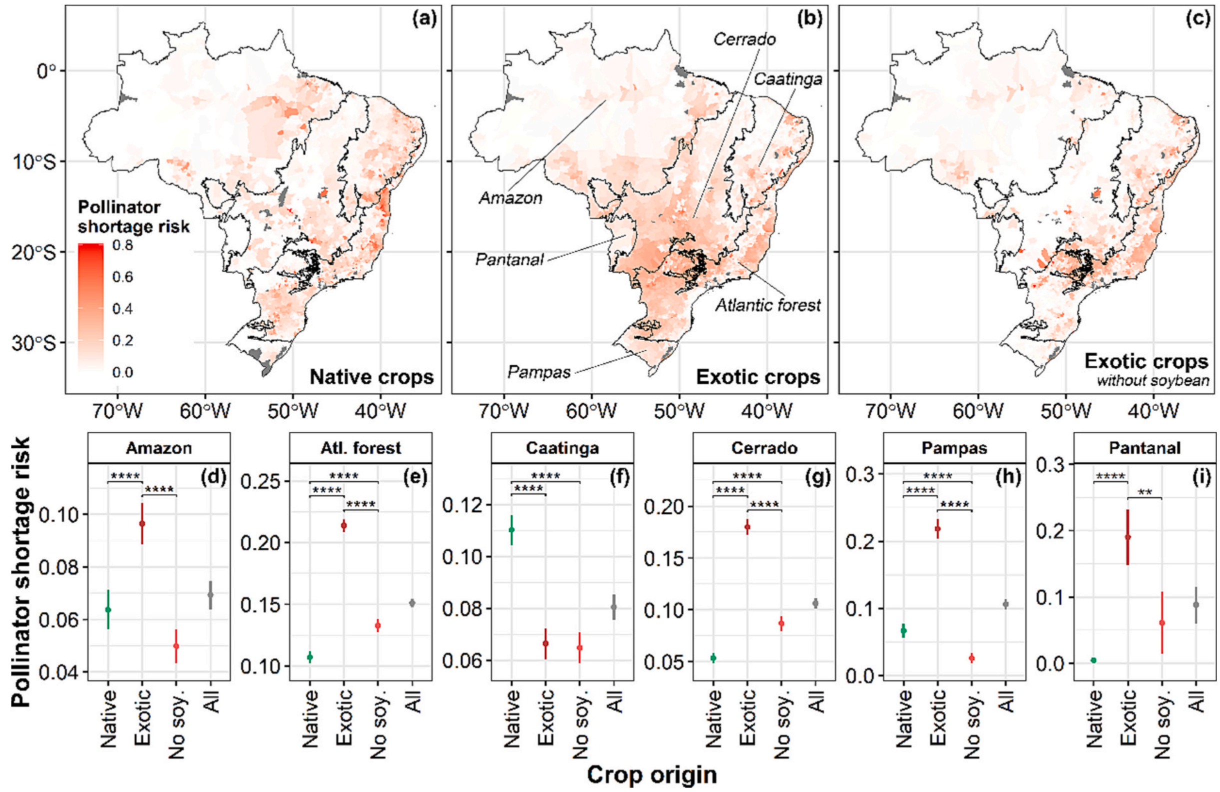

Fig. 6. Maps representing the spatial distribution of pollinator shortage risk of (a) native croplands, (b) exotic croplands, and (c) exotic croplands without soybean across the counties of Brazil. Panels from d to i represent the differences in pollinator shortage risk between native and exotic croplands (also after removing soybean, under "*No soy.*") within each of the major biomes of Brazil. Points in the middle of bars in plot (b) represent the mean area, while the bars represent its 95% possible confidence interval. Lines above bars in panels c to h represent the pairwise comparisons between crop origin within each biome. In this way, "****" is $p < 0.0001$ and "*" is $p < 0.05$, as returned by the post-hoc Tukey test. If no lines are shown above a pair of bars, then they do not differ in crop area (i.e., $p > 0.05$). For the results of the pairwise comparisons between biomes, see Appendix S5.

(Fig. 6I), and lower than the native crops in the Pampa (Fig. 6H).

4. Discussion

Our findings indicate that over half (53.77%) of the food crops growing in Brazil are native, and most of this crop diversity is concentrated in the Atlantic forest. These crops rely heavily on biotic pollination, particularly from bees. Overall, we found that socioecological patterns of food plants are distributed unevenly across Brazil, with different regions and crops from different origins presenting contrasting patterns. Although the diversity of pollinators associated with food plants does seem to be different between native and exotic crops, the diversity of crops cultivated across Brazil differed between native and exotic plants. The North region of Brazil is where the diversity of native crops is higher, in contrast with the South and Southeast of Brazil, where the diversity of exotic crops is higher than anywhere else. Most counties in Brazil produce more exotic crops than native and this pattern is consistent across all six major biomes of the country. Approximately 81% of the total agricultural area is dedicated to exotic crops, primarily self-compatible commodities with low to modest dependence on pollinators. Although the richness of exotic crops always surpasses the richness of native crops in the different biomes, cropland area patterns are not as consistent. However, if we removed soybean from our analysis, these differences between the area devoted to exotic and native crops always decreased, becoming equal to the area devoted to native crops in the Atlantic forest. Indeed, soybean cover nearly half of the entire agricultural land, leading the list of the top five with the highest Economic Value of Pollination (EVP), contributing to nearly 60% of Brazil's total EVP. These findings highlight the dominance of soybean production across Brazil, which is the largest exporter of soybeans in the world (FAO, 2016). Although agriculture thrives in Brazil, some biomes may be at risk of losing >20% of their yields due to pollinator shortage. These are areas in which biotic pollination dependence of the production is high and natural vegetation surrounding these croplands is low, where natural resources may not be enough to support the demand for the pollination ecosystem service. Based on these findings, we argue that the expansion of exotic monocultures in Brazil's agricultural areas could impact the provision of pollination services. This impact stems from various factors associated with the expansion of exotic crops, such as habitat fragmentation and loss, which can harm native pollinators and ecosystem services.

Worldwide, the expansion of agricultural frontiers has been driving diverse environmental damages, clearing natural forests and reducing biodiversity (Foley et al., 2011; Laurence et al., 2014; Schmitz et al., 2014), affecting ecosystems and, consequently, the maintenance of the provision of several ecological processes and ecosystem services (e.g. Tilman et al., 2017), which is more critical in tropical regions (Tilman et al., 2001; Foley et al., 2005; Laurence et al., 2014). Thus, the human-induced disturbances through the conversion of many natural habitats into agricultural landscapes, mostly those poorly diversified patches of agricultural lands devoted to the cultivation of monocultures, have been leading to the loss of biodiversity (Laurence et al., 2014). Here, we documented large cropland areas in Brazil devoted to the cultivation of exotic commodities, mainly soybean, which occupies almost half of the total area. Besides, a great portion of the economic value of pollination is from commodities that rely to some extent on pollinators, which reinforces the export role of Brazil in the international food trade. The deforestation of tropical forests is strongly driven by the expansion of commodities and croplands destined for the global food trade, mainly for industrialized countries (DeFries and Rosenzweig, 2010; Chaudhary and Kastner, 2016). For instance, over the past two decades, the demand for soybean in China has increased exponentially, growing the imports from Brazil by 2000%, mostly to feed the animals and meet China's consumption patterns (Fuchs et al., 2019). In this way, because of production on a large scale for exportation to countries like China and the USA, the soybean expansion in Brazil has been a strong driver of forest clearing, directly converting 3.4Mha of natural forests into soybean croplands between 2001 and 2016, of which 44% was located in the Brazilian Cerrado (Song et al., 2021). Considering the percentage of forest loss in the Brazilian biomes due to the conversion to soybean cultivation, the Cerrado was the most affected biome, losing about 17% of the natural areas, followed by Pampa, Atlantic forest, and Amazon (Song et al., 2021). Therefore, understanding the impacts of commodities expansion on biodiversity is important to emerge mitigative approaches to maintain the natural forests and the ecosystems goods delivered by them, and rethink the trends of agricultural production, food trades, and human diet based on the consumption patterns.

Deforestation and climate change have been major factors in the degradation of natural habitats, especially in tropical regions (Laurence et al., 2014; Potts et al., 2010; IPBES, 2016). In this scenario, the Atlantic forest and the Caatinga dry forest are two Brazilian biomes that historically have been intensely threatened (e.g., Silva et al., 2017; Solórzano et al., 2021). Some native plants cultivated in these regions, such as pitanga/Brazilian cherry, umbu/Brazilian plum, cashew and passion fruit, depend critically on pollinators for reproduction (Klein et al., 2007; BPBES/REBIPP, 2019). This pollinator dependence creates a direct link with the food security of the populations that inhabit these areas since biodiversity and food production are intrinsically associated (IPBES, 2016). In fact, the North and Northeast regions of Brazil and along the Atlantic coast have the municipalities with the greatest diversity of crops dependent on pollinators. On the other hand, the areas of deforestation in the Atlantic forest, for example, coincide with the areas with the greatest demand for pollination (Bergamo et al., 2021). Therefore, areas with a greater degree of dependence on pollinators in agricultural production are strongly associated with areas that have less vegetation cover, which is related to the expansion of monoculture cultivation (Bergamo et al., 2021). Furthermore, as the Atlantic forest domain is home to the majority of the Brazilian population, intensifying the importance of its preservation (IBGE, 2010), a collapse in the pollination service thus represents a significant threat to the food security of a large portion of the population. In this context, it is important to rethink the current practice of agricultural expansion, which has been responsible for the decline in populations of several groups of pollinators (e.g., Giannini et al., 2017, 2020; Sales et al., 2021).

There is a huge lack of knowledge in terms of pollinator dependence and the economic value of pollination for many species, especially those native. We also highlight that many native species cultivated in Brazil are neglected from the reproductive perspective, even though being used for food. Globally, native and wild species are used by many societies in the world for food, medicine, and income, mainly for those people with socioeconomic vulnerability (IPBES, 2022). For instance, it is estimated that at least 70 % of poor people depend to some extent on wild species for subsistence and food needs (IPBES, 2022). The current summary for policymakers and of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services also highlighted the potential contributions of sustainable use of wild species to meet some of the targets of the Sustainable Development Goals, such as zero hunger (IPBES, 2022). In Brazil, some ethnobotanical studies considering the socioeconomic variables have been conducted in many regions where indigenous people and local communities live, aiming to investigate, understand and use the local knowledge and perception about the use of wild plant species for food demand, also identifying promising species that could be used and that also need further investigations (e.g., Cruz et al., 2014; Jacob et al., 2020; Medeiros et al., 2021; Pilnik et al., 2023). Thereby, expanding and diversifying the use of native plants can result in a range of new potential nutritious foods, which will diversify agricultural trade and human diet, and generate income for small-scale farmers that depend on agriculture for subsistence (FAO, 2016).

Nevertheless, although some studies have been conducted, the potential use of many wild food species, including information about consumption, propagation, and nutritional aspects remains unknown (e.g., Medeiros et al., 2021). The lack of knowledge on pollination aspects could imply raising some approaches to maintaining plant reproduction, delivery of ecosystem goods, and sustainable food. Efforts are then needed to improve the knowledge of wild food plants for local communities and the whole country, reducing the limitations of understanding the potential uses of such plants for food. A recent study carried out in the Caatinga dry forest reveals that this biome can offer a high diversity of food resources, but still needs efforts to advance the ethnobotanical and nutritional knowledge of such plants (Jacob et al., 2020). Also, in the Caatinga dry forest, it was reported that the pollination of some wild species with edible fruits used for food by local people could be jeopardized by the increasing intensity of chronic anthropogenic disturbances (Oliveira et al., 2022). Therefore, we emphasize here that the use of wild plant species associated with reduced human disturbances on natural ecosystems could emerge as a possible alternative for sustainable diets and reductions in biodiversity loss caused by different sources of land-use change, such as the clearing of old-growth forests due to the commodity expansion, for example. Native conventional and non-conventional and other wild species can be sources of nutrients, vitamins, and minerals for humans, as evidenced by >200 species of wild plants with edible fruits in India, (Sawian et al., 2007), about 160 species of wild plants in China (Kang et al., 2012), 89 native species used as food by indigenous peoples in the western Brazilian Amazon (Pilnik et al., 2023), and 196 promising neglected species (Singh et al., 2019). Therefore, biodiverse foods can complement the human diet and safeguard food security by providing essential micronutrients, mainly for people living in rural areas and who face food insecurity (Gomes et al., 2023). However, currently, only 15 cultivated plants contribute to 90% of human food energy and with global food production such as rice, wheat, and soybeans (Kew, 2020). Generally, these native plants are primary sources of essential micronutrients for humans and are mostly dependent on biotic pollination services, thus the collapse of this key ecosystem service has a direct impact on food security (e.g., Ellis et al., 2015). Therefore, it is urgent that more native and wild species be studied in relation to their use by local communities so that it is possible to identify promising species to diversify human food, ensure food sovereignty, and reduce ecological costs.

The impacts of the expansion of industrial agricultural frontiers on biodiversity make it difficult to produce sustainable food with minimal impacts on ecosystems and the ecosystem services provided by them (Bommarco et al., 2013). In this context, ecological intensification emerges as a nature-based strategy that integrates reduced impacts of land use change and pesticides on nature, developing an agricultural system concerned with maintaining biodiversity and food production (Dicks et al., 2016; IPBES, 2016). Therefore, without the need to expand more croplands into natural areas, ecological intensification can safeguard pollinator diversity, maintain the provision of pollination services for several crops that rely on pollinators to set fruits and seeds, and also ensure the agricultural production in a sustainable way (Altieri and Nicholls, 2008, 2017; Garibaldi et al., 2016; Nicholls and Altieri, 2018), which is in agreement with some targets of life on land and zero hunger of the Sustainable Development Goals. As human beings, we need to be compromised in reducing food waste, including a great diversity of native food plants in our diet, which could help the nations with the challenge of ending food insecurity and hunger, mainly for those poor and vulnerable people who are the most impacted by socioeconomic inequities. Brazil is a large agricultural producer, but ending hunger is again a huge challenge, also the current policy actions that have been jeopardizing family farming, which corresponds to 77 % of all agricultural establishments in the country, distancing the chances of reaching the target of sustainable food production without biodiversity losses

(IBGE, 2019; Oliveira et al., 2023). Therefore, we also call the attention of policymakers to put into discussion and include as a central issue in the political agendas the urgent need to achieve the Sustainable Development Goals, also including the popularization and use of many nutrient-rich native food plants into the human diet, stimulating more scientific researches for those that still are poorly studied or unknown, which could help to reduce the expansion of more croplands.

Concluding remarks.

Our results indicate that soybean has a great impact on Brazilian agriculture, being responsible for disguising some of our main evidence. Overall, despite Brazilian counties producing more exotic food plants than native ones and most of these exotic species being generally self-compatible and with low to modest pollinator dependence, when soybean is excluded, the areas devoted to exotic decreased, and in some cases, it is equal to that of native. Additionally, our results show that some Brazilian biomes may be at risk due to pollinator shortage, which will be more severe in the Caatinga dry forest and the Atlantic forest for native crops. Therefore, the expansion of monocultures across the Brazilian territory could reduce the provision of pollination services, mainly due to the expansion of agricultural lands on natural habitats, leading to habitat fragmentation and loss, which in the long term could also result in several impacts on agricultural production and, consequently, affect the food security not only of the nation as Brazil is the 3rd largest world agricultural producer and exporter (Schneider et al., 2021).

In addition, we also highlight that data and investigation at the local, regional, or country scale are necessary to detect trends and reduce the gaps in terms of pollination of native crops and the impacts of exotic crops on the biodiversity and ecosystem services, also reinforcing the urgent need to develop effective actions for the conservation of the Brazilian biodiversity. Therefore, it is important to consider the native food species and the interactions of such species with their pollinators in the conservation agenda. In this way, policymakers must drive policy actions aiming to support nature-based solutions that promote both human-sustainable food access and biodiversity maintenance in Brazil's agriculture. The current food insecurity paradox in Brazil illustrates how commodity overexpansion can be a severe driver in reducing the chances of people having food access and food diversification, heightening food insecurity, and the challenge to achieve zero hunger by 2030, as proposed by the Sustainable Development Goals. The chronic hunger that plagued Brazil again is a political emergency, which reflects political actions uncommitted to sustainable food production, especially for the poorest and most vulnerable people, who are most marginalized from access to safe food (Oliveira et al., 2023). Unlocking the potential of native and wild crops is very important for global food security and achieving some targets of the Sustainable Development Goals. For this, policymakers must amplify this debate and formulate policies to investigate and popularize the uses of potential species.

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CRediT authorship contribution statement

Willams Oliveira: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Lucas F. Colares:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Rafaella G. Porto:** Conceptualization, Data curation, Writing – review & editing. **Blandina F. Viana:** Writing – review & editing. **Marcelo Tabarelli:** Writing – review & editing, Funding acquisition, Resources. **Ariadna V. Lopes:** Conceptualization, Data curation, Investigation, Methodology, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.169147.

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