Bee and non-bee pollinator importance for local food security

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Abstract

Pollinators are critical for food security; however, their contribution to the pollination of locally important crops is still unclear, especially for non-bee pollinators. We reviewed the diversity, conservation status, and role of bee and non-bee pollinators in 83 different crops described either as important for the global food market or of local importance. Bees are the most commonly recorded crop floral visitors. However, non-bee pollinators are frequently recorded visitors to crops of local importance. Non-bee pollinators in tropical ecosystems include nocturnal insects, bats and birds. Importantly, nocturnal pollinators are neglected in current diurnal-oriented research and are experiencing declines. Integrating non-bee pollinators into scientific studies and conservation agenda is urgently required for more sustainable agriculture and safeguarding food security for both globally and locally important crops.

Keywords: Agriculture; Biodiversity; Crop yield; Ecosystem services; Local food production; Pollination

Contribution of bee and non-bee pollination service for human well-being

Worldwide, nearly 90 percent of wild flowering plant species depend to some degree on animal-mediated pollination for reproduction [1,2], including a broad range of crop species [3,4]. **Crop yield** (see **Glossary**) and crop quality of more than three quarters of the global leading crop types depend on animal pollinators to some degree [3,4], accounting for 5-8 percent of global crop production [5]. Many fruit, vegetable, seed, nut and oil crops are pollinator dependent, supplying major proportions of micronutrients, vitamins, and minerals to the human diet [4,6]. Furthermore, agriculture's reliance on pollinator-dependent crops has increased in volume by more than 300 percent over the last five decades [5] and pollination limitation due to lack of pollinators is a common cause for lower crop yield [3,7,8].

A diverse community of pollinators generally provides more effective and stable crop pollination than any single species [8]. Pollinator diversity, including non-bee species such as flies, wasps, beetles, butterflies and moths, contributes to crop pollination even when managed species (e.g. the Western honey bee *Apis mellifera*) are present in high abundance [8]. Overall, it is estimated that non-bee insects perform 25–50% of the floral visits of globally-important crops [9]. Moreover, crop fruit set increased with non-bee insect visits independently of bee visits, highlighting the complementary role of non-bee pollinators in crop pollination [9,10]. In addition, the floral structure and the blooming activity (e.g. diurnal *vs.* nocturnal bloom) of many cultivated plants can restrict the mutualistic interaction to mostly non-bee pollinator species. This is important for some crop species with a high value for global markets [9]. However, it is especially important for other minority crops that are very valuable for local people (e.g. açai palm *Euterpe oleracea*, durian *Durio zibethinus*).

While similar stress factors are expected to impact bees and non-bee pollinators [2,11–14] alike, in the last few decades, more effort has been put into assessing global trends of increasingly decimated bee populations [4], than similar trends of declining non-bee pollinators and their association pollination services [9,10,15,16]. Here, we review the role, the diversity, and the conservation of non-bee species in crop production. In addition to assessing the broad range of crops visited by non-bee species, we evaluated their overall implication in supporting **food security**.

Role and diversity of bee and non-bee pollinators in crop production

Bees have traditionally been considered the most important group of crop pollinators worldwide [3,17]. Their pollinating efficiency is linked, among other things, to (*i*) their diet consisting predominantly of resources derived from flowers [18]; (*ii*) their bodies covered with branching hairs which allow for efficient attachment and transport of pollen grains; (*iii*) their floral fidelity to a given species during the same foraging trip or even during their lifetime [19,20]. Recent studies, however, highlight the important contribution of other non-bee insects in crop production, such as flies, butterflies, moths, wasps, beetles, thrips [9,21], as well as other groups, such as mammals or birds [22,23]. For example, Rader *et al.* [9] explicitly evaluated the role of non-bee insects on crop pollination. They found that flowers of all analyzed crops (n = 20) were visited by both bee and non-bee insect species, suggesting that the role of non-bee pollinators has been overlooked. However, these studies have focused mainly on crops important for global trade, potentially excluding crops of local importance for food production.

We extensively searched the published literature to gather data on bee and non-bee floral visitors considered as pollinators (while a pollinator, *sensu stricto, is* a floral visitor that deposits pollen and contributes to flower fertilization) in crop production using the *Web of Knowledge* [24] (**Supporting Information, Section S1**). We selected articles that published original data on the diversity of pollinators visiting crops with local importance for people (i.e. fruit and/or seeds of considerable economic, nutritional and cultural value for local communities; **Box 1**) or of global market importance (i.e. the crop produced is dominantly exported and thus present in the FAOSTAT database [25]), which produced 154 studies (see **Section S1** for more details on the literature search methodology). For each study we recorded (*i*) the study country of origin, (*ii*) the crop species, and whether its production was of importance for the global market or for local people, and (*iii*) the sampling method used to estimate the abundance and diversity of floral visitors. Interestingly, we found that, depending on the sampling method used, 67 studies (44%) focused only on bees as crop pollinators, and thus did not assess the diversity of pollinators visiting crops. This can introduce a methodological bias of bees' importance for crop pollination, which is currently questioned relative to the contribution of other insect pollinators [9,10]. Therefore, we excluded these 67 studies from the analysis.

Overall, the dataset comprised 83 crops with 31 crops described as important for global food markets, 48 crops described as important for local people, and four crops described as globally and locally important crops (avocado *Persea americana*, blueberry *Vaccinium sect.*, common bean *Phaseolus vulgaris*, fennel *Foeniculum vulgare*, **Table S1**). The synthesis covered 39 countries (**Figure 1**). We then classified the diversity of pollinators across 12 taxonomic groups, including bees and 9 groups of non-bee insects: Blattodea, Diptera, Coleoptera, Hemiptera, non-bee Hymenoptera, Lepidoptera, Neuroptera, Odonata, and Orthoptera, but also two groups of vertebrates: bats and birds. Overall, bees were the most common crop floral visitors (with 91% of presence occurring in all crops), followed by other insects such as Diptera (67%), Lepidoptera (i.e., butterflies and moths, 44%), Coleoptera (33%), non-bee Hymenoptera (i.e. wasps and ants, 25%) and Hemiptera (18%). Blattodea, Neuroptera, Odonata and Orthoptera were observed less than 2% of the time overall; thus, we excluded these groups thereafter.

Bees have been shown as the dominant group of pollinators visiting the vast majority of global food market crops [9,10], however, these results could be biased by the sampling methods that are commonly used. Indeed, we found that a large number of studies focused exclusively on bee sampling (44%). Moreover, only 31% of the pollination studies focusing on globally important crops had no species-specific restrictions on their sampling method. All these studies recorded non-bee and non-Diptera species as floral visitors, suggesting that pollination mediated by commonly overlooked animal groups could be more frequent than previously reported. For instance, we found that non-bee pollinators routinely visit several crops of global importance, including cocoa (*Theobroma cocoa*), coffee (*Coffea arabica*), common bean, onion (*Allium cepa*), sunflower (*Helianthus annuus*), and apple (*Malus domestica*) (**Figure 2a**).

Although the diversity of non-bee insects confirms the results from Rader *et al.* [9], we show that non-bee pollinators are also more frequent floral visitors of locally-important crops (**Figure 1**) and sometimes the only floral visitors (e.g. atemoya *Annona squamosa* × *cherimola*, salak *Salacca edulis*, pitayas *Stenocereus queretaroensis*, banana *Musa acuminata*, calabash *Lagenaria siceraria*, langsat *Lansium domesticum,* petail *Parkia speciosa* and snake gourd *Trichosanthes anguina*; **Figure 2b**). Hence, our results suggest that supporting the yield of locally important crops cannot rely exclusively on bee pollinators. Floral visitors of such locally important crops also included non-insect species such as bats (9%) and birds (4%), which can represent more than 30% of floral visits in tropical crops (e.g. in

Malaysia and Mexico, **Figure 1**). Furthermore, the floral visit frequency by Diptera, Coleoptera, Lepidoptera, non-bee Hymenoptera and Hemiptera is also higher in locally important crops compared to globally important crops, while pollination from bats and birds are mainly related to locally important crops (**Figure 1**). For instance, bats and birds are frequent visitors of several tropical crops for which bees have never been observed (e.g. pitayas, banana, langsat, and petai; **Figure 2**). Therefore, despite bees being dominant as pollinators in many studies, and disregarding the bias, non-bee pollinators can play an important role in local food security. This calls for consideration of local food crops and their pollinators in developing conservation programs to enhance **ecosystem services** for food security.

Nocturnal pollinators are neglected

Bats were found as nocturnal pollinators in several tropical crops, but some insects also provide this service (**Figure 1**) and their contribution remains understudied on crops of local and global importance [26]. In the recent CropPol global database on crop pollination recording insect pollinators of global crops [27], we focused on night-active Lepidoptera and Coleoptera [28,29] among those identified to, at least, the family level (restricted to a 77% of the records). We identified 27 coleopteran and 6 lepidopteran species as potential nocturnal pollinators of oilseed rape, sunflower, ridge gourd (*Luffa acutangular*) and bottle gourd (*Lagenaria siceraria*) (**Table 1**). To assess the possible pollinating role of these insects, we analyzed the visitation rate of flowers by night-active Lepidoptera and Coleoptera in the CropPol database. We identified three species as potential nocturnal pollinators of sunflower: *Lampyris noctiluca* (Coleoptera, Lampyridae), *Lagria hirta* (Coleoptera, Tenebrionidae) and *Hyles euphorbiae* (Lepidoptera, Sphingidae) [27]. However, identification of nocturnal pollinators is limited as many of the coleopteran and lepidopteran pollinators listed in the CropPol database are only identified to higher taxonomic levels. Thus, CropPol potentially underestimates the contribution of nocturnal pollination. For instance, this global database does not record nocturnal pollination of apple and cucurbits; however, recent exclusion experiments showed that their contribution to pollination is significant [30–32].

The underestimation of nocturnal pollination is likely related to current diurnal-oriented research; common sampling techniques used to date are not adapted to the study of nocturnal pollinators. As an example, we analyzed the effectiveness of insect sampling techniques to record nocturnal pollinators in the CropPol database (i.e. the 27 coleopteran and 6 lepidopteran species) (**Figure 3**). Overall, five sampling techniques are commonly used either as passive 24h-day sampling (e.g. pitfall trap and pan trap or bee bowl) or active daytime sampling (sweep net, focal observations and transects). Pitfall traps are efficient to collect night-active coleopteran pollinators, but fail at collecting lepidopteran pollinators. Other passive 24h-day sampling techniques show few records of both coleopteran and lepidopteran pollinator species. Interestingly, the active daytime sampling techniques are able to record nocturnal pollinators, in particular those of crepuscular activities, with higher efficiency in recording lepidopteran pollinators than coleopteran pollinators (**Figure 3**). However, all of those common diurnal-oriented research techniques are limited in their robustness to measure pollination activity at night. The few techniques that ensure the accurate monitoring of nocturnal pollinators imply the observation of flowers at night [33]. Moreover, the use of camera traps is a promising option to collect diurnal and nocturnal information [34] to better understand and reconsider the role of nocturnal pollinators in crop production [35].

Importance of non-bee pollinators for local food security

Pollinator-dependent species encompass many fruit, vegetable, seed, nut and oil crops, which supply major proportions of micronutrients, vitamins and minerals to the human diet [36–38]. Therefore, pollination directly benefits rural people who gain both their food and income from agriculture [2,39]. This is of particular importance for low-income families that lack access to marketed food, and where animal-pollinated crops contribute to a large part of their vitamin intake [40].

Most food is produced at a small scale by family farmers and traded locally or regionally, whereas about 15% is traded globally [25]. Therefore, these locally produced crops can be equally, if not more, important for food security [41]. As locally produced crops can substantially contribute to food security, especially for the poorest and most rural people, there is a potential significant connection between pollination, local production and food security [38]. For example, in several countries, such as Brazil and Mexico, poor and rural people rely heavily on pollinator-dependent crops [42].

Non-bee pollinators can also be relatively more important for local livelihoods than for globally traded crops overall. Although complementary pollination systems exist, in which both bee and non-bee species simultaneously play an important role in crop production [8,9], some crops are almost exclusively pollinated by non-bee species (**Figure 2b**) [9,10], as is the case for atemoya, banana, calabash, langsat, petail, pitayas, salak and snake gourd, which are important crops for local production and economies. Certain non-bee pollinated crops are both globally and locally important. Cocoa is an emblematic example of a non-bee pollinator-dependent crop [43], which also requires cross-pollination to produce viable seeds [44]. The majority of cocoa pollination studies suggest that ceratopogonids (Diptera) are the most common and main pollinators [45–48]. Beyond the global importance of this crop, the World Cocoa Foundation estimated the number of people that depend on cocoa farming for their livelihood is 40-50 million worldwide [49]. Exports of cocoa products overall generated $US 20.7 billion [50] with more than 4.7 million tons produced in 2017 [51]. Another example, less systematically studied, is African oil palm (*Elaeis guineensis*). This tropical crop is grown mainly to produce palm oil that is obtained from the seeds and fleshy pulp of palm fruits. Although it is native to West Africa, cultivation has spread throughout the tropics and it is currently the most cultivated and traded vegetable oil in the world. Its low price and the fact that it can be used for many purposes (e.g. cooking oil, cosmetic product base, conservation method for processed food or as biofuel [52]) have contributed to its popularity. Although palm oil can be pollinated by wind in dry environments, high crop yields depend almost exclusively on pollination mediated by a subfamily of weevils (Derelominae) among which the species of the genus *Elaeidobius* are the most efficient pollinators [53]. Crop yield has been historically higher in plantations located within the areas where the weevils are native and abundant (e.g. Cameroon).

The New World leaf-nosed bats (Phyllostomidae) and the Old World fruit bats (Pteropodidae) provide unique and valuable pollination services to several crop species of local and global importance [54]. For example, most species of the genus *Agave* (Asparagaceae) are heavily dependent on phyllostomid bats for seed production [55], which are usually produced for selling. For their part, the pteropodid bats are critical pollinators of several important commercial food species such as the honeytree (*Madhuca longifolia*) in India [54], or the petai [56] and durian [57,58]. In Southeast Asia other locally-consumed food and fiber plants depend on non-bee pollinators [59]. Vertebrates such as birds, and especially bats, play an important, and often overlooked, role in tropical crop pollination [60–62]. Bats may be the main pollinators for up to 1,000 species of plants across the tropics, including many of socio-economic importance such as durian, mango and pitayas [60,63,64]. Additionally, wild plants sometimes play an important role in guaranteeing food security, especially in times of crop failure. For instance, the miombo ecosystem of southern Africa contains over 150 species of edible plants, which contribute to both nutrition and income [65], and several of which (e.g. *Kigelia africana*) rely greatly on bats for pollination [66,67].

If estimations of the importance of pollination services have mainly focused on globally-traded crops, the importance of pollinators for local food security has likely been underestimated, especially the contributions of non-bee pollinators. Therefore, it is important to make sure that locally-produced, non-commodity crops are not overlooked when estimating pollination dependence for food and nutritional security. This is also applicable for **orphan crops** and underutilized crops, many of which are thought to depend on animal-mediated pollination [65,68] and are recognized as important for food security [65,69,70]. The lack of knowledge as to what extent, not only non-bee pollinators, but pollinators in general, contribute to local and regional crops, important for food security, is *per se* a call for future studies on these issues.

Conservation status of non-bee pollinators

Due to the expansion of anthropogenic activities, animal-plant interactions, including pollination, are in decline globally. IUCN Red List assessments indicate that many of the non-bee pollinator species are threatened, including 16.5% of vertebrate pollinators, which increases to 30% for island species, [57]. Regan *et al.* [58] calculated that 10% and 6% of the described birds and mammal species, respectively, (1089 birds and 343 mammals) act as pollinators. In general, pollinating birds and mammals are slightly less threatened than non-pollinator birds and mammals, except for bats. Pollinating bat species are more threatened than non-pollinating species. In particular, bat populations are severely threatened in many parts of the world – 80% of bat species require conservation actions [71]. Abundance and diversity of butterflies have also declined in northwest Europe and North America [2] and general insect declines have been widely reported [72]. Overall, the lack of information on population trends of many pollinators is especially worrying [73].

Concluding remarks and future perspectives

Non-bee species are common floral visitors to crops of global and local importance. For certain crops non-bee species are the primary, often specialized, pollinators (e.g. banana, calabash, langsat, petai, and snake gourd). For example, bats and birds are common pollinators of tropical crops for which bees have never been observed visiting flowers. For other crops, non-bee species contribute by enhancing the abundance and diversity of floral visitors. Pollination provided by a wide range of taxa is expected to confer crop stability in the short and long term, as they are functionally complementary (e.g. different floral visitors might be active under different weather conditions).

Non-bee species are critical contributors to food production as pollinators, especially for locally important crops, but also for other ecosystem services. Given their particular life history traits, many non-bee pollinator species provide seed dispersal, pest control, or nutrient cycling (see **Outstanding questions**). Moreover, in local cultures, non-bee species act as sources of inspiration for art, music, literature, religion, traditions, technology and education. Despite their importance, we found that non-bee pollinators are less studied than bee pollinators because sampling methods for floral visitors focus mostly on bees. In particular, the absence of sampling schemes for nocturnal pollinators is noteworthy [35]. Also, most habitat restoration studies focus on bee species, while their impact on many non-bee floral visitors is unclear.

Non-bee floral visitors might respond differently to land-use change than bee species (see **Outstanding questions**). Certain groups of non-bee floral visitors such as some Diptera species (e.g. hoverflies) seem to be more tolerant to anthropogenic pressures than bees, providing crop insurance in places where bee populations have declined [74]. Overall, however, non-bee species are not the exception to current biodiversity declines and are threatened all over the world. To revert the loss of non-bee contributions, current management of agricultural and forest landscapes needs to transition to systems that conserve both bee and non-bee pollinators [16]. Alternatives to conventional production systems, such as ecological intensification, exist already with successful examples of applications found throughout the world [75].

Declaration of interests

The authors declare no conflicts of interest.

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Figure Legends

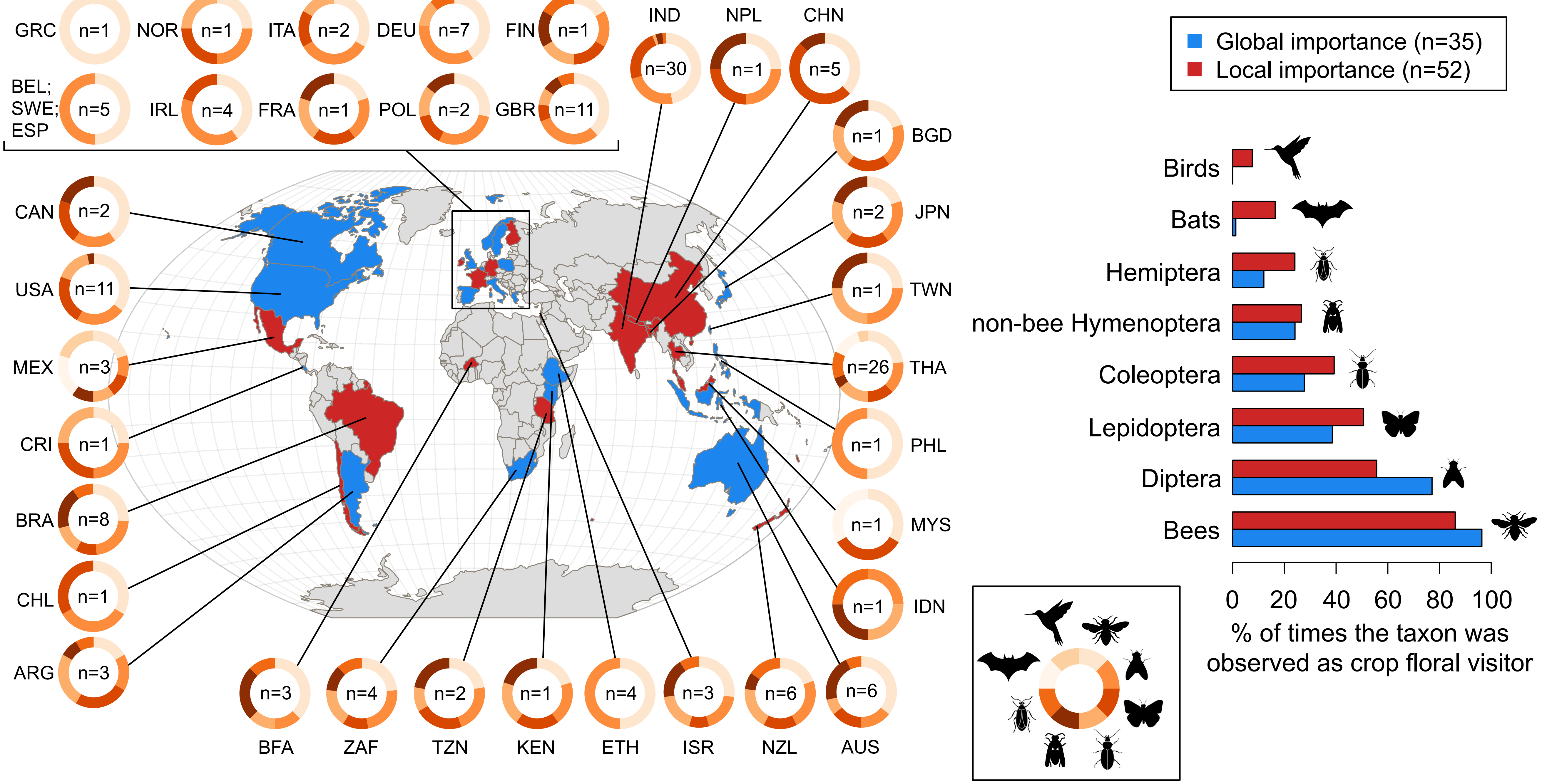
Figure 1. Global synthesis of crop pollinators reveals shared high-level diversity of non-bee species including Diptera, Coleoptera, Lepidoptera, non-bee Hymenoptera, Hemiptera, but also non-insect pollinators such as bats and birds, with differences between species group for crops with global food market importance and those of importance for local people. N represents the number of monitoring studies per country. Countries are colored according to the density of globally vs. locally important crops (e.g. countries in blue whenever two third of the crops studied are of global importance). Acronyms show the country names following the abbreviation ISO 3166 ALPHA-3. Icons: www.freepik.com

Figure 2. List of crops with (a) global food market importance or (b) importance for local people, and their observed species group of floral visitors including Diptera, Coleoptera, Lepidoptera, non-bee Hymenoptera, Hemiptera, bats and birds. Pollinator symbols follow Figure 1. Color gradient in the pie charts represents the density of floral visitors for which several studies were available. Icons: www.freepik.com

Figure 3. Methodological bias of common sampling techniques for monitoring crepuscular or nocturnal pollinators based on the pollinator CropPol global database [27]. Bars represent the proportion of crepuscular or nocturnal pollinators recorded among the total lepidopteran and coleopteran pollinators depending on the sampling methods. Numbers in the bar chart represent the total number of combinations (study × monitoring site × pollinator) for which we were able to determine that the species or family exhibited diurnal, crepuscular or nocturnal activities. Icons: www.freepik.com

Table 1. List of pollinators with crepuscular or nocturnal activities in crops based on the pollinator CropPol global database [27].

Figure 1



GRC n=1
NOR n=1
ITA n=2
DEU n=7
FIN n=1
BEL; SWE; ESP n=5
IRL n=4
FRA n=1
POL n=2
GBR n=11
IND n=30
NPL n=1
CHN n=5
CAN n=2
USA n=11
MEX n=3
CRI n=1
BRA n=8
CHL n=1
ARG n=3
BGD n=1
JPN n=2
TWN n=1
THA n=26
PHL n=1
MYS n=1
IDN n=1
BFA n=3
ZAF n=4
TZN n=2
KEN n=1
ETH n=4
ISR n=3
NZL n=6
AUS n=6
Global importance (n=35)
Local importance (n=52)
Birds
Bats
Hemiptera
non-bee Hymenoptera
Coleoptera
Lepidoptera
Diptera
Bees
0
20
40
60
80
100
% of times the taxon was observed as crop floral visitor

Figure 2

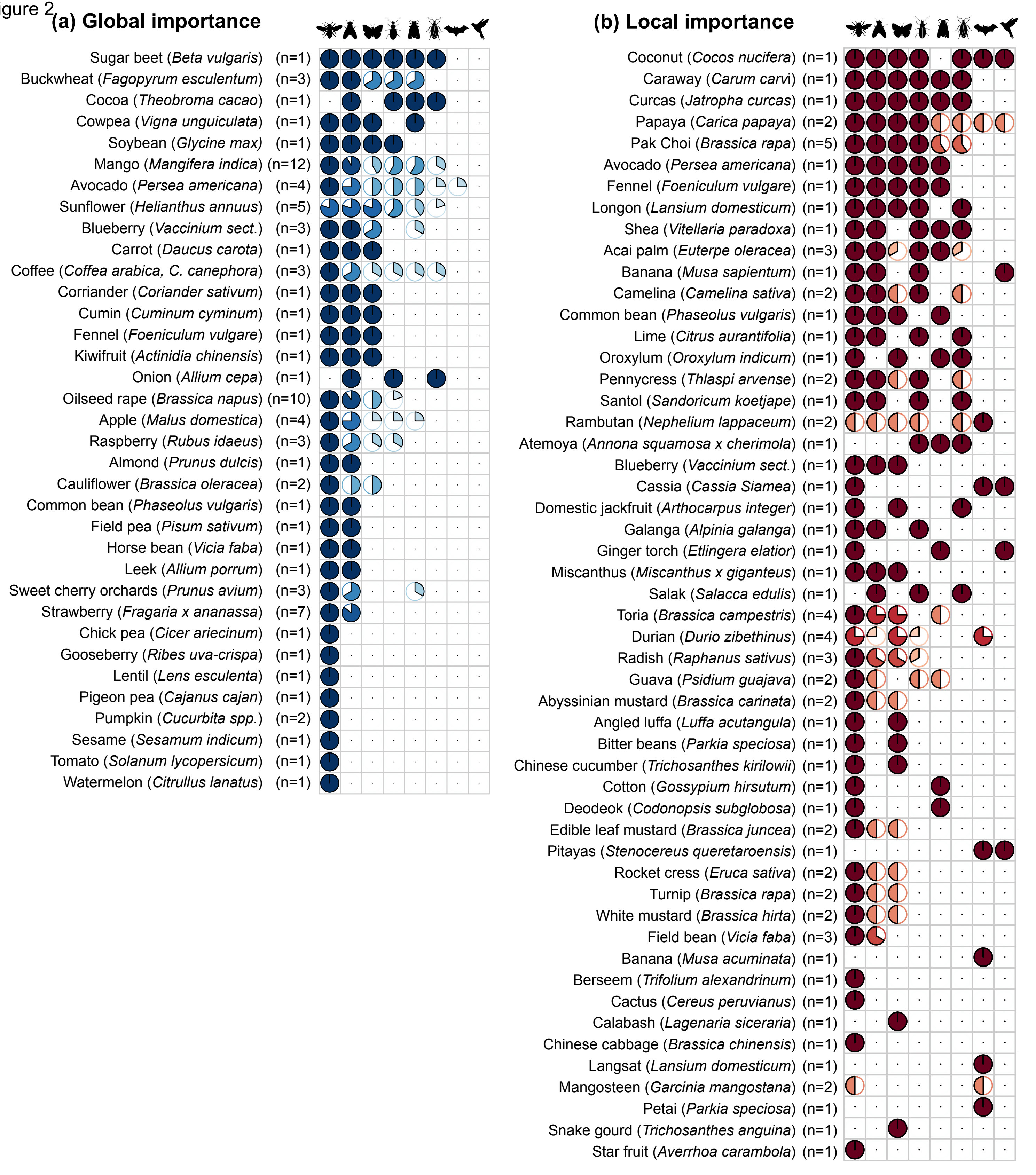
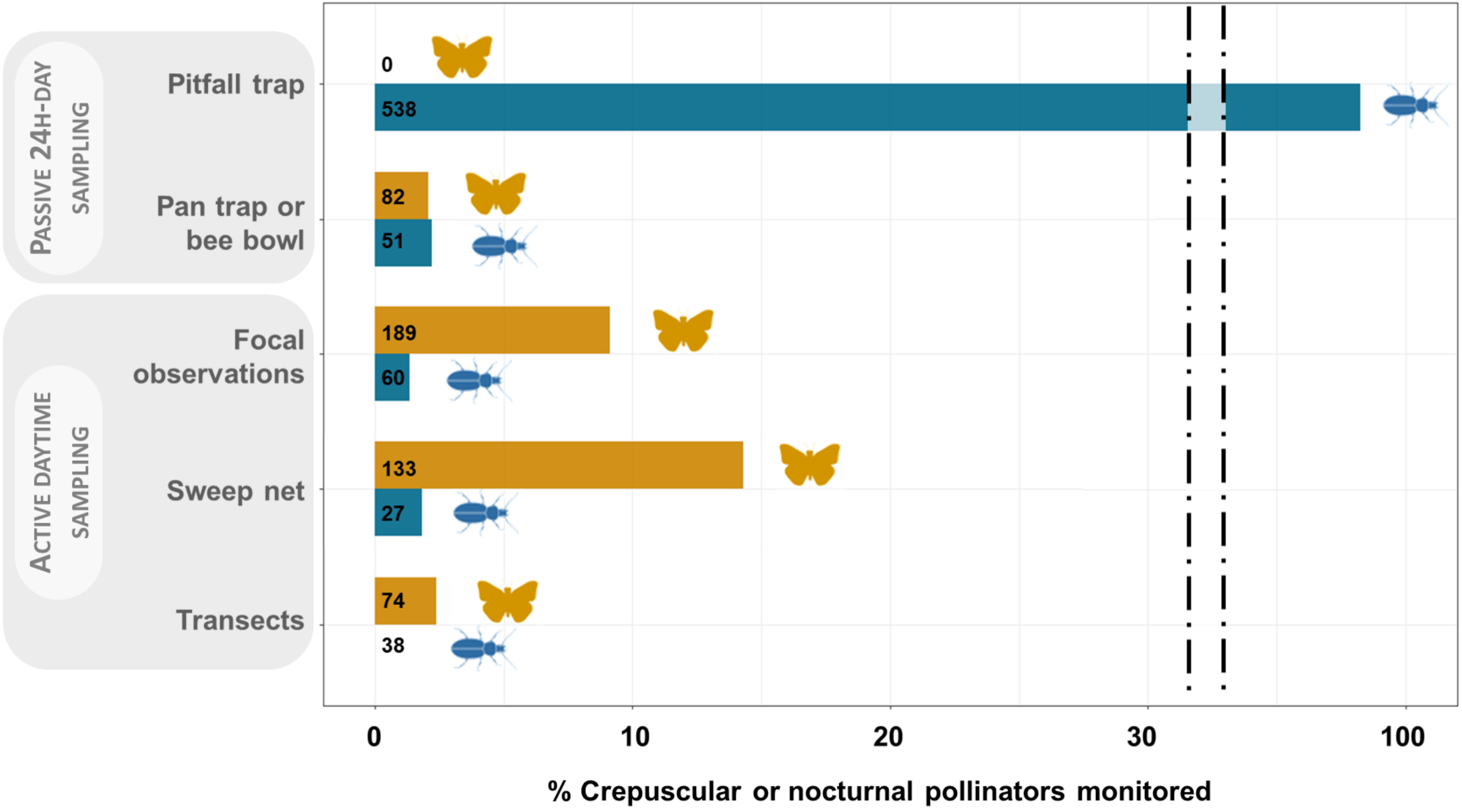

(a) Global importance
Sugar beet (Beta vulgaris) (n=1)
Buckwheat (Fagopyrum esculentum) (n=3)
Cocoa (Theobroma cacao) (n=1)
Cowpea (Vigna unguiculata) (n=1)
Soybean (Glycine max) (n=1)
Mango (Mangifera indica) (n=12)
Avocado (Persea americana) (n=4)
Sunflower (Helianthus annuus) (n=5)
Blueberry (Vaccinium sect.) (n=3)
Carrot (Daucus carota) (n=1)
Coffee (Coffea arabica, C. canephora) (n=3)
Corriander (Coriander sativum) (n=1)
Cumin (Cuminum cyminum) (n=1)
Fennel (Foeniculum vulgare) (n=1)
Kiwifruit (Actinidia chinensis) (n=1)
Onion (Allium cepa) (n=1)
Oilseed rape (Brassica napus) (n=10)
Apple (Malus domestica) (n=4)
Raspberry (Rubus idaeus) (n=3)
Almond (Prunus dulcis) (n=1)
Cauliflower (Brassica oleracea) (n=2)
Common bean (Phaseolus vulgaris) (n=1)
Field pea (Pisum sativum) (n=1)
Horse bean (Vicia faba) (n=1)
Leek (Allium porrum) (n=1)
Sweet cherry orchards (Prunus avium) (n=3)
Strawberry (Fragaria x ananassa) (n=7)
Chick pea (Cicer ariecinum) (n=1)
Gooseberry (Ribes uva-crispa) (n=1)
Lentil (Lens esculenta) (n=1)
Pigeon pea (Cajanus cajan) (n=1)
Pumpkin (Cucurbita spp.) (n=2)
Sesame (Sesamum indicum) (n=1)
Tomato (Solanum lycopersicum) (n=1)
Watermelon (Citrullus lanatus) (n=1)
(b) Local importance
Coconut (Cocos nucifera) (n=1)
Caraway (Carum carvi) (n=1)
Curcas (Jatropha curcas) (n=1)
Papaya (Carica papaya) (n=2)
Pak Choi (Brassica rapa) (n=5)
Avocado (Persea americana) (n=1)
Fennel (Foeniculum vulgare) (n=1)
Longon (Lansium domesticum) (n=1)
Shea (Vitellaria paradoxa) (n=1)
Acai palm (Euterpe oleracea) (n=3)
Banana (Musa sapientum) (n=1)
Camelina (Camelina sativa) (n=2)
Common bean (Phaseolus vulgaris) (n=1)
Lime (Citrus aurantifolia) (n=1)
Oroxylum (Oroxylum indicum) (n=1)
Pennycress (Thlaspi arvense) (n=2)
Santol (Sandoricum koetjape) (n=1)
Rambutan (Nephelium lappaceum) (n=2)
Atemoya (Annona squamosa x cherimola) (n=1)
Blueberry (Vaccinium sect.) (n=1)
Cassia (Cassia Siamea) (n=1)
Domestic jackfruit (Arthocarpus integer) (n=1)
Galanga (Alpinia galanga) (n=1)
Ginger torch (Etlingera elatior) (n=1)
Miscanthus (Miscanthus x giganteus) (n=1)
Salak (Salacca edulis) (n=1)
Toria (Brassica campestris) (n=4)
Durian (Durio zibethinus) (n=4)
Radish (Raphanus sativus) (n=3)
Guava (Psidium guajava) (n=2)
Abyssinian mustard (Brassica carinata) (n=2)
Angled luffa (Luffa acutangula) (n=1)
Bitter beans (Parkia speciosa) (n=1)
Chinese cucumber (Trichosanthes kirilowii) (n=1)
Cotton (Gossypium hirsutum) (n=1)
Deodeok (Codonopsis subglobosa) (n=1)
Edible leaf mustard (Brassica juncea) (n=2)
Pitayas (Stenocereus queretaroensis) (n=1)
Rocket cress (Eruca sativa) (n=2)
Turnip (Brassica rapa) (n=2)
White mustard (Brassica hirta) (n=2)
Field bean (Vicia faba) (n=3)
Banana (Musa acuminata) (n=1)
Berseem (Trifolium alexandrinum) (n=1)
Cactus (Cereus peruvianus) (n=1)
Calabash (Lagenaria siceraria) (n=1)
Chinese cabbage (Brassica chinensis) (n=1)
Langsat (Lansium domesticum) (n=1)
Mangosteen (Garcinia mangostana) (n=2)
Petai (Parkia speciosa) (n=1)
Snake gourd (Trichosanthes anguina) (n=1)
Star fruit (Averrhoa carambola) (n=1)

Figure 3



PASSIVE 24H-DAY SAMPLING
ACTIVE DAYTIME SAMPLING
Pitfall trap
Pan trap or bee bowl
Focal observations
Sweep net
Transects
0
538
82
51
189
60
133
27
74
38
0
10
20
30
100
% Crepuscular or nocturnal pollinators monitored

Table 1. List of pollinators with crepuscular or nocturnal activities in crops based on the pollinator CropPol global database [27]. * Species with a potential role of pollinator of the crop since they were collected in sessions where the visitation rate of their order was strictly greater than zero.

Guild	Crop	Species or family		References
Coleoptera	*Brassica napus*	*Abax parallelepipedus*	*Nebria brevicollis*	[33,78–81]
		Agonum muelleri	*Nebria salina*	
		Amara similata	*Notiophilus aestuans*	
		Anchmenus dorsalis	*Notiophilus palustris*	
		Bembidion obtusum	*Platynus assimilis*	
		Bembidion tetracolum	*Poecilus cupreus*	
		Carabus granulatus	*Pterostichus anthracinus*	
		Carabus monilis	*Pterostichus melanarius*	
		Carabus nemoralis	*Pterostichus nigrita*	
		Clivina fossor	*Pterostichus vernalis*	
		Harpalus affinis	*Stomis pumicatus*	
		Harpalus rufipes	*Trechus quadristriatus*	
		Loricara pilicornis	Elateridae spp	
	Helianthus annuus	*Lagria hirta* *	Lathrididae spp	[81]
		Lampyris noctiluca *		
Lepidoptera	*Brassica napus*	*Pieris brassicae*	Pieridae spp	[28,82,83]
		Plutella xylostella	Sphingidae spp	
		Noctuidae spp		
	Helianthus annuus	*Eudalaca exul*	*Utetheisa pulchella*	[28,84,85]
		Hyles euphorbiae *	Noctuidae spp	
	Lagenaria siceraria	Noctuidae spp	Sphingidae spp	[28,83]
	Luffa acutangula	*Melanitis leda*	Sphingidae spp	[28,83,86]

Box 1. Global and locally important crops

Crops of global importance are defined as those crop species that were mainly produced for exportation in the global market. The trade of these crops is regulated by stock exchanges and international organizations such as the World Trade Organization. These crops are therefore listed in the FAOSTAT database (e.g., coffee *Coffea arabica*, oilseed rape *Brassica napus*, strawberry *Fragaria x ananassa*) [25]. Conversely, crops of local importance to people are defined as fruits and seeds of considerable economic, nutritional and cultural value for communities. For instance, production is consumed directly by these communities, or has high cultural value due to the perpetuation of traditional agronomic practices. Specifically, we categorized crops as of local importance when meeting one of the two following criteria: *i*) crop species that do not appear in the FAOSTAT database (e.g., acai palm *Euterpe oleracea*, durian *Durio zibethinus*, petai Pa*rkia speciosa*) or *ii*) crop species that appear in the FAOSTAT database but authors of the original papers from which pollinator information was gathered, explicitly considered the target crop species as important for local people (e.g., papaya *Carica papaya* in Thailand [63], banana *Musa acuminata* in Thailand [59] and common bean *Phaseolus vulgaris* in Tanzania [76], **Table S1**).

Highlights

- One third of pollination studies focus exclusively on bees, introducing a potential bias in their importance for crop yield
- Non-bee pollinators can have relatively high importance for local crops with cultural and food values
- Nocturnal pollinators were commonly cited as critical pollinators of locally important tropical crops, however, their contribution is currently neglected in crop pollination studies
- The general decline of non-bee pollinators calls for an urgent conservation agenda not only for buffering the alarming global loss of biodiversity but also for safeguarding food security and local livelihoods.

Outstanding Questions

- What is the contribution of nocturnal pollination provided by non-bee animals to crop production? The role of nocturnal pollinators is often overlooked in pollination studies, in particular for global food market crops. However, certain nocturnal pollinators, in particular bats, are known to contribute to pollination of crops such as banana and mango.
- Is the demand for pollination services provided by non-bee species increasing? The global increase in the production of pollinator-dependent crops raises the question of the identity of the pollinators able to provide pollination services to these crops, since managed honey bees are not always the optimal solution. Indeed, pollinators vary in pollination efficiency and more diverse pollinator assemblages are known to provide better crop pollination services than single-species assemblages.
- Are non-bee pollinators more resilient to anthropogenic disturbances than bee pollinators? Bee pollinators are the focus of many studies, and thus their responses to anthropogenic disturbances are relatively well understood, in particular in agricultural landscapes. However, as non-bee pollinators have not received the same attention, their resilience to these disturbances is not so well established.
- What is the contribution of non-bee pollinators to the provisioning of additional ecosystem services (regulatory, material and non-material) when compared to bee pollinators? Beyond bees that exclusively feed on pollen and nectar during all their adult life stages, numerous non-bee pollinators such as vertebrates or other insect taxa (e.g. beetles, ants) can be considered as potential biocontrol agents or seed dispersers as well as a source of inspiration for art, literature, religion, traditions, technology an education. However, few studies focus on documenting the whole range of potential positive side effects of non-bee conservation in agricultural landscapes.
- How much do locally important crops depend on different pollinator species, especially in the global south? Little is known about the species of pollinators that visit crops which benefit local communities, particularly in the global south. However, some of these crops are known to attract interesting non-bee

pollinator assemblages (e.g. bats, flies) which provide essential pollination services.

Glossary

Crop yield: Defined by the FAO as a numerical measure of a harvested crop per unit area of land on which it is grown.

Ecosystem services: Term popularized by the Millennium Ecosystem Assessment, refers to the ecological processes which benefit human societies. Ecosystem services are divided into four categories: provisioning services (e.g. crop pollination), regulatory services (e.g. climate regulation), cultural services (e.g. recreational interactions with nature), and supporting services (e.g. nutrient cycling).

Food security: According to FAO, food security exists when [… all people, at all times, have physical and economic access to sufficient, safe and nutritious food that meets their dietary needs and food preferences for an active and healthy life] [77].

Orphan crops: Underused, lost, indigenous, minor, promising, or future crops in a state of neglect and abandonment despite their grossly underexploited food and nutritional potential that can contribute to food and nutrition security.

Supporting Information

Section S1. Literature synthesis of bee and non-bee pollinators in crop production.

We extensively searched the published literature to gather data on non-bee pollinators in crop production using the *Web of Knowledge* [S1]. We configured the search string with “[TS=Crop pollination]”, with TS meaning “Topic”, to collect information on both globally important crops and other crops of more local importance. We included all literature from January 1975 until September 2022 and we focused on Articles as “Document types”. The initial search identified 827 papers worldwide. Based on title and abstract, we then restricted our search to empirical studies with original data, excluding opinion papers, reviews, meta-analyses, and theoretical works. We also restricted the data synthesis to crops –excluding pollination studies on flowering plants without link to food production– and to “in-crop” census of pollinators –excluding landscape-scale inventories of pollinators. We finally selected studies that recorded free-ranging flower visitors of crops, and thus we excluded greenhouse, lab works, and all studies for which the diversity of pollinators is controlled or artificially restricted (e.g. using trap nests or managed pollinators). The data synthesis produced 154 references for which we recorded the location of the study (at country scale), the name of the crop and whether the production is rather of global food market importance or of importance for local people (food security and local livelihoods), the method of flower visitor monitoring and their diversity. We excluded 67 studies (44%) that focused only on bees as crop pollinators, and thus did not assess the diversity of pollinators visiting crops. Therefore, the review considered 87 references. We then classified the diversity of pollinators among 12 groups, including Bees, and 11 non-bee pollinators: bats, birds, Blattodea, Diptera, Coleoptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Odonata, Orthoptera.

Table S1. Crops of global and local importance from our global synthesis of crop flower visitors**.** Given that the trade of global important crops is regulated by stock exchanges and international organizations such as the World Trade Organization, we categorized these crops as listed in the FAOSTAT database [S2]. We present the mean cultivated area of global important crops, and the proportion that represents this crop for the total cultivated area based on the FAOSTAT data from 2011 to 2020. Conversely, we categorized crops as of local importance when they met any of the two following criteria: *i*) crop species that do not appear in the FAOSTAT database or *ii*) crop species that appear in the FAOSTAT database but authors of the original papers from which pollinator information was gathered, explicitly considered the target crop species as important for local people.

Country	Crop (*Latin name*)	Importance	Crop cultivated area (ha)	Crop proportion area (%)	References
Argentina	Soybean (*Glycine max*)	Global	18086507	51.60	[S3]
	Sunflower (*Helianthus annuus*)	Global	1608995	4.59	[S4,S5]
Australia	Apple (*Malus domestica*)	Global	17805	0.08	[S6]
	Atemoya (*Annona squamosa x cherimola*)	Local	NA	NA	[S7]
	Blueberry (*Vaccinium sect.*)	Global	1452	< 0.01	[S8]
	Raspberry (*Rubus idaeus*)	Global	243	< 0.01	[S8]
	Sunflower (*Helianthus annuus*)	Global	22682	0.10	[S9]
	Sweet cherry orchards (*Prunus avium*)	Global	2219	< 0.01	[S6]
Bangladesh	Pak Choi (*Brassica rapa*)	Local	NA	NA	[S10]
Belgium	Sweet cherry orchards (*Prunus avium*)	Global	1144	0.20	[S11,S12]
Brazil	Acai palm (*Euterpe oleracea*)	Local	NA	NA	[S13–S15]
	Coffee (*Coffea arabica, C. canephora*)	Global	1988747	2.65	[S16]
	Common bean (*Phaseolus vulgaris*)	Global	2926563	3.90	[S17]
	Mango (*Mangifera indica*)	Global	85883	0.11	[S18,S19]
	Star fruit (*Averrhoa carambola*)	Local	NA	NA	[S20]
Burkina Faso	Cotton (*Gossypium hirsutum*)	Local	NA	NA	[S21]
	Sesame (*Sesamum indicum*)	Global	327445	4.67	[S21]
	Shea (*Vitellaria paradoxa*)	Local	NA	NA	[S22]
Canada	Blueberry (*Vaccinium sect.*)	Global	39493	0.14	[S23]
	Strawberry (*Fragaria x ananassa*)	Global	3146	0.01	[S24]
Chile	Blueberry (*Vaccinium sect.*)	Local	NA	NA	[S25]
China	Angled luffa (*Luffa acutangula*)	Local	NA	NA	[S26]
	Calabash (*Lagenaria siceraria*)	Local	NA	NA	[S26]

	Chinese cucumber (*Trichosanthes kirilowii*)	Local	NA	NA	[S26]
	Deodeok (*Codonopsis subglobosa*)	Local	NA	NA	[S27]
	Snake gourd (*Trichosanthes anguina*)	Local	NA	NA	[S26]
Costa Rica	Mango (*Mangifera indica*)	Global	5677	1.10	[S19]
England	Apple (*Malus domestica*)	Global	16032	0.36	[S28]
	Oilseed rape (*Brassica napus*)	Global	616149	13.95	[S29]
	Strawberry (*Fragaria x ananassa*)	Global	4714	0.11	[S30]
Ethiopia	Coffee (*Coffea arabica, C. canephora*)	Global	645784	4.13	[S31]
	Field pea (*Pisum sativum*)	Global	239996	1.54	[S31]
	Horse bean (*Vicia faba*)	Global	478375	3.06	[S31]
	Mango (*Mangifera indica*)	Global	15361	0.10	[S31]
Finland	Caraway (*Carum carvi*)	Local	NA	NA	[S32]
France	Fennel (*Foeniculum vulgare*)	Local	NA	NA	[S33]
Germany	Camelina (*Camelina sativa*)	Local	NA	NA	[S34]
	Field bean (*Vicia faba*)	Local	NA	NA	[S35]
	Pennycress (*Thlaspi arvense*)	Local	NA	NA	[S34]
	Strawberry (*Fragaria x ananassa*)	Global	14242	0.16	[S36–S38]
	Sunflower (*Helianthus annuus*)	Global	22125	0.25	[S39]
Greece	Tomato (*Solanum lycopersicum*)	Global	20543	0.78	[S40]
India	Abyssinian mustard (*Brassica carinata*)	Local	NA	NA	[S41,S42]
	Berseem (*Trifolium alexandrinum*)	Local	NA	NA	[S42]
	Carrot (*Daucus carota*)	Global	34492	0.02	[S41]
	Cauliflower (*Brassica oleracea*)	Global	419161	0.21	[S41,S42]
	Chick pea (*Cicer ariecinum*)	Global	9223773	4.62	[S42]
	Chinese cabbage (*Brassica chinensis*)	Local	NA	NA	[S42]
	Coffee (*Coffea arabica, C. canephora*)	Global	411245	0.21	[S43]
	Corriander (*Coriander sativum*)	Global	1018358	0.51	[S41]
	Cumin (*Cuminum cyminum*)	Global	1018358	0.51	[S41]
	Edible leaf mustard (*Brassica juncea*)	Local	NA	NA	[S41,S42]
	Fennel (*Foeniculum vulgare*)	Global	1018358	0.51	[S41]
	Lentil (*Lens esculenta*)	Global	1443162	0.72	[S42]
	Mango (*Mangifera indica*)	Global	2411297	1.21	[S19]
	Oilseed rape (*Brassica napus*)	Global	6450875	3.23	[S41,S42]
	Pigeon pea (*Cajanus cajan*)	Global	4259446	2.14	[S42]
	Radish (*Raphanus sativus*)	Local	NA	NA	[S41,S42]
	Rocket cress (*Eruca sativa*)	Local	NA	NA	[S41,S42]
	Toria (*Brassica campestris*)	Local	NA	NA	[S41,S42,S44]
	Turnip (*Brassica rapa*)	Local	NA	NA	[S41,S42]
	White mustard (*Brassica hirta*)	Local	NA	NA	[S41,S42]
Indonesia	Cocoa (*Theobroma cacao*)	Global	1687280	3.85	[S45]

Ireland	Apple (*Malus domestica*)	Global	660	0.21	[S46]
	Miscanthus (*Miscanthus x giganteus*)	Local	NA	NA	[S47]
	Oilseed rape (*Brassica napus*)	Global	10917	3.39	[S47,S48]
Israel	Cactus (*Cereus peruvianus*)	Local	NA	NA	[S49]
	Curcas (*Jatropha curcas*)	Local	NA	NA	[S50]
	Mango (*Mangifera indica*)	Global	1797	0.61	[S19]
Italy	Leek (*Allium porrum*)	Global	400	0.01	[S51]
	Oilseed rape (*Brassica napus*)	Global	15641	0.23	[S52]
Japan	Buckwheat (*Fagopyrum esculentum*)	Global	60364	2.05	[S53,S54]
Kenya	Avocado (*Persea americana*)	Global	13513	0.24	[S55]
Malaysia	Durian (*Durio zibethinus*)	Local	NA	NA	[S56]
Mexico	Avocado (*Persea americana*)	Global	169207	1.06	[S19]
	Papaya (*Carica papaya*)	Local	16103	0.10	[S57]
	Pitayas (*Stenocereus queretaroensis*)	Local	NA	NA	[S58]
Nepal	Toria (*Brassica campestris*)	Local	NA	NA	[S59]
New Zealand	Avocado (*Persea americana*)	Global	4250	1.55	[S19]
	Onion (*Allium cepa*)	Local	NA	NA	[S60]
	Pak Choi (*Brassica rapa*)	Local	NA	NA	[S61–S64]
Norway	Raspberry (*Rubus idaeus*)	Global	367	0.12	[S65]
Philippines	Mango (*Mangifera indica*)	Global	195860	1.37	[S19]
Poland	Buckwheat (*Fagopyrum esculentum*)	Global	73264	0.74	[S37]
	Sunflower (*Helianthus annuus*)	Global	3154	0.03	[S66]
Scotland	Raspberry (*Rubus idaeus*)	Global	1543	0.04	[S67]
	Strawberry (*Fragaria x ananassa*)	Global	4714	0.11	[S67,S68]
South Africa	Apple (*Malus domestica*)	Global	22758	0.42	[S69]
	Avocado (*Persea americana*)	Global	17211	0.32	[S19]
	Mango (*Mangifera indica*)	Global	4063	0.08	[S19,S70]
Spain	Almond (*Prunus dulcis*)	Global	591194	4.68	[S71]
Sweden	Oilseed rape (*Brassica napus*)	Global	102433	8.46	[S37,S72]
Taiwan	Mango (*Mangifera indica*)	Global	15898	2.32	[S19]
Tanzania	Avocado (*Persea americana*)	Local	NA	NA	[S55]
	Common bean (*Phaseolus vulgaris*)	Local	1045014	6.68	[S73]
Thailand	Banana (*Musa acuminata*)	Local	63958	0.31	[S74]
	Banana (*Musa sapientum*)	Local	63958	0.31	[S75]
	Bitter beans (*Parkia speciosa*)	Local	NA	NA	[S75]
	Cassia (*Cassia Siamea*)	Local	NA	NA	[S75]
	Coconut (*Cocos nucifera*)	Local	177096	0.85	[S75]
	Domestic jackfruit (*Arthocarpus integer*)	Local	NA	NA	[S75]
	Durian (*Durio zibethinus*)	Local	NA	NA	[S74–S76]
	Galanga (*Alpinia galanga*)	Local	NA	NA	[S75]
	Ginger torch (*Etlingera elatior*)	Local	9774	0.05	[S75]
	Guava (*Psidium guajava*)	Local	NA	NA	[S75,S77]
	Langsat (*Lansium domesticum*)	Local	NA	NA	[S74]
	Lime (*Citrus aurantifolia*)	Local	16078	0.08	[S75]

	Longon (*Lansium domesticum*)	Local	NA	NA	[S75]
	Mango (*Mangifera indica*)	Global	335712	1.60	[S75]
	Mangosteen (*Garcinia mangostana*)	Local	NA	NA	[S74,S75]
	Oroxylum (*Oroxylum indicum*)	Local	NA	NA	[S75]
	Papaya (*Carica papaya*)	Local	5602	0.03	[S75]
	Petai (*Parkia speciosa*)	Local	NA	NA	[S74]
	Rambutan (*Nephelium lappaceum*)	Local	NA	NA	[S74,S75]
	Salak Palm (*Zalacca edulis*)	Local	NA	NA	[S75]
	Santol (*Sandoricum koetjape*)	Local	NA	NA	[S75]
UK	Field bean (*Vicia faba*)	Local	NA	NA	[S37,S78]
	Gooseberry (*Ribes uva-crispa*)	Global	276	< 0.01	[S79]
	Oilseed rape (*Brassica napus*)	Global	616149	13.95	[S78]
	Sugar beet (*Beta vulgaris*)	Global	109535	2.48	[S80]
USA	Blueberry (*Vaccinium sect.*)	Global	34495	0.03	[S81]
	Camelina (*Camelina sativa*)	Local	NA	NA	[S82]
	Cowpea (*Vigna unguiculata*)	Global	11735	0.01	[S83]
	Kiwifruit (*Actinidia chinensis*)	Global	1619	< 0.01	[S84]
	Mango (*Mangifera indica*)	Global	42	< 0.01	[S85]
	Oilseed rape (*Brassica napus*)	Global	666027	0.66	[S82]
	Pennycress (*Thlaspi arvense*)	Local	NA	NA	[S82]
	Pumpkin (*Cucurbita spp.*)	Global	35431	0.04	[S86,S87]
	Radish (*Raphanus sativus*)	Local	NA	NA	[S88]
	Watermelon (*Citrullus lanatus*)	Global	45502	0.05	[S89]

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