

Buzziness as usual? Questioning the global pollination crisis

Jaboury Ghazoul

Imperial College London, Silwood Park, Ascot, Berkshire, UK, SL5 7PY

Concerns have been raised that invertebrate pollinators of crops and wild plants are in decline as a result of modern agricultural practices, habitat degradation, and introduced pests and diseases. This has led to demands for a response by land managers, conservationists and political decision makers to the impending 'global pollinator crisis'. In questioning this crisis, it becomes apparent that perceptions of a pollinator crisis are driven mainly by reported declines of crop-pollinating honeybees in North America, and bumblebees and butterflies in Europe, whereas native pollinator communities elsewhere show mixed responses to environmental change. Additionally, few staple food crops depend on pollinator services, and most crops that do are grown at small scales in diversified agro-ecosystems that are likely to support healthy pollinator communities, or in highly managed systems that are largely independent of wild pollinators. Consequently, justifying conservation action on the basis of deteriorating pollinator services might be misplaced. Nevertheless, existing initiatives to monitor pollinators are well founded, given the uncertainty about the dynamics of pollinator populations.

An unfolding crisis?

The spread of agriculture at the expense of natural vegetation has greatly reduced the local biodiversity of temperate regions [1,2] and is doing so at unprecedented rates in the tropics [3]. This biodiversity crisis has been linked to the degradation of ecosystem services [4], such as nutrient cycling and water purification, which is touted as a major threat to the well being of economic systems and human welfare ([4,5]). Pollination is generally presented as a crucial service in decline [6–9], a concern promoted in scientific and policy circles, as well as among the wider public. For example, Allen-Wardell *et al.* [6] refer to the management and protection of wild pollinators as 'an issue of paramount importance to food supply systems', a view popularized by Buchmann and Nabhan [9]. Pollinating insects (Figure 1) have also entered the political arena (Box 1): the International Pollinators Initiative, established by the Fifth Conference of Parties to the Convention on Biological Diversity in 2000, declared an 'urgent need to address the issue of worldwide decline of pollinator diversity'. These initiatives are justified not so much by concern for pollinators *per se* but rather for the crops that

they visit, as Kearns *et al.* [8] remind us 'humans depend on animal pollination directly or indirectly for about one-third of the food they eat'. Statements about worldwide and potentially catastrophic extinctions of pollinator populations implying a global collapse of crop production systems are powerful messages that, if true, justify immediate conservation action and management remediation. I do not necessarily imply that such statements are false, and agree that there is strong evidence for the decline of some pollinator species in at least part of their ranges, and that yields of some crops might suffer as a result. Rather, I wonder about the weight of evidence upon which wider pronouncements on pollinator declines and their implications are based.

Here, I explore our knowledge of the decline of invertebrate pollinator abundance and diversity, and evaluate this in the context of current and future crop vulnerability and productivity. I also consider evidence for reproductive failure among wild plant species resulting from anthropogenically driven changes to pollinator communities. Well documented cases of specific pollinator declines notwithstanding, it is my view that an extrapolation from our current knowledge to imply worldwide pollinator and crop production crises is inappropriate and pre-mature.

Parameters of a pollinator-mediated food crisis

First, I consider the parameters of a pollinator-mediated food crisis. The loss of some pollinator species need not necessarily affect crop yields if crops are wind or self-pollinated, or if they are insured against specific losses by a diverse array of pollinator visitors. Crop productivity might also be limited by other considerations, such as nutrient or water availability. Thus, pollinator declines are only likely to cause an agricultural crisis for crops that are pollinator dependent, pollinator limited and pollinator specific (Figure 2). A first step, therefore, in assessing the agricultural impact of the 'global pollinator crisis' would be to identify those crops that are most vulnerable to pollinator losses.

Vulnerability of crop plants

Few major crop species depend on animal pollinators (Figure 2). Cereals, including wheat, rice and maize, are either wind pollinated, or their seed production does not require fertilization. Food from crops such as potatoes, yam and cassava is dependent on vegetative growth of tubers, and (self-) pollination is only needed for seed

Corresponding author: Ghazoul, J. (j.ghazoul@imperial.ac.uk).

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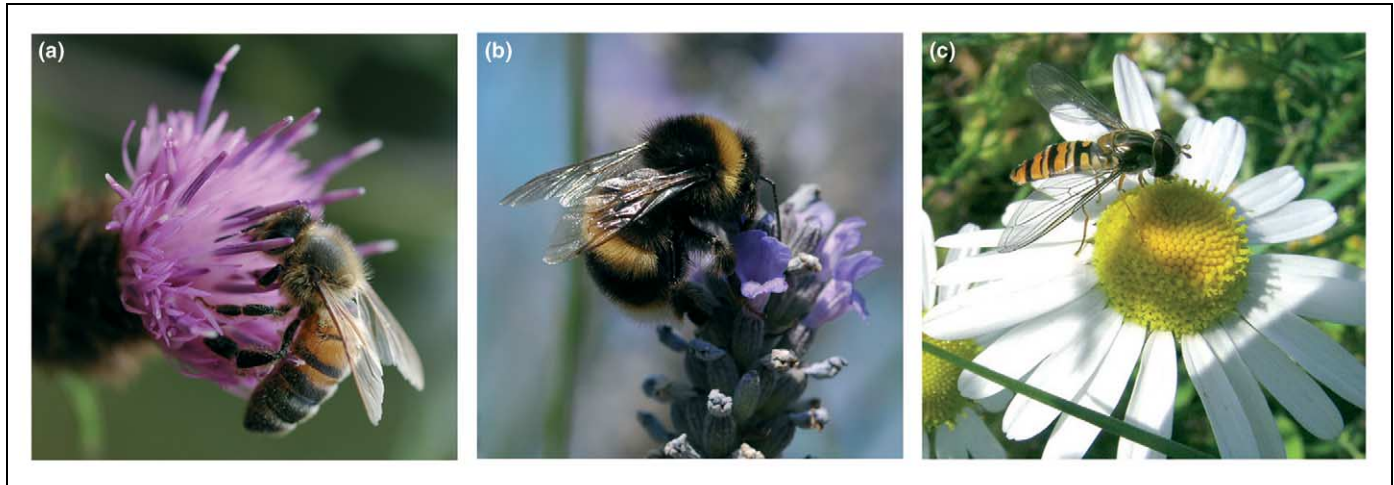


Figure 1. Examples of pollinating species. (a) The honeybee *Apis mellifera* provides essential pollinator service to many intensively grown crops particularly in North America. The decline of managed honeybee colonies owing to a combination of pests and diseases has been central to the calls for concern over an impending pollinator crisis. (b) The bumblebee *Bombus terrestris* is a common widespread pollinating species. However, several European bumblebee species have declined in recent decades, probably as a result of a combination of changing land use and pesticides. It is thought that declining bumblebee species tend to be more specialist in their foraging or habitat requirements. (c) The syrphid fly *Epsirphus balteatus* is not only a pollinator, but also provides a natural pest control service because its larvae feed on aphids. Arable fields adjacent to flower-rich field margins harbour greater densities of this fly [33]. (a) and (b) Reproduced with permission from Dave Goulson.

distribution. Many fruit and seed crops require neither pollinators (e.g. lentils, groundnut and soya) nor pollination (e.g. bananas and figs) for production [10,11]. Others are self-fertile, although animal pollination increases the quantity and quality of fruit production (e.g. oil-seed rape, sunflowers, cotton, pepper and tomatoes) [10,11].

Although most monoecious (separate male and female flowers on the same individual) species are self-fertile and wind pollinated, productivity of some monoecious plants is enhanced by insect visitation (e.g. coconut) or even dependent on it (e.g. cucumber, pumpkin, mango and jackfruit) [10,11]. Large-scale commercially grown

Box 1. International and regional initiatives on pollinators

Pollinators have gained considerable recognition through the Convention on Biological Diversity (CBD) and several regional initiatives that aim to monitor their status and promote their conservation. A short history of these pollinator initiatives is presented here.

The Sao Paulo Declaration (1999)

The Sao Paulo Declaration (<http://www.biodiv.org/doc/case-studies/agr/cs-agr-pollinator-rpt.pdf> [76]) was prepared as a contribution to the implementation of Decision III/11 (Conservation and sustainable use of agricultural biological diversity) of the third meeting of the Conference of Parties (COP). The Declaration recommended that COP5 formally establish the International Pollinators Initiative based on a framework of action that addressed taxonomic impediment, monitoring the status and decline of pollinators, addressing the causes of the decline, evaluating the economic importance of pollinators and establishing conservation, restoration and sustainable use programmes and guidelines.

International initiative for the conservation and sustainable use of pollinators (2000)

Heeding the recommendations of the Sao Paulo declaration, and working within the framework of Decision III/11 (COP3), the Fifth Meeting of the COP (Nairobi, Kenya, 15–26 May 2000) established the International Initiative for the Conservation and Sustainable Use of Pollinators (Decision V/5; <http://www.biodiv.org/programmes/areas/agro/pollinators.asp>) as a cross-cutting initiative within the programme of work on agricultural biodiversity. Section 16 of Decision V/5 specifically invited the Food and Agriculture Organization of the United Nations to facilitate and coordinate the Initiative and to establish a mechanism with which to respond to the recommendations of the Sao Paulo Declaration on Pollinators. The principle objectives of this Initiative are:

- (i) Monitor pollinator decline, and its causes and impact on pollination services.
- (ii) Address the lack of taxonomic information on pollinators.

- (iii) Assess the economic value of pollination and the economic impacts of declining pollinator populations and services.

- (iv) Promote the conservation, restoration and sustainable use of pollinator diversity in agriculture and related ecosystems.

The Initiative was expected to produce a preliminary report in 2004 (now due in 2005) with the first comprehensive report on results of monitoring programmes and economic analyses by 2010.

Regional initiatives

Several regional initiatives coordinate action on pollinator assessment and conservation, and they include: the European Pollinator Initiative (<http://www.europeanpollinatorinitiative.org/>), which has representatives from 17 European regions; the North American Pollinator Protection Campaign (<http://www.nappc.org/>), which includes Mexico, Canada and the USA; International Centre for Integrated Mountain Development Initiative from South Asia (<http://www.icimod.org/index.htm>); the Brazilian Pollinators Initiative; and the African Pollinators Initiative (<http://www.up.ac.za/academic/entomological-society/rostrum/apr01/page5.html>), with representatives from 15 countries. There are also plans for an Australian and New Zealand Pollinators Initiative. The objectives of these regional initiatives are broadly similar:

- (i) Assessment: quantifying the loss of pollinators and the risks associated with the loss of pollination services.
- (ii) Adaptive management: identifying the best management practices and technologies to overcome declines in pollinators and the services that they provide.
- (iii) Capacity building: mainly by strengthening networks and building taxonomic expertise.
- (iv) Raising awareness: by coordinating local, national and international action in pollinator research, education and awareness, policies, conservation and restoration, and supporting national plans for the conservation and sustainable use pollinators.
- (v) Species management: notably honeybees, stingless bees and solitary bees.

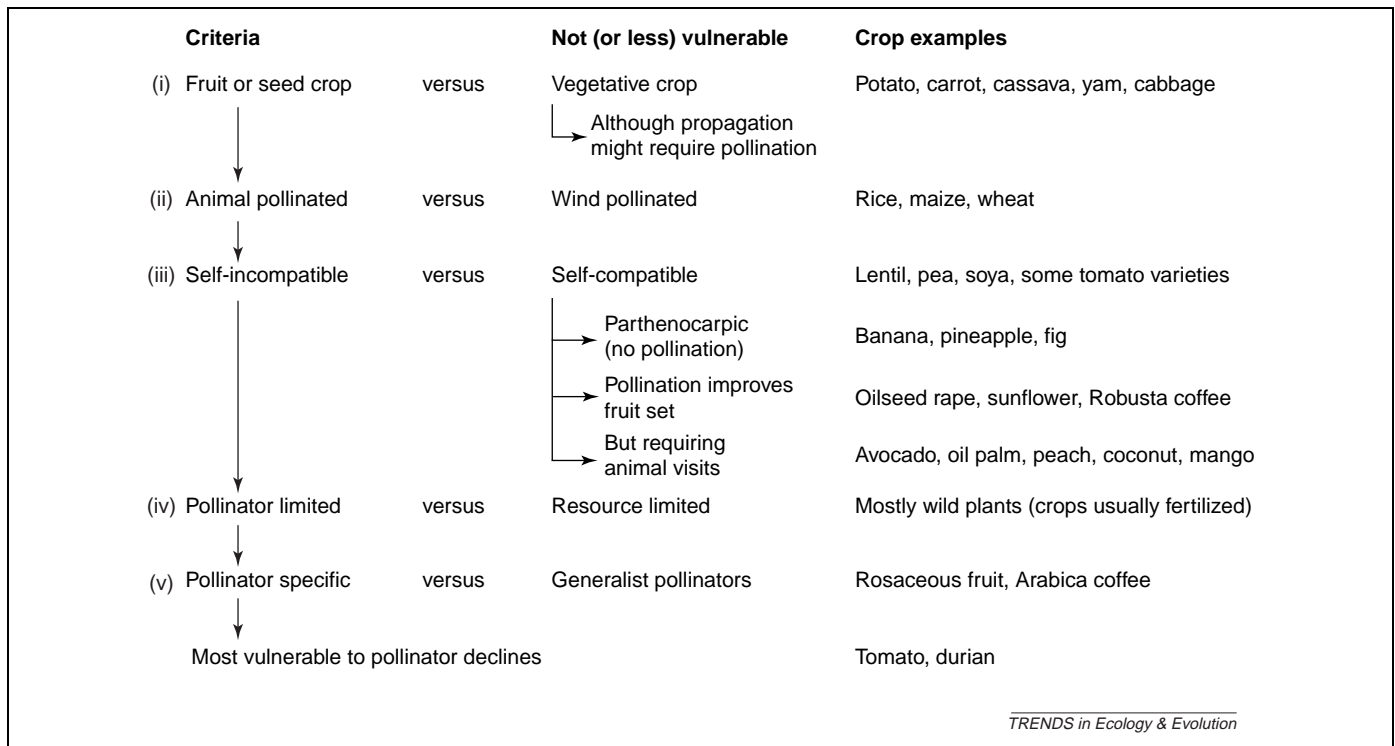


Figure 2. The sensitivity of crop productivity to pollinator declines. Crop productivity is likely to be sensitive to a decline in pollinators only if the crop species fulfils several criteria associated with the nature of the product and reproductive system. The more criteria that are fulfilled, the more vulnerable a crop plant is likely to be. Even species that are obligately dependent on specific pollinators, and therefore expected to be highly vulnerable to pollinator declines, might not be because they are produced in highly managed agricultural systems (e.g. tomato).

self-incompatible plants that depend on animal pollination include the 'robusta' variety of coffee, cardamom, and many fruit crops within the Rosaceae (e.g. apple, pear, plum, cherry and almond). However, most obligately animal-pollinated crops are economically minor species that are grown on a small scale (e.g. in home gardens or agroforestry plots) with predominantly local markets [10]. These crops typically occur in high-diversity low-input agricultural or agroforestry systems that favour the persistence of pollinator richness and abundance, or are products that are collected directly from wild plants growing in natural or semi-natural conditions.

Animal-pollinated crops in temperate zones, mostly legumes (e.g. peas and beans) or fruits (e.g. apples and pears), are increasingly grown in large-scale intensive systems with the liberal application of pesticides and herbicides. In these modern agricultural systems, intensive farming practices create massive demands for pollinator services by raising crop densities while simultaneously removing nutrient and water limits to productivity by applying fertilizers and irrigation. In such intensive agricultural settings, native pollinators might not need to decline at all for pollination limitation to be expressed. California, for example, produces one-third of the world's almonds and even the import of honeybee colonies does not satisfy the demand for pollinators [12]. Inappropriate pesticide use and the elimination of larval food plants or nesting sites can only exacerbate this situation [13]. In Europe, 84% of the 264 crop species are animal pollinated [14], but most are grown in non-intensive systems, where pollinator decline and pollination limitation are unlikely to be experienced [10]. For

other crops, the agricultural product is vegetative (e.g. potatoes and carrots), or the plant is self-fertile, although production is often improved by cross-pollination (e.g. sunflower and olives).

Nevertheless, valuations of pollinator services are invariably impressive. Pollinator services in the USA have been valued at US\$1.25 billion annually, and it is estimated that seven out of the 60 agricultural crops that are crucial to the North American economy (e.g. alfalfa) would be lost if the insects that pollinate them became extinct [9]. Dramatic as this might seem, one should also be curious about the likelihood of such catastrophic pollinator declines occurring.

Vulnerability of wild plants

Many studies attribute the reproductive decline of wild plants to pollination failure (reviewed in [15]), but few of these suggest that reproductive output is limited directly by a regional decline in pollinator abundance. Rather, localized depression of pollinator activity resulting from a limited capacity of pollinators to move between isolated plants in fragmented habitats repeatedly emerges as the predominant explanation. Regardless of the reason, seed production of non-crop plants is likely to be more resource limited than it is for crop plants (which are generally fertilized) and, furthermore, plant recruitment might not even be limited by seed production [16].

A perception among ecologists of a tendency to specialism of tropical plant–pollinator mutualisms has raised concerns of a disproportionate susceptibility of tropical communities to pollinator declines [8,17]. Recent studies dismiss the existence of such tropical–temperate

trends as marginal at best [18] and emphasize the predominance of generalized plant–pollinator interactions [19]. Furthermore, interaction asymmetry appears to be the norm among pollinator and seed-disperser networks [20]: specialist pollinators tend to visit plants that accept many pollinator species, whereas the pollinators of plants that are specialized in their pollinator requirements are themselves generalists; for example, *Dolichandra cynanchoides*, a vine from the Chaco Serrano forests of Argentina, is pollinated exclusively by three hummingbird species that are themselves generalist pollinators of many different plant species [20]. Thus, the loss of specialized pollinators mainly affects generalist plants that are buffered from such losses by the other pollinators that they also attract [21]. Asymmetric specialist–generalist interactions among plants and pollinators might therefore explain why specialist plants appear no more susceptible than generalists to fragmentation or other disturbances that might cause pollinator losses [21,22]. Consequently, although pollinator declines are undoubtedly regrettable, their impact on plant reproductive processes, even those that are obligately dependent on only a few pollinating species, is likely to be muted [21,22].

Are pollinators declining?

The central assumption of the pollinator crisis is that pollinating species are declining. European honeybees (Figure 1a) in North America have suffered dramatic declines (up to 50% of managed colonies [23]) as a result of introduced parasitic mites and excessive pesticide use [24]. To a small extent, these losses are offset by the spread of Africanized honeybees that have greater resistance to mites, disease and certain pesticides [24]. Africanized honeybees have been successfully integrated into agricultural practices in several regions of Latin America, where they have replaced European honeybees [25,26] and might even be superior to European bees for the pollination of certain crops [27,28]. Africanized honeybees do, however, present several problems for commercial pollination of crops in that they have smaller forager populations, forage closer to the nest, and suffer higher mortality following relocation [11,29,30]; they are also notoriously aggressive. Integrating Africanized honeybees into US agricultural practices is considered unworkable because of the dependence of modern agriculture on highly mobile and managed bee colonies to pollinate crops such as almond [31,32]. The ability of native American pollinators to compensate for a decline in honeybee number is considerable, provided that less-intensive agricultural practices, such as reduced pesticide application and retention of weedy field borders [33,34], are adopted and remnant natural habitat is retained in the landscape [35]. Several temperate studies have shown that landscape structure (the proportion of semi-natural habitats and features that increase habitat heterogeneity) promote butterfly and bee diversity and abundance, although different groups respond at different scales [36,37].

In Europe, concern for bumblebees [38] and butterflies [39–41] has stimulated major initiatives to track regional changes in their distributions (e.g. [39]). Destruction of semi-natural habitats and changing land management

has caused disproportionate declines among butterflies that are rare habitat specialists [40,42]. However, generalist butterflies (such as *Pararge aegeria* and *Polygonia c-album* [43]) have expanded their ranges [44,45] probably in response to more favourable climates [40,45], as have many bees, such as *Colletes hederæ*, *Lasioglossum paxillum*, and wasps, *Philanthus triangulum* (Stuart Roberts, personal communication). The decline of bumblebees in the UK (and continental Europe) is similarly disproportionately associated with rare and specialized species [38,46,47], which are particularly vulnerable to the agricultural intensification that is typical of the landscape of southern England [38]. As for butterflies, bumblebees that remain common (Figure 1b) are (on the whole) catholic in their food plant and habitat preferences, and it is these generalist species that are most useful as crop pollinators. Indeed, the abundance of resources provided by mass flowering crops, such as oilseed rape, has been shown to support bumblebee densities at the landscape scale [48].

A few tropical studies report declining pollinator abundances in human-dominated landscapes. In South-East Asia, the absolute abundance of bees in relatively undisturbed forest fragments was higher than in disturbed forest sites, but disturbed sites supported many more species of solitary bees, giving these sites higher species richness [49]. Other studies on tropical bees show a surprising degree of resistance to habitat fragmentation [50–52]. Powell and Powell's [53] study on fragmentation-induced declines among euglossine bees, which are important neotropical pollinators, has now been thoroughly refuted [51,52] and euglossines seem largely unaffected by forest fragmentation. In Panama, considerable interannual variation in the abundance of euglossine bees did not show any consistent directional trend over a 22-year period [50]. Over longer timescales, native bees and wasps used by the Incas 500 years ago are still extant [28] in spite of substantial land-use change. Similarly, native bee communities in Illinois, USA, first surveyed during the late 1800s, remained remarkably similar when resurveyed 75 years later [54]. These studies suggest that many bee species are remarkably resistant to changes in land use and cumulative pesticide applications.

Nevertheless, there are clear examples of plant reproductive decline, attributable to pollinator losses, among wild plants (e.g. *Banksia goodii* [55]), although most of these are of insular populations pollinated by vertebrates [56]. Oceanic island pollinators are susceptible to extinction owing to small population sizes and little or no possibility of rescue through immigration. Pollination systems are vulnerable because depauperate island communities have little capacity for compensating the loss of particular pollinators. For example, 79% of canopy tree species on Samoa are pollinated by two species of fruit bats *Pteropus* spp. that have declined as a result of hunting, habitat destruction, introduced predators and periodic cyclones [56]; on Hawaii, 31 species of Campanulaceae have become extinct, apparently because of the extinction of their bird pollinators [56].

It is, of course, an important conservation issue that rare species appear to be getting rarer, but justifying

conservation policy on the basis of pollinator services might be inappropriate if common generalist pollinators remain abundant. This, coupled with the considerable gaps in our knowledge of changing pollinator abundances, suggests that it is pre-mature to call for a crisis in pollination, notwithstanding pollinator extinctions on oceanic islands.

Thus, is there a problem?

The scientific information relating to pollinator services or declines must be evaluated critically before a crisis is declared lest we overplay our hand in demanding conservation action for the wrong reasons. It is possible that a global pollination crisis is, indeed, in progress, but I do not believe that evidence for such a crisis is currently strong. I suggest that the observed decline in managed honeybee colonies in the USA, and similar concerns about declining bumblebees in Europe, has driven much of the rhetoric on the degradation of pollinator services. In Europe, there is no evidence to indicate that declining bumblebees have depressed crop productivity, whereas in the North America, lower yields of bee-dependent crops, such as alfalfa, almonds and blueberries, are partially a reflection of excessive intensification that has created an unprecedented demand for a pollinator service met by an over-reliance on a few species.

However, one should not become complacent. The simplified agricultural landscapes that characterize much of Europe and North America, and increasingly much of the tropics, lack natural or semi-natural habitats that insects, birds and bats favour. The loss of suitable forest habitat is of particular concern for solitary (e.g. *Xylocopa*, *Osmia* and *Chalicodoma* spp.) and social (*Trigona* spp.) bees [37,57–59] that nest in dead wood or in living trees (although ground-nesting bees, such as *Halictus* and *Lasioglossum* spp., prefer unshaded open ground and might be well suited to many agro-ecosystems [60]). For example, pollination services by native (non-*Apis*) bees on watermelon in California [37] and coffee in Sulawesi [60], Brazil [61] and Costa Rica [62] decline with increasing distance to natural habitats. For these crops pollinator diversity also contributes to productivity, either because of year-to-year variation in community composition [35], or increased pollination efficiency [63]. This implies that even loss of a small subset of the pollinator community might have economic ramifications.

To bee or not to bee

In spite of some scepticism portrayed here about the reality of a global pollination crisis, environmental crises are, almost by definition, belatedly recognized. In view of this, some simple management recommendations could ensure that a pollinator crisis remains largely a myth.

Given that the heavy-dependence of modern agriculture on honeybees for pollination is at the heart of the pollination crisis [64,65], diversifying the suite of crop-pollinating species has been proposed as an appropriate management response [64,66]. Most crop species are receptive to a broad range of pollinators, not least because generalized pollination systems facilitate their domestication in regions beyond their natural range where their

usual pollinators might be absent. Therefore, many non-*Apis* species are potential candidates for providing pollinator services and attempts have already been made to encourage or domesticate carpenter bees *Xylocopa* spp., stingless bees (Meliponinae) and various solitary bees for this purpose [59,67–69].

Natural or semi-natural habitat remnants provide nesting sites and reliable food sources for pollinators. Proximity to such remnants has been shown to enhance the quantity and quality of coffee yields [60–63] and to contribute important pollinator services to cashew [70], macadamia [57] and mango [71]. Conserving such fragments in human-dominated landscapes would benefit biodiversity generally [72] and, arguably, could make good economic sense in terms of improved crop productivity [61,73]. However, transformation to intensive monoculture systems raises yields several-fold (e.g. [74]), indicating that pollination services either persist or at least do not limit production. Thus, the preservation of diverse tropical agroforestry systems, ranging from home gardens in Yucatan to shade coffee plantations in India, should be encouraged, although the opportunity costs of doing so need to be recognized and compensated.

Finally, because pollinator populations are highly dynamic at local scales [50,75], detecting long-term directional trends requires coordinated regional sampling strategies over many years. In this sense, the International Pollinators Initiative is a worthy development albeit based on uncertain supposition.

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