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POLLINATION SERVICES FOR SUSTAINABLE AGRICULTURE
EXTENSION OF KNOWLEDGE BASE



Chapter 3

SUSTAINABLE YIELDS, SUSTAINABLE GROWTH OR NEITHER?

3.1 THE POTENTIAL FOR INSECT POLLINATORS TO ALLEVIATE GLOBAL POLLINATION DEFICITS AND ENHANCE YIELDS OF FRUIT AND SEED CROPS

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3.1.1 Introduction

Land use has changed at an unprecedented rate during the past century. Agricultural lands, pastures, tree plantations and urban areas have expanded concomitantly with the consumption of agricultural products, energy, water and chemical inputs [1]. Those changes have caused widespread environmental degradation and major biodiversity loss that affect the ecosystem services on which human livelihoods depend [1], including crop pollination by wild insects [2, 3]. This chapter provides a general framework for understanding the contribution of animal pollination to crop yield. It also describes global patterns of pollinator abundance and diversity, pollinator dependence, pollination deficits, and the pollination efficiency of honey bees (*Apis mellifera*) and wild insects. It concludes with recommendations for improved agricultural sustainability from the enhancement of pollinator biodiversity, pollination services and crop yield.

3.1.2 Pollen as a resource that limits crop yield

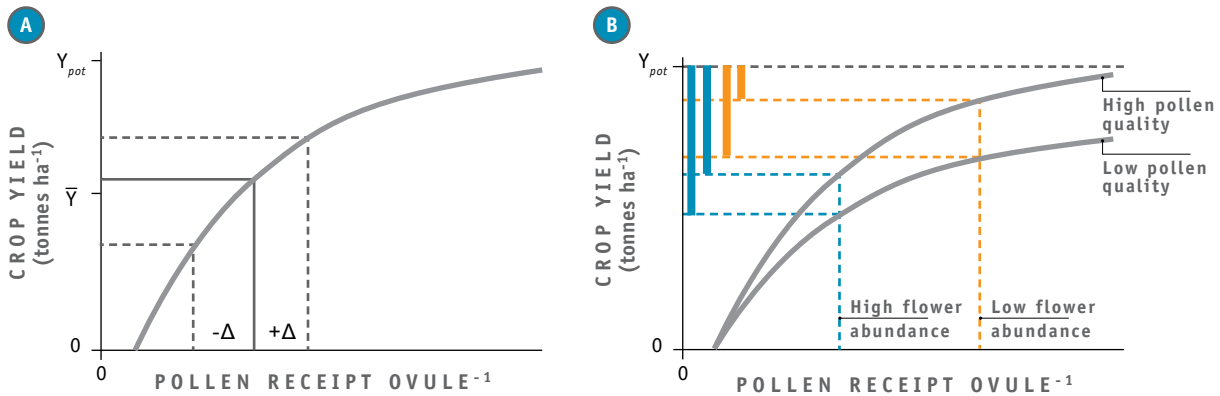
Crop yield (tonnes ha⁻¹) [1 tonne = 1.1 US tons] increases asymptotically with the delivery of resources in general, and for most fruit or seed crops with the pollen delivered to the stigmas [4–10]. The relation can be summarized generally as

$$Y = Y_{pot} \cdot (1 - e^{-b \cdot Pollen})$$

where Y is realized yield, $Pollen$ is the mean number of pollen grains per stigma, and b governs the rate of approach to the "asymptote, Y_{pot} ", which is the potential yield (Figure 3.1a). Given such a saturating relationship, the temporal (e.g. among years) or spatial (e.g. among agricultural fields) variation in pollen receipt both increases variability (reduces stability) of crop yield, and reduces its mean. The latter result arises because the yield increase resulting from Δ units of pollen receipt above the average during a good year ($+\Delta$ in Figure 3.1a) is smaller than the yield decrease caused by pollen receipt Δ units below the average during a bad year ($-\Delta$ in Figure 3.1a).

Figure 3.1

CROP YIELD INCREASES WITH POLLEN QUANTITY AT A DECELERATING RATE, WITH PREDICTABLE IMPLICATIONS FOR THE RESPONSES OF MEAN YIELD AND YIELD STABILITY TO VARIATION IN POLLINATION AND POLLEN QUALITY



(A) Variability in pollen receipt (Δ) increases yield variability, but also reduces its mean (\bar{Y}), where \bar{Y}_{pot} is the potential yield. (B) Effects of pollen quality and flower abundance. The blue and orange rectangles indicate the pollination deficit (potential minus the realized yield) under high and low flower abundance, respectively.

Source: L.A. Garibaldi

Pollination deficit is thus a shortfall in the yield of fruit and seed crops which could be alleviated by improved pollination, expressed here as the difference between potential and realized yield (Figure 3.1b) [11]. The model described above can be elaborated to incorporate the influence of pollen quality, which can affect pollination deficit through change in ovule fertilization and embryo development [8, 12]. Unlike pollen quantity, better pollen quality, resulting in enhanced cross-fertilization and reduced inbreeding depression [8, 12], can increase both potential yield Y_{pot} and the rate of increase in crop yield with increasing pollen quantity, as influenced by b (Figure 3.1b). Thus, even if other inputs are provided, a reduction in the quantitative component of pollination deficit will not maximize yield unless pollinators deliver a sufficient quality of pollen. Management practices mostly ignore this component of pollination deficit; however, encouraging pollinators that move frequently among plants will improve overall pollen quality and reduce the deficit [13, 14]. Further enhancement of outcrossing rates might be achieved by considering the floral display, inflorescence architecture and particularly the genetic composition

of the cultivated crop. Finally, management practices usually enhance the abundance of crop flowers per hectare, which may alleviate pollination deficits by promoting pollinator arrival or recruitment (i.e. higher pollinator attractiveness). However, these practices more commonly increase deficits by saturating the local pollinators, thus reducing the number of visits per flower, and therefore pollen receipt per ovule. In other words, the combination of monocultures with sparse, poor pollinator assemblages exacerbates the pollination limitation experienced by many crops (Figure 3.1b). Practices should therefore not try to increase floral resources, unless other measures are in place to increase the abundance and/or diversity of pollinators.

3.1.3 Pollinator dependence in fruit and seed crops

As with wild plants, fruit and seed crops, which are the subject of this volume, differ greatly regarding the extent to which animal pollinators increase yield, ranging from little or no improvement (e.g. obligate wind or self-pollinated crops such as walnuts or cereals) to complete dependence (e.g. Brazil nut,

cocoa, kiwi, melon and papaya) [15]. In general, animal pollination enhances the sexual reproduction of about 90 percent [16, 17] of all angiosperms. Among crops, the estimates are similar, amounting to 85 percent of 264 crops cultivated in Europe [18] and 70 percent of 1 330 tropical crops, many of which have not received study [19]. Globally, animal pollination enhances the yield of 75 percent of the 115 most important crops, as measured by food production [15, 20] and economic value [21], including crops with a high domestication investment, such as soybean, sunflower and canola [13, 22, 23].

Such estimates consider crops to be of two kinds – completely unaffected by animal pollination, or at least partially dependent on animal pollination, whereas from a farmer's perspective the pollinator dependence of crops varies quantitatively. This dependence can be measured according to the extent of yield reduction in the absence of pollinators (percent dependence) compared to potential yield (Figure 3.1). The contribution of animal pollination to global agriculture has been estimated based on the pollinator dependence of the 87 most important crops, using yearly data for 1961–2006 provided by the Food and Agriculture Organization of the United Nations (FAO) [20]. Those crops were classified into five (average) dependency categories: 0 (no dependence), 5 percent, 25 percent, 65 percent and 95 percent (extremely high dependence) [15]. Thus, with no animal pollination, the estimated reduction in total agricultural production – considering these different categories of dependency – is 3 percent to 8 percent, depending on the year and local economic perspective [20]. These estimates are lower than previous ones by about 30 percent, which were derived without considering the degree of pollinator dependence [15]. However, the extra cultivated area needed to compensate for the < 10 percent production loss, under a hypothetical scenario of complete pollinator collapse, is much higher because of the lower yields of pollinator-dependent crops [20]. The increased area ranges from 15 percent to 42 percent, with the largest estimates for developing countries,

where two-thirds of global agricultural land is farmed [20]. Furthermore, analyses of temporal trends for cultivated area and production reveal that, although animal pollination accounts for a relatively small share of total crop production, agriculture became steadily more pollinator dependent (> 50 percent increase) during 1961–2006 [20]. Therefore, the expansion of cultivated area, driven in part by pollinator loss, contributes to global environmental degradation, particularly in developing countries.

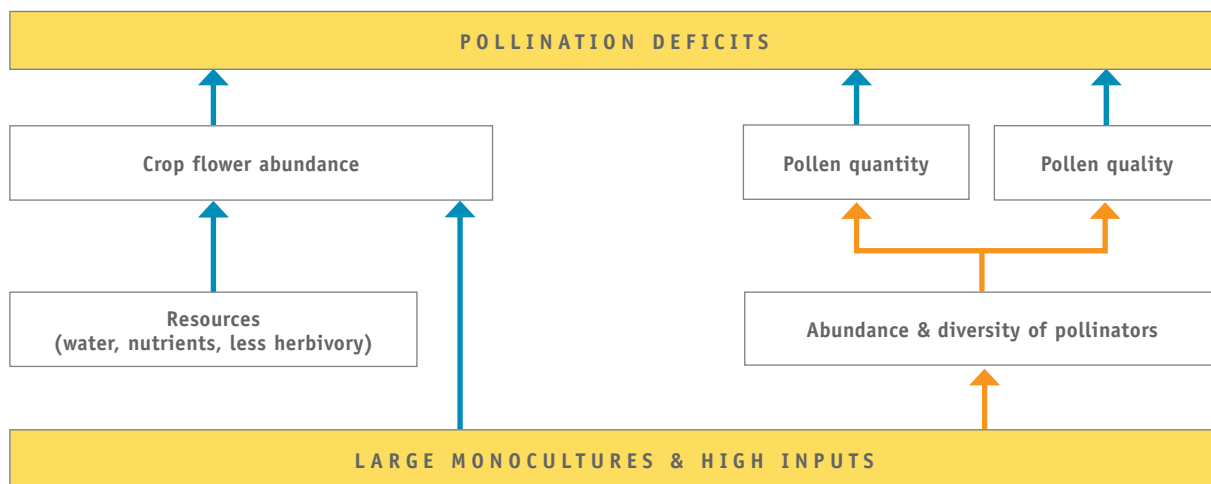
3.1.4 Are pollination deficits common?

The preceding section describes the magnitude of the pollination deficit that would occur if all pollinators disappeared. By analysing temporal trends in the growth and stability of crop yield, this section asks whether pollination deficits are common [24].

Pollination deficits are common among wild plants [25] and are thus expected among crops in general. Indeed, pollination deficits occur frequently in natural pollinator communities and ecosystems [25], just as crops can be nutrient limited even in non-degraded soils [26]. Despite many floral mechanisms that promote efficient pollen transfer, cross-pollination is intrinsically an uncertain process [9]. However, pollination deficits are aggravated in agricultural landscapes for several reasons. First, intensively managed agricultural landscapes usually provide poor habitats for pollinators [2, 3]. Furthermore, unlike crop loss due to herbivores, weeds, pathogens and their vectors, which are usually highly regulated by agricultural practices, pollination is usually subject to only minimal management and occurs almost entirely naturally, as an "ecosystem service" [27]. Worsening this situation, pollinator abundance and diversity are declining in many agricultural landscapes [2, 28, 29], further reducing the quantity and quality of pollen delivered to flowers [30] (Figure 3.2). Finally, current agricultural practices often involve the cultivation of extensive and massively flowering monocultures, increasing pollination demands for brief periods [19, 31]. The demands cannot be satisfied by the local pollinator pool (Figure 3.2), which is itself diminished by the practice.

Figure 3.2

POSSIBLE CONSEQUENCES OF AGRICULTURAL PRACTICES TO POLLINATION DEFICITS



Agricultural landscapes often are homogeneous environments including large monocultures and high chemical inputs, which may either cause pollinator deficits or alleviate some of them (see text). The blue arrows indicate most positive inputs, while orange arrows suggest where abundance, diversity and pollen factors may be negatively affected, while still contributing to overall crop production.

Source: L.A. Garibaldi

Given such conditions, crops with greater pollinator dependence will have a lower mean and stability of yield growth than less dependent crops, despite other practices that increase yield in most crops, such as fertilizer application and irrigation [24]. This prediction is supported by FAO data collected annually from 1961 to 2008, comprising 99 crops that accounted for 95 percent of global cultivated area during 2008. As a consequence of the lower mean and stability of yield growth, the cultivated area increased at a faster rate for crops with higher pollinator dependence such that production can match the demanded levels. That is, yield growth decreased but area growth increased with crop pollinator dependence (see [24] for more details). These results reveal that insufficient and variable pollination quantity and (or) quality reduce yield growth of pollinator-dependent crops, decreasing the temporal stability of global agricultural production, while promoting compensatory land conversion to agriculture.

The conversion of land to agriculture, described above, leads to a concomitant reduction in natural and semi-natural areas within agricultural landscapes, and decreases the abundance and richness (number of species) of wild pollinators (Figure 3.2). Such land conversion increasingly isolates crop plants from wild pollinators, aggravating pollination deficits (Figure 3.2). In particular, a synthesis of 29 studies [2] reveals that a 1 km separation between natural and semi-natural areas reduces flower visitor richness by 34 percent, visitation rates to crop flowers by all insects except honey bees by 27 percent, and the proportions of a plant's flowers or ovules that develop into mature fruit or seeds (fruit and seed set, respectively) by 16 percent [2]. Such separation similarly reduces spatial and temporal pollination stability, defined as the inverse of spatial variation within fields or of among-day variation within fields, respectively. Specifically, spatial stability decreases by 25 percent, 16 percent and 9 percent for richness, visitation and fruit set, respectively, whereas temporal

stability decreases by 39 percent and 13 percent for richness and visitation, respectively [2]. To the extent that pollination deficits and low pollination stability have stimulated any change in agricultural practice, they have traditionally been addressed by managing a single pollinator species, usually honey bees, which are the most abundant crop pollinator species worldwide [2]. Potential effects of distance to source for honey bees are circumvented by deployment in crop fields and, during floral scarcity, by food supplements and other management measures (see Chapter 20). In addition, honey bees forage farther than most wild pollinators, and can locate and use discrete flower patches scattered in the landscape by means of scouting and directed recruitment [32–34]. However, whether an application of honey bees reduces most potential deficits efficiently remains an open question (see Part IV).

3.1.5 Can honey bee management alone reduce pollination deficits?

Honey bees occur both as wild and managed colonies nesting in transportable hives. Hived colonies can be placed in almost any habitat, depending on the demand for commercial pollination or honey production. Therefore, honey bees can alleviate the negative effects of isolation from natural or semi-natural areas on crop seed or fruit set. However, focusing on honey bees alone for pollination management may not provide sustainable pollination for several reasons.

First, an increased abundance of honey bees complements, but evidently does not replace, the pollination provided by diverse assemblages of wild insects. Wild insects pollinate most crops more effectively than honey bees, as revealed by a recent global synthesis of 600 fields in 41 crop systems [35]. In that study, fruit set varied positively with flower visitation by honey bees in only 14 percent of the sampled crops. In contrast, flower visitation by wild insects increased fruit set in every study crop. The relatively weak influence of honey bees detected by this analysis may reflect their tendency to limit single foraging bouts to small flower patches, and sometimes

the flowers of a single plant [13, 14]. If this occurs regularly, cross-pollination is limited and elevated self-pollen interference and inbreeding depression are likely (Figure 3.1) [8].

Second, even for crops pollinated by honey bees, the current commercial availability of colonies may not suffice. Despite a global increase in the number of hives of approximately 50 percent during the last five decades, global agriculture dependent on animal pollination has tripled [36]. These disparate rates strongly suggest a rapidly expanding demand for pollination services provided by wild insects and other pollinators. Furthermore, honey bee numbers have increased unevenly among countries, with strong growth in major honey-producing countries, such as Argentina, China and Spain, but declines elsewhere, including the United Kingdom, the United States and many western European countries [36, 37]. Growth in honey bee numbers in one country is unlikely to contribute to the pollination of crops in another, although many queens and nuclei are distributed internationally (Chapter 16). In most countries except the United States [38], beekeepers profit more from producing honey than from renting colonies for pollination. Therefore, as is increasingly realized, the use of honey bees as crop pollinators will remain low unless payments for pollination increase.

Third, species of flower visitors respond differently to environmental change (response diversity), and thus biodiversity plays an important role in stabilizing ecosystem services, including crop pollination [39]. Indeed, some studies predict an increased role for wild bees given global warming [40]. Another study reported contrasting responses of wild insects and honey bees to wind conditions [41], such that this response diversity may stabilize crop pollination. The effects of response diversity may be especially relevant in the tropics, where impacts of climate change on pollinators are expected to be the greatest [42]. In summary, wild insects play a critical but underappreciated role in modern agriculture, and their importance will increase even more in the future. It is therefore essential to make better use of them for crop pollination.

3.1.6 Why do wild insects contribute to crop yield?

Fruit and seed set are key components of crop yield and reflect pollination success when other resources (e.g. nutrients) are not limiting factors [43]. Positive effects of wild insects on fruit set occur regardless of geographic location, sample size of the study, relative proportion of honey bees in the pollinator assemblage (their relative dominance), pollinator dependence of the crop, or whether the crop species is herbaceous or woody, native or exotic [35]. Such consistency is expected from the generalized nature of plant-pollinator interactions, whereby multiple pollinator species can profit from pollen and nectar of the same plant species [44]. This generalization does not mean that all pollinators interacting with a given crop are equally effective, but rather that various pollinators have comparable pollination efficiency.

The number of pollinator species (species richness) by itself may increase the mean and the stability of crop yield through several mechanisms [45]. First, a rich pollinator fauna displays more individual niche complementarity, with a variety of pollinators active across different flower patches and during different periods, individual days or a crop's entire flowering season, thus providing more consistent pollination overall [39, 46, 47]. Second, different pollinator species can act synergistically. For example, wild insects enhance the pollination behaviour of honey bees, presumably by un-aggressively displacing them from flowers, thus potentially driving both pollination quantity and quality, and enhancing outcrossing [13, 14, 30]. Third, because of a simple sampling effect, richer pollinator assemblages are more likely to include an efficient pollinator for a given crop than poor species assemblages [48]. By these and other mechanisms [49, 50], pollinator diversity contributes critically to an increased, sustained yield.

3.1.7 Sound practices that reduce pollination deficits

Land use changes during the past century have aggravated pollination deficits. Global fertilizer and herbicide use and the irrigation of crop areas

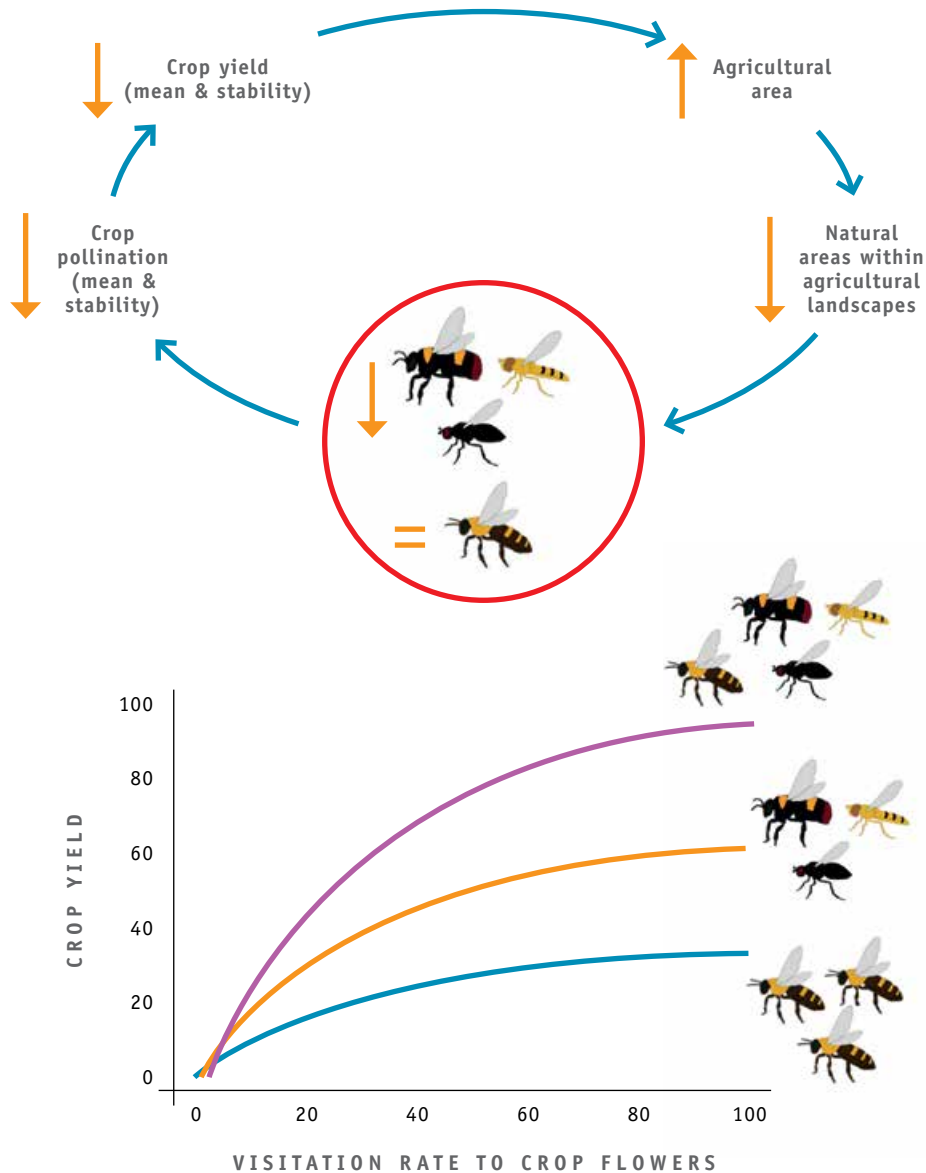
have increased rapidly during recent decades, concomitant with the cultivation of mass-flowering crops [1]. In particular, herbicides – which have seen the most rapid growth in use among pesticides worldwide – are also implicated in the creation of agricultural environments devoid of pollen and nectar resources [50]. As discussed above, the combination of monocultures with sparse, poor pollinator assemblages exacerbates the pollination limitation experienced by many crops (Figure 3.3). In addition to the lack of habitat heterogeneity in those landscapes, high pesticide input further impoverishes wild insect assemblages (Figure 3.3). As argued here, the introduction of exotic pollinators does not seem to be an environmentally sensible practice to mitigate pollination deficits.

Varied practices increase the abundance and species richness of wild insects [51]. Indeed, wild pollinator species richness and flower visitation rate – a reflection of pollinator abundance – correlate strongly across agricultural fields [35]. Therefore, practices that enhance species richness may also increase aggregate pollinator abundance, and vice versa. Practices that should enhance the carrying capacity of habitats for wild insect assemblages and associated crop pollination services include:

- conservation and restoration of natural and semi-natural areas within landscapes dominated by crops [2, 3];
- planting hedgerows and flower strips along field edges [52–54];
- the addition of nesting resources (e.g. reed internodes) [55];
- implementation of organic practices within landscapes dominated by conventional farming [23, 56–58];
- the development and implementation of pollinator safety guidelines when applying insecticides [59–63];
- enhancement of farmland heterogeneity [39, 56, 64, 65];
- reduction of crop field size [66];
- actions to increase flowering plant richness within crop fields [14, 61, 62, 67, 68].

Figure 3.3

THE CYCLE OF WILD POLLINATOR DECLINE IN AGRICULTURAL SYSTEMS AND ITS EXPECTED CONSEQUENCES FOR CROP YIELD



Pollen limitation hinders yield growth of pollinator dependent crops, decreasing temporal stability of production, and promoting compensatory land conversion to agriculture at the expense of natural and semi-natural areas. These land use changes decrease the species richness and abundance of wild pollinators (represented by upper three insects in red circle) and crop pollination, but do not affect honey bee abundance (represented by lower insect in red circle). Increasing the visitation rate (visits flower⁻¹ hour⁻¹) of only honey bees adds pollination and crop yield (tonnes ha⁻¹), but does not compensate for pollination losses from fewer wild insects.

Source: L.A. Garibaldi, reprinted from [50]

The effectiveness of such practices is context dependent, and relatively more successful when and where background floral resources, and natural nesting substrates, are scarce [69]. Where diverse floral resources are already available, preserving this diversity is likely to be the most cost-effective mitigation practice. In general, the effectiveness of large-scale practices (e.g. restoration of semi-natural areas) depends on smaller scale practices (e.g. increasing plant diversity within fields), and vice versa. The effects of such management depend on how far the various pollinators will fly from their nests, which is poorly studied. Flight distances are expected to vary positively with body size [70]. However, strong fidelity to small habitats, irrespective of body size, has also been documented [71]. Therefore, small-scale practices can strongly affect pollinators and crop pollination [52, 72]. Maintenance of biodiversity in agricultural landscapes is expected to support ecosystem services generally, and there is already strong evidence [35] that this is the case for the diversity of wild insects and the pollination services they provide.

3.1.8 Natural history of bees and their potential for crop pollination

Bees (Hymenoptera, Anthophila) are the single most important group of pollinators because they depend on flowers for nourishment at all active lifecycle stages, and visit flowers regularly and consistently. Nevertheless, the estimated > 20 000 species of bees [73] do not have equivalent potential as effective crop pollinators because of differences in geographic ranges and natural history, including abundance, phenology and habitat requirements. Thus, from an agricultural rather than a purely conservation perspective, management practices that promote suitable species are more likely to result in improved yields.

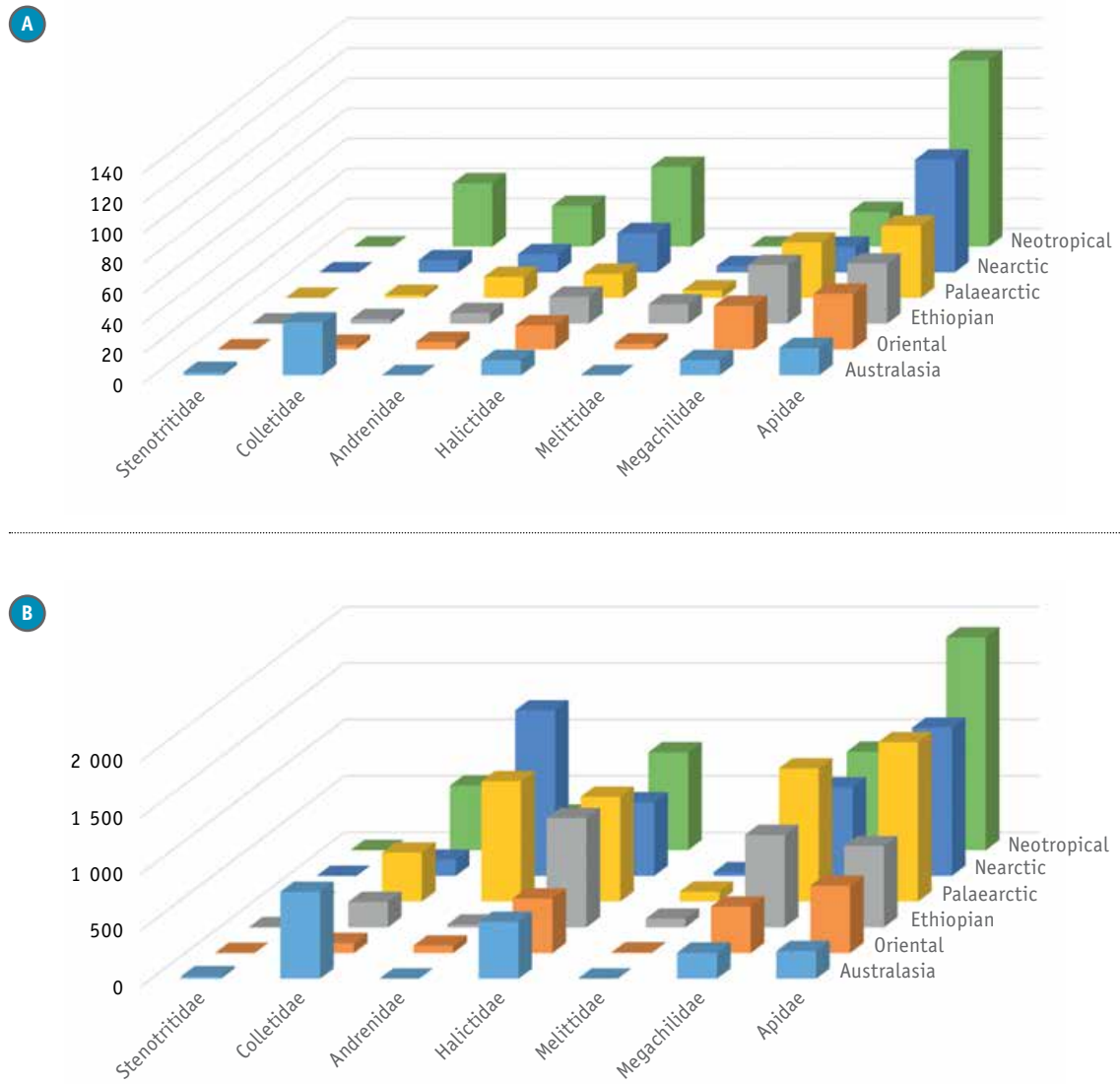
Bees are not equally spread geographically, but instead are most diverse in arid and semi-arid habitats, perhaps as a consequence of their purported evolutionary origin in drier parts of Gondwana [74,

75]. The preponderance of different bee taxonomic groups also varies with habitat and continent. Some higher-level taxa are geographically restricted, such as Stenotritidae and Euryglossinae, which are native only to Australia (Figure 3.4). Others are restricted, or largely restricted, to specific biomes. Stingless bees, Meliponini, are almost entirely tropical whereas the most species-rich bee genus, *Andrena*, is largely a north-temperate taxon (Figure 3.5a). Still other taxa are almost ubiquitous: *Hylaeus* is found on all continents except Antarctica, which has no bees.

To be suitable for crop pollination, wild bees must be active simultaneously with crop flowering. Eusocial bees are often more suitable in this regard, because they are active throughout the growing season. They include the native *Apis* and *Bombus* species that extend from northern Africa to Asia, and in the case of *Bombus* also into the Americas. Those genera have had their ranges extended further by human introduction (below), and commonly exploit crops [35]. Most social Halictini, on the other hand, have pulses of activity, although their nests are often closed between brood-producing periods [76]. Solitary bees with a single generation per year rarely forage for more than a few weeks, and the activity periods of specialist species are often tightly linked to the flowering periods of their preferred hosts. Nevertheless, such phenological matching can be used to advantage for crop pollination if a specialist species frequents wild relatives of the crop, as is the case for the nomiine *Dieunomia* and sunflowers [77].

The activity periods of solitary bees also vary taxonomically. For example, although most *Andrena* are active during spring, North American species of the subgenus *Cnemidandrena* fly during late summer or autumn [78]. Similarly, species of the *Colletes inaequalis* group are among the first bees active during spring in northeastern North America [79], whereas species of the *Colletes succinctus* group are active during late summer and autumn in Europe [80]. Such phenological characteristics exclude many bee species as potential crop pollinators, despite their contribution to the pollination of native plant species.

Figure 3.4
NUMBERS OF GENERA (A) AND SPECIES (B) OF BEES OF DIFFERENT FAMILIES FROM DIFFERENT ZOOGEOGRAPHICAL REALMS

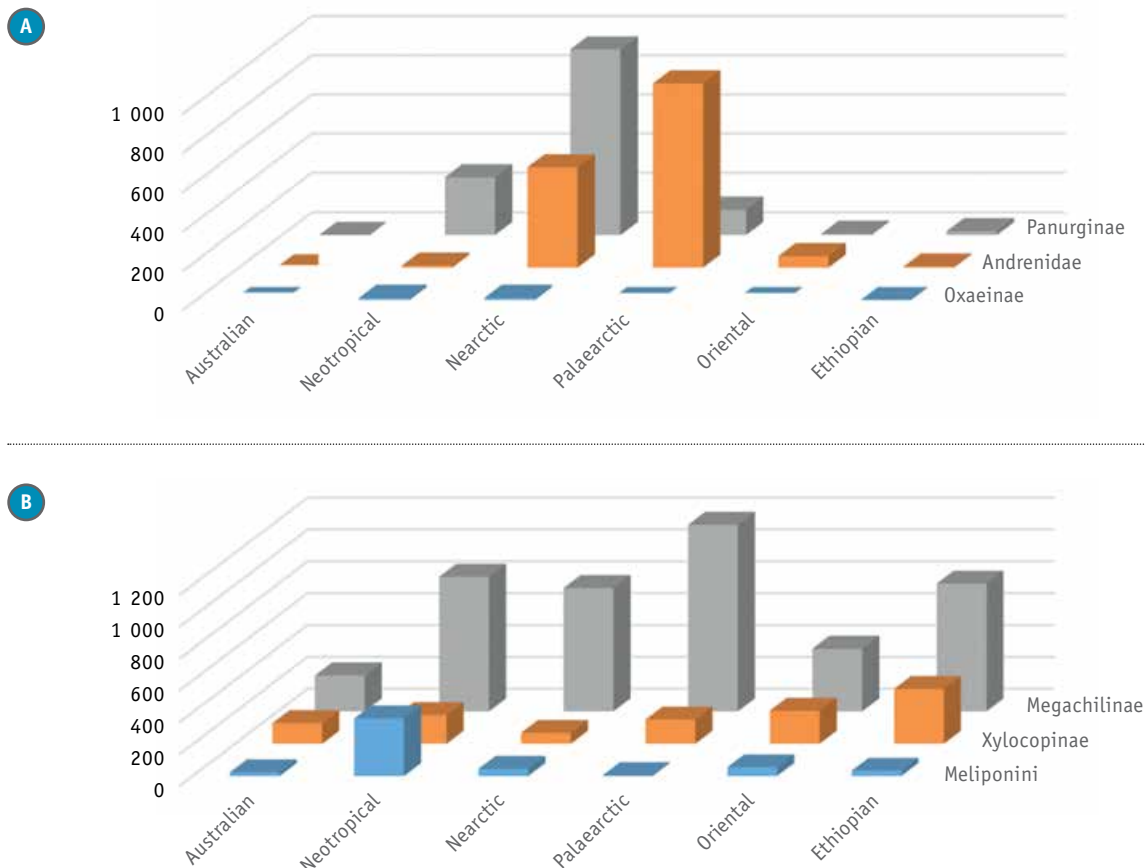


These data were obtained from [129] with the different regions delimited by national boundaries as close to those of the realms as possible. The greater generic diversity in the Neotropics for Colletidae, Halictidae and Apidae is evident, as is the low generic diversity of bees, except the Colletidae, in Australia. The pattern for species shares some similarities, such as the high diversity of Apidae in the Neotropics, but also some differences, such as the diversity of Halictidae in the Ethiopian realm. Some of the variation among regions likely reflects different intensity of study of bee taxonomy

Source: L.A. Garibaldi, reprinted from [50]

Figure 3.5

GEOGRAPHIC VARIATION IN THE NUMBERS OF SPECIES IN (A) THE THREE SUBFAMILIES OF ANDRENIDAE AND (B) THE THREE TAXONOMIC GROUPS OF BEES TO WHICH MOST MANAGED BEES BELONG (OTHER THAN *APIS* OR *BOMBUS* SPP.) AND FROM WHICH ADDITIONAL SPECIES MAY BE MOST SUITABLY EXAMINED FOR USE IN CROP POLLINATION



Source: L.A. Garibaldi

In addition to food requirements, the maintenance of viable wild bee populations in agricultural landscapes requires the provision of suitable nesting conditions. All Andrenidae, Melittidae and Stenotritidae, as well as the vast majority of Halictidae, nest in soil.

However, details of the preferred soil type, degree of shading and so on are known for comparatively few species [81, 82]. As a result, appropriate management practices are unclear. It is noteworthy that the most intensively managed ground-nesting pollinator, the alkali bee (*Nomia melanderi*), has specific and

somewhat unusual substrate requirements, including silty, sub-irrigated soils with salty surfaces [83] (Chapter 5). Other ground-nesting bees used for crop pollination include *Amegilla* spp. for tomatoes in Australian greenhouses [84] and cardamom in India [85] and New Guinea [86], and both *Augochloropsis* and *Exomalopsis* for tomato pollination in Mexico [87] among others (see Part III).

Some bee subfamilies nest primarily in wood or pithy stems, including most Hylaeinae, Megachilinae and Xylocopinae, which makes them particularly amenable to management, because suitable

materials can be readily provided. The first of these are comparatively hairless bees that carry foraged pollen internally, and so are not suitable for crop pollination. *Xylocopa* are effective pollinators of blueberry and passion fruit (see Chapters 9 and 15), as well as greenhouse tomatoes and melons [88]. However, the clearing of woody debris prior to planting of passion fruit vines, a usual agricultural practice, results in crop failure [89]. In contrast, *Xylocopa* in artificial domiciles have been introduced effectively into passion fruit orchards in Brazil [90]. They also colonize unoccupied nest sites within the fields, although the placement of unoccupied nests in fields does not attract bees from outside [90].

Megachilidae have the largest number of managed solitary bees, but are also the family with the most diverse nesting requirements [91, 92]. Most species nest in pithy stems or holes in wood, but for some species almost any cavity is used for nesting (they have even been found in the fuel lines of downed aircraft [93]). There is a large literature on the use of alfalfa leafcutter bees and various orchard bee species [94, 95], but one recent study also demonstrates the importance of nest dispersion. Specifically, *Osmia lignaria* (the "Blue Orchard Bee") prefers to nest in plots with a high density of nest boxes (100 per plot) with few cavities (100 per box), rather than in plots with a lower density of nest boxes (25 per plot) with many cavities (400 per box), despite the same overall density of potential nest sites [96]. Such details of nest box design and spacing will impact bee reproductive success and potential for sustainable management.

The use of wild bees as agricultural pollinators must embrace more aspects of their biology than mentioned above. Those of particular relevance are population dynamics [97] and features of the mating system, such as the potential impact of diploid males [98] on the persistence of small bee populations. Variation in ecological traits among bees of different taxonomic groups must be considered when habitat is modified to enhance crop pollination by native bees. Consequently, the expanded use of wild bees in food production will require increased expenditure

on basic taxonomy and natural history [99]. Tropical stingless bees (Meliponini) provide a prime example. These eusocial bees have long been managed for honey production [100, 101], and one genus, *Melipona*, is increasingly used for pollination of crops such as tomato, eggplant and *Capsicum* peppers [102–105]. Their use is expanding in Africa [105, 107], Australia [106] and Latin America [101, 108] (see Part IV). The group includes hundreds of species that may be used in agriculture (Figure 3.5b). However, the pollen and nectar preferences of only few species are known, and even less is known about their pollination performance on particular crops [109].

3.1.9 Bee introductions

Motivated first by desire for honey and then by crop pollination problems, humans have promoted a few bee species and moved them beyond their original ranges. Accidental introductions can lead to successful colonization, even from a single, mated female [110]; however, some of the most problematic invasions have followed purposeful introduction for honey production or crop pollination [111, 112]. Most notably, honey bees and *Bombus terrestris* native to the Western Palaearctic have been spread around the world with human assistance. Both domesticated and wild varieties of honey bee are now nearly ubiquitous, and several European *Bombus* species have become naturalized in North and South America, Japan, New Zealand and Tasmania [113, 114]. In some regions, the alien bees have become superabundant, such as Africanized honey bees in the Neotropics [114–116] and *B. terrestris* in Patagonia [111]. In these cases, invasive bees overexploit flowers of both native and crop species, in some instances reducing fruit set because of intensive pollen theft [117] or flower damage [10]. Although exotic bees usually comprise only a small proportion of local bee diversity [118, 119], their abundance at a site can thus increase dramatically over time [114, 120] and spread rapidly upon introduction [111, 121], with the potential for large-scale ecological [47] and agricultural impacts [122].

In addition to reducing fruit and seed set as a result of over-visitation [10], introduced pollinators

may diminish the reproduction of both cultivated and wild plants if they displace more effective native pollinators. Evidence for such impacts is varied. It is not clear whether the natural abundance of native bees decreases following invasion of the Africanized honey bee [47, 113, 114, 123]. Furthermore, visitation by wild bees to crop flowers sometimes varies independently of honey bee visitation [34]. However, invasion of Africanized honey bees has changed the preferences of native plant species by wild insects [47, 114]. Other studies have shown that the presence of managed honey bees can reduce the reproduction or fecundity of native bees, presumably through resource competition [124]. More seriously, the abundance of medium and large-bodied native bees declined following the arrival of *B. terrestris* in Israel in 1978 [125]. Similarly, the invasion of northwest Patagonia by *B. ruderatus* and then by *B. terrestris* during the last two decades has driven the native bumblebee *B. dahlbomii* to the brink of extinction [111]. The latter population collapse probably resulted from the susceptibility of the native bumblebee to pathogens transmitted from the invading congeners, rather than resource competition [126].

In summary, bee introduction can impose high environmental costs, while its benefit for crop pollination is arguable. As discussed, honey bees are often not particularly efficient pollinators. Their importance is likely to be greatest when the native pollinator community is so reduced that only managed honey bee hives can replace the missing ecosystem service. Introduced bumblebees can be highly damaging to flowers when abundant, or cause the demise of other, more efficient, pollinators. Little information is available on the impact of other introduced bees [113], but available evidence suggests that future pollinator introduction should be strongly discouraged. Instead, pollination management practices should, wherever possible, promote diverse and healthy assemblages of native pollinators.

3.1.10 Conclusion

Humanity faces a major challenge as agricultural intensification and growth of cultivated areas increase to satisfy greater demands from a human population of growing size and affluence [127, 128]. However, with long-term, sustainable agricultural practices, higher agricultural production does not necessarily require further loss of biodiversity or major environmental degradation [127, 128]. Crop yield (tonnes ha⁻¹) is a key driver of farm profits, livelihoods and agricultural decisions, which influence land use at both local and global scales. This chapter discussed how yield could be limited by pollen quantity and quality. Pollination deficit is the difference between realized yield and potential achieved under optimal pollen quantity and quality conditions. Pollination deficits can arise for crops because, unlike other limits, such as nutrients and pests, pollen delivery is not managed directly in most agricultural systems. Consistent with these observations, global patterns of yield reveal that pollination deficits are common for crops dependent on animal pollination.

Pollination deficits reduce the yield growth of pollinator-dependent crops and also promote the cultivation of a larger area to satisfy production demands. Indeed, planting of pollinator-dependent crops is expanding three times faster than the managed honey bee population, potentially exacerbating chronic pollination deficits exhibited by many crops. As a consequence, crop yield increasingly depends on pollination services provided by wild insects, which contribute significantly to fruit or seed set, regardless of crop origin (exotic or native) and life history traits (herbaceous or woody, etc.). Honey bees supplement the role of wild insects but cannot replace them, so that efforts to maximize pollination require the conservation or enhancement of all available pollinators. However, managed and wild populations of pollinators are declining in many agricultural landscapes, and further introductions of alien species should be discouraged because of their manifold environmental impacts. This situation strongly motivates conservation or restoration of natural and semi-natural areas within agricultural landscapes.

Restoration is promoted through land use heterogeneity, the addition of diverse floral and nesting resources, and respect for pollinator safety when applying pesticides and herbicides. Natural history traits of local wild pollinators can often be used to improve the effectiveness of pollinator-supporting practices. In general, the potential management of

wild bees for crop pollination is still largely unrealized. Practices that enhance wild insects and associated crop pollination will usually provide resources for managed honey bee colonies, and can also enhance other ecosystem services, thereby creating positive feedback between healthy agricultural environments and high and stable crop yields.

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