This publication provides an approach for the socio-economic valuation of pollinator-friendly practices at a landscape/farm level. The text was prepared as part of the Global Environment Fund (GEF) supported

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THE POLLINATION OF CULTIVATED PLANTS

A COMPENDIUM FOR PRACTITIONERS

Volume 1

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POLLINATION SERVICES FOR SUSTAINABLE AGRICULTURE

THE POLLINATION OF CULTIVATED PLANTS

A COMPENDIUM FOR PRACTITIONERS

Volume 1

Edited by
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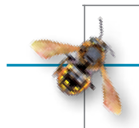
This publication provides information on the management of bee pollinators in apple orchards.

The text was prepared as part of the Global Environment Fund (GEF) supported project 'Conservation and management of pollinators for sustainable agriculture, through an ecosystem approach' implemented in seven countries – Brazil, Ghana, India, Kenya, Nepal, Pakistan and South Africa.

The project is coordinated by the Food and Agriculture Organization of the United Nations (FAO) with implementation support from the United Nations Environment Programme (UNEP).



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PREFACE
TO THE SECOND EDITION

Pollinators such as bees have been declining in diversity, if not abundance, ever since people began to replace their habitats with those suited for human use. Humans are largely responsible for this problem and, thus, might also be expected to remedy it. How to achieve this, however, is not yet exactly clear. Furthermore, there is now increasing awareness that an intact ecosystem has values determined by social, political, economic and a host of other human devices, which are often in conflict with ecological processes that form and maintain ecosystems and the services they provide to humanity [1–3].

Many advocate the use of "sustainable" approaches in crop pollination. However, it is prudent to draw on the knowledge of experts in related fields. One such group is the sustainable forestry cadre, which encompasses both the so-called developed and developing worlds. In their words, [4] sustainable forestry is not the same as sustainable forests. In the present context, sustainable pollination is not the same as sustainable pollinators. Which pollinators are to be sustained, how and for whom?

There are obvious trade-offs. In the case of agriculture, managed pollinators are brought in when local pollinator numbers are too low in the surrounding environment to pollinate crops at an acceptable level. However, when the environment itself is the source of pollinators, and property boundaries are already set, some difficult decisions are required. How much land or habitat should remain underutilized by agriculture or other activities to sustain pollinators? In other words, how many crops or other materials can be voluntarily sacrificed for the sake of producing fruit and seeds that are only obtained from pollination by wild animals? In larger farms or monocultures, the question is more complex, but similar. If fewer pollinators result in a smaller yield, is it less costly to increase planting density or area, to hire a pollinator service provider (PSP) or to sacrifice arable land for "pollinator reserves" [5]? Finally, biocides almost invariably reduce pollinator populations [6, 7]. Is the cost of such chemical input compensated by the increased saleable produce and the profit margin, compared to lost production due to a pollination/pollinator deficit?

As if this were not already complicated enough, bee keepers are hard pressed to maintain their profit margins, which seem to hover at a level of net profit being just shy of 10 percent of the gross profit [8]. In other words, no one is getting rich, but commercial beekeeping is sustainable – meaning that it can continue and is not going "into the red". The fact that nature is deemed sustainable only when such a decline is avoided is a sure sign of trouble. Nature must not only continue, but advance by a process known as natural selection, to keep pace with the mounting challenges posed both by environmental change and human impact. Without the appropriate habitat and populations it supports, that cannot occur.

The present compendium for practitioners shows the reader how to strive to maintain important checks and balances, taking into consideration pollinators in croplands, both large and small, and within the world's temperate and tropical realms. While it describes a range of methods and goals, it does not advocate any particular product or copyrighted item. Thanks are due to FAO for its service in furthering applied pollination science.

David W. Roubik
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A NOTE ON REFERENCES

Several of the chapters and sections included in this publication appeared in earlier forms in the previous edition of this Compendium: *Pollination of Cultivated Plants in the Tropics* (1995). The presentation of the references in these chapters has remained the same, with the inclusion of newer publications where these are mentioned in the text. New chapters and sections use a numbered reference system. All chapters have been revised and updated for this second edition.

Part I
INTRODUCTION

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Chapter 1

LESSONS LEARNED OVER THE LAST 20 YEARS

D.W. Roubik

1.1 SUSTAINABLE POLLINATION AND POLLINATORS

The year 2012 marked the 50th anniversary of a landmark book by Rachael Carson entitled *Silent Spring*, which first drew attention to the real dangers of biocides. Today, lessons regarding the hazards of toxic pesticide are still being re-learned, with the consequences of usage most evident in pollinators. In 1995, FAO published *The Pollination of Cultivated Plants in the Tropics*, which introduced readers to various aspects of natural and insect pollination. Now, over 20 years later, it is timely to revise, update and expand this publication. While there is much new information to be added to the knowledge base on pollination, much of what was known 20 years ago bears repeating.

The practical concerns of pollination studies are not difficult to understand. The largest crops – rice, wheat, sugar cane and corn – are pollinated by wind, but the proportion of crops that requires pollination by animals has increased steadily. Only a few crops used for fruit, seeds or fibre (e.g. olives, pistachio, pineapple and banana) have no need for pollination by animals [4, 5]. The utility of pollination also extends to crops beyond food and fibre. For example, a number of important biofuels (aside from sugarcane and corn) benefit from pollinators including: sunflower, canola, African oil palm, coconut, *Jatropha* and soybean [6, 7, 44 and see Chapter 9.3].

Yet, problems still arise in getting the pollinator-pollination message across, despite concerted efforts [8–24]. Notwithstanding progress in farming techniques and diverse farm management strategies, many limitations persist in basic and applied knowledge of pollinators and their environment, especially among small farms. In such environments, pollinators cannot be rented or purchased; they must be incorporated into farming itself. And if they are lost, *some* (see below) will likely vanish forever. Most of the pollinators in any kind of agro-ecosystem certainly seem to require conscious attention and management innovations, if not intervention or regulation.

Not all pollinators are amenable to management, however. Those that are possess certain distinguishing characteristics that require attention, especially now. The main pollinators serving agriculture in addition to "pollen bees" (Chapter 4) are "persistent pollinators". They nest along roadways, open areas, human-created landscapes and often forage in weedy vegetation. They are pre-adapted to disturbances such as land clearing or aridity, and opportunistically use available nesting and food resources during much of the growing season. Their pioneer habits make them potentially invasive and able to fill biological gaps and loose niches. Individuals and companies that have achieved economic success as "pollination service providers" produce and sell adaptable or at least manageable bees, such as *Apis, Osmia, Centris, Xylocopa, Bombus* and *Megachile*. Such species forage on a wide range of plants and crops and are amenable to nesting in spaces expressly created for them. Most importantly, they appear to compensate for biodiversity loss in pollinator species by their sheer number and persistence, a fact that is still underappreciated.

Thus, it is true that, over the short term, pollination may be preserved at the expense of certain pollinators by substituting the rich diversity of pollinators in natural systems with certain "default pollinators" in agricultural systems. A conservationist views such novel pollinators as a mixed blessing, because they may displace the original pollinators. Many of those original pollinators, however, prefer their normal habitat and will be primarily found there, not in the agro-ecosystem. Although the most flexible species will remain accessory pollinators in agriculture and silviculture, more sensitive species will not be found nearby. The majority of pollinators, outside of particular reserves, will be a small subset of the original pollinators in any geographic area. These will be the pollinators that are managed, and will include the most adaptable and opportunistic species that rapidly colonize, reproduce and compensate for environmental stressors. In rare cases, they might also include species that can partly withstand biocides, fire, rising global temperature and tillage. The most obvious alternative scenarios in the agro-pollination network seem implausible: people are unlikely to abandon farming in favour of forest gardening within semi-natural communities; the continuation of widespread habitat poisoning until all wildlife, including pollinators, is driven to extinction seems inconceivable; and agronomists are unlikely to find the means of converting all important crops into self-pollinating or pollen-free varieties. Pollinators, some of them living in the wild and some of them under human care, will continue to form the basis for successful agriculture and silviculture. The only rational definition of success is sustainability, in its best sense.

1.1.1 Tropical and temperate zones

When the first edition of this book was completed, in 1993, several important facts were evident. The majority of plants cultivated in the tropics had not received much attention with respect to pollination requirements, breeding system or pollinators. Most cultivated plants and their fruit, seed and edible parts had therefore survived without applied human knowledge or management. This statement also applied – and still applies – reasonably to the temperate zone, in addition to the tropics and subtropics [25–31]. Moreover, although agrarian knowledge is formidable on fruit, nut, vegetable and seed crop management [32, 33], the paucity of concrete pollination data for tropical and temperate crops remains unchanged. Several new chapters here serve to demonstrate the range of important tests and variables that are needed to supply that badly needed, detailed information on pollination.

Because tropical crops grown in the highlands usually originate in the temperate zone, tropical pollination information already contains much that is relevant to temperate climates. At the same time, the tropical crops consumed in the temperate zone are much more diverse than temperate zone crops consumed in situ. It is therefore important to study and monitor them, especially in the global marketplace. One region and set of practices also informs others, which constitutes a significant advantage for the goal of sustainable pollination and sustainable pollinators worldwide.

In the tropics, the last 20 to 30 years mirror past dynamics in the temperate zone with at least one major difference. A basic ecological turning point is approaching: the tropics are quickly losing a significant proportion of natural habitats, including a large part of the world's species [34], and routinely depend upon this often underappreciated wildlife. Temperate latitudes have already passed through changes that led to the adoption of different, manageable pollinators, either to supplement or replace those in agricultural settings. As Krell (Chapter 10.5) points out, creating infrastructure for improving pollination is expensive and difficult, and the best alternative is to conserve pollinators while they still exist (Chapter 3.1). While the situation in the temperate zone is being managed – more or less – this is often not the case in the tropics as far as pollinators and pollination are concerned. Economies in these regions are, therefore, especially vulnerable to a pollinator decline [e.g. 35]. However, one distinct advantage in the tropics is the continuous breeding and activity of pollinators and plants. If this persists, and does not have to be artificially restored, there are many benefits, including potential recovery following negative impacts.

Somewhat contrary to the above scenario, there have been significant new advances in applied and managed pollination, at least at the descriptive level. Some of the most comprehensive and detailed efforts relate to tropical zones. For instance, a catalogue of Neotropical bees led to a broad summary of passion fruit management in Brazil, and also to an enumeration of common bees found at flowering crops in that diverse tropical country [99, 119, 120]. In the temperate zone, detailed manuals now supply the natural history enthusiast with the means to identify species of bumblebees [36]. The subjects of pollinator application, restoration and gardening to fulfil pollinator needs have been treated by recent introductory guides and manuals, both supported with international funding and by societies dedicated to pollinators and their conservation, and are generally available on the World Wide Web [e.g. 86, 107, 109, 119].

This revised edition of the original compendium, first published in 1995, examines the tropical and temperate zones together. It incorporates and updates several sections from the first edition and adds many new chapters and authors. These emphasize not only the present state of knowledge and its application but, in general, approaches and methods for *getting things done* in various farming environments. In order to introduce those subjects to a new generation of readers, the following paragraphs outline the general similarities and differences of tropical and temperate zones.

Pollinators can be divided essentially into two groups: those dedicated to visiting flowers and those that make only occasional use of them. Bees, certain wasps and flies are the *only* animals that specialize in harvesting pollen, using its protein to make their offspring. These insects are indispensable for pollination. They remove pollen from the anthers, handle it and occasionally pass it on to a receptive stigma, but otherwise pollen is destined for brood, the earth or personal consumption by such dedicated flower visitors.

The tropics are distinguished not only by continuous growing seasons, and a potentially greater build-up of diseases or herbivores, but also by a much wider variety of general pollinators – primarily honey-making social bees with colonies active year round [17, 22, 37, 38]. Those bees are termed "general pollinators" because they may interact with a large proportion of the local flowers. More importantly, such bees recruit hundreds to thousands of colony members on the best available blooms. This results in distinctive behaviour with bees visiting flowers and leaving in a comparatively abrupt manner, particularly in large patches such as croplands. Once the blooms are over or if they have not satisfied the colony, the bees continue their search for more. Colonies can live for years and reproduce, visiting one flower species after another or many at the same time.

In the temperate zone, other bee groups and varied pollinating animals often seek a narrower variety of flowers. However, in both the temperate zone and among certain tropical habitats and species, the individual pollinator has a brief active season. During a favourable period at any point on the globe, a particular bee or other flower-visiting animal may reproduce and then disappear from view for around 48 weeks. Such varied pollinator schedules call for fundamental differences in management outlook and approach in croplands. The tropics and some subtropical areas are naturally endowed with bees that visit flowers throughout the year; however, their value as adequate or manageable pollinators, as shown in several chapters here, is only now being realized.

Among all the world's pollinators – including flies, wasps, bees, beetles, thrips, butterflies and moths, through bats, birds, marsupials and the odd ant, crickets, cockroaches, squirrels, lizards and molluscs – about half of tropical flowering plants depend on bees. This proportion rises in farms and wildlands of the temperate zone, where the majority of flowering plants are visited and pollinated by bees, birds and flies. When searching for crop pollinators with the aim of increasing their abundance – and believing that this will also help pollinate native flora – a fairly rigorous plan of study and experimentation is needed to provide evidence that such hopes are well founded. Although this area remains beyond the scope of the present publication, the tools needed to investigate the subject are presented here and have been updated since the original edition.

1.1.2 Pollinator backup and restoration

Although animals pollinate flowers everywhere, among crops the most widely employed pollinator is usually a single species of honey bee. This social animal provides a critical backup role in the pollinator realm. As a manageable bee that also produces marketable honey and wax, *Apis mellifera* has few counterparts in the pollinator world – most notably the tropical and subtropical "stingless honey bees", now increasingly utilized. Those honey-making animals are equally regarded as a basis for "productive conservation", perhaps because they have multiple uses and provide economic benefits. They may be good for sustaining a certain kind of agriculture, much as teak plantations prevent erosion or leguminous cover crops improve soil nitrogen, but whether they should constitute the principal basis for agricultural pollination is rightly questioned (see Chapter 3).

Although crops that require animal pollination do not provide the bulk of food for human consumption, their individual nutritional value is often higher [35, 39]. At the high end of crop value, biofuels and seed, fruit, nut and beverage crops increasingly demand bees and other pollinators, which must be managed to fulfil such demands [29, 40–45].

By diversifying the species that are put to work for those purposes, and by working to understand their biology, experts come closer to finding adequate insurance for both human needs and general conservation. Perhaps some time in the future, pollinators managed for crop production or invasive ones that have naturalized (e.g. megachilids, bumblebees or honey bees in the Americas, Australia, New Zealand and elsewhere) may provide a backup or even the sole pollination services for certain native wildland plants, as they now readily support a variety of invasive flora. The vast crop fields, if varied in their composition and managed in a "pollinator friendly" manner, may in turn help to restore *some* pollinators to their native habitat. The essential fact remains that a species in an assemblage is sustainable in the proper community, while all else is unsustainable without added input. This publication is an effort to define the parameters of that needed human input.

1.2 THE EXTENT OF PROGRESS TO DATE

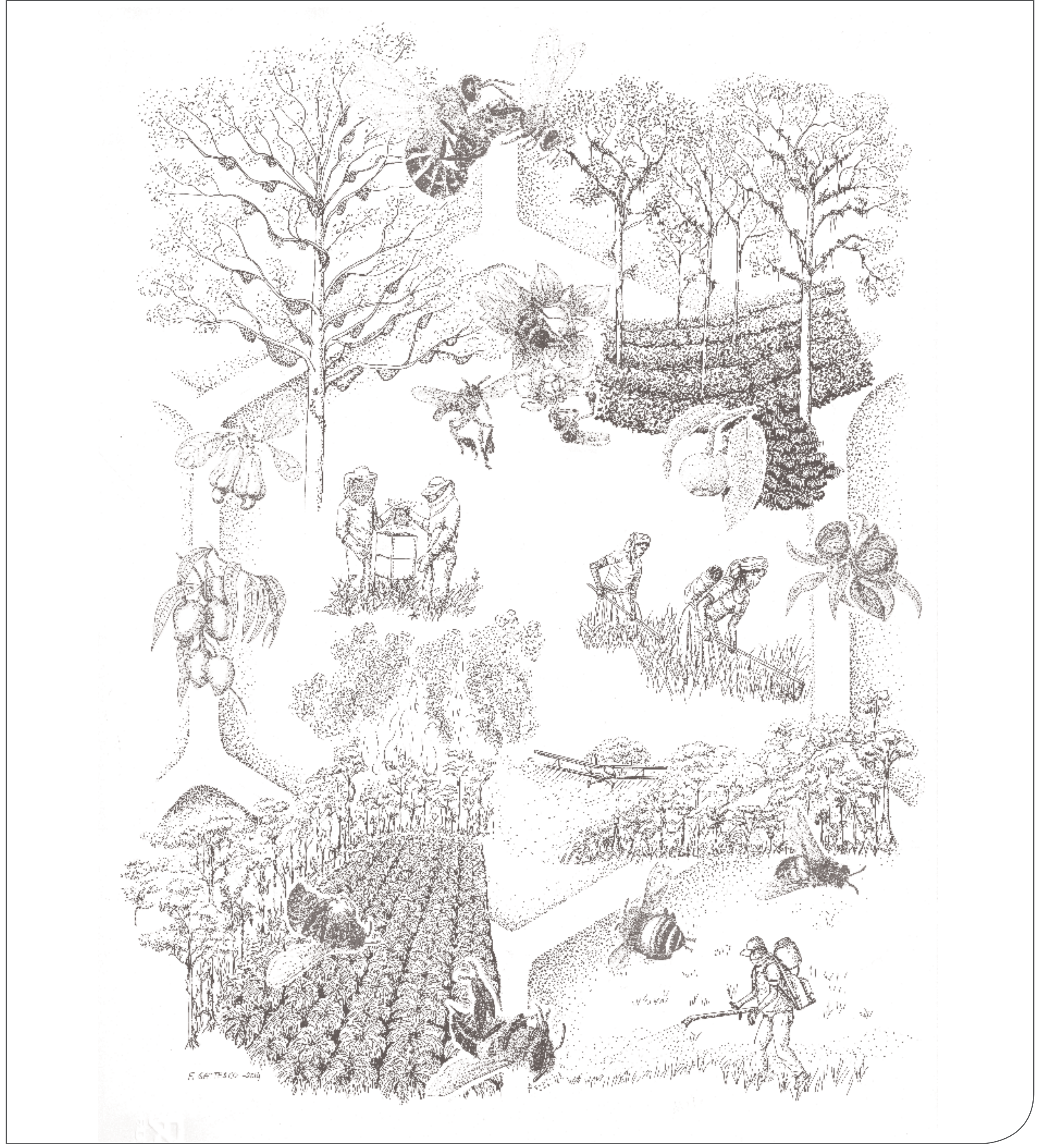
1.2.1 An ecological overview

Fifty years ago, it was known that pollinators for agricultural plants can fail, just like the rains or a vernalization period, and that growers often "place all their eggs in one basket" – at least for a year or two [45]. Then, as now, small farmers in tropical zones cut and burn forest to sow crops in a cycle resembling "predatory farming" [46] – using up one set of resources and then passing to another, but at a small scale and with a rapid farm recovery period. However, more extensive land use by more people, and greater demands, leads to soil and land becoming increasingly depleted.

Less traditional and larger-scale styles of farming spread rapidly removing existing habitats and organisms, including pollinators, more or less completely and for relatively long periods. All such practices inevitably affect huge landscapes, but the tropics and the temperate zone also harbour substantial areas of natural vegetation and wildlife. These natural ecosystems nonetheless experience drought, flooding and a certain degree of regular, substantial fluctuation.

Figure 1.1

SCENES OF HUMANS, CULTIVATION AND POLLINATORS FROM AROUND THE GLOBE



Above left depicts a mating and nesting aggregation of the giant honey bee, *Apis dorsata*, in Asia, and a mating drone with queen flying nearby. Flies and stingless honey bees (meliponines) are shown below, working on the flowers of mango. Shaded coffee plantings, pollinated by diverse bees, are presented along with forest clearing and burning, traditional tillage and beekeeping with a hive of honeybees, and the chemical applications of herbicide and pesticide (by air) in paddy rice, next to a young plantation of African oil palm, pollinated by beetles and not requiring biocwide utilization (in the Neotropics, contrasted with Asia and Africa). Ripe fruit of mangosteen, mango, cashew and lychee are shown.

Source: Drawing and design by F. Gattesco and D.W. Roubik

Figure 1.2

WHAT THE BEES HAVE GIVEN US

Food is shown in the form of honey and pollen from both stingless honey bees (above right), with two worker bees in flight and a fecund, non-flying queen next to a few brood cells and honey pots, while the worker *Apis mellifera* (above left) flies near its comb and brood containing a few drones and queens. Food and beverage take the form of products of plants whose flowers bees forage from and deliver pollen to (below left), with a worker bumblebee cradled next to some coffee beans and leguminous seeds. Seeds for growing plants with multiple uses are also shown (bottom right), including forage for livestock (the "leafcutter" bee female shown at its nest, a managed pollinator for lucerne), biofuels (sunflower seeds), and squash and melon seeds.

Source: Drawing and design by F. Gattesco and D.W. Roubik

They are by no means stable, regardless of latitude or elevation, and their original pollinators and floral resources experience peaks and lows. Thus, an important contrast with agricultural areas is not only the presence of abundant native pollinators, including some that are managed, but an abundance suitable for pollination. That relative stability is certain to be a goal of management, rather than a given feature obtained merely by preserving pollinator reserves or management areas.

A curious "boom or bust" resource pattern also exists for flower visitors. Of particular relevance to the main subject of this publication, is the important role played by ENSO (El Niño–Southern Oscillation) events [59, 74] in heavily agricultural areas particularly in Southeast Asia, tropical America and Africa. An extensive flowering period occurs every few years, in which a large variety of woody plants flower concurrently, usually within a few months. Among mass flowering crops, and in those natural systems affected by the dry years of ENSO, pollinators are attracted in large numbers to resources that last only a short time. There, the pollinators are forced to adjust though a combination of food hoarding, diapause (hibernation) and dispersal (migration, especially the honey bee), when no such large resource blooms occur. In the temperate zone, in general, most pollinators are highly seasonal, and their adult activity matches that of preferred floral resources [106]. A brief active pollinator period in the drier regions often follows rain showers. In the moister regions, the emergence of adult insects that pollinate flowers coincides most often with a dry period. Thus, while agricultural ecosystems are challenging habitats for pollinators to persist within, they are not entirely different from the challenges of resource swings in natural environments, to which pollinators have always had to adjust. As discussed below, the threat of agricultural chemicals poses an entirely different kind of challenge, found only in human-created ecosystems.

1.2.2 Major shifts in pollination landscapes

The world is now experiencing a "sea change" in the pollination landscape, and must decide how to usher in the best alternatives to the original, natural communities. Two contemporary events, in addition to much publicized and debated pesticide use and habitat conversion, are having a strong global impact on pollinators and pollination. One is repeated introduction of Asiatic native honey bee pests (primarily *Varroa*, a large parasitic mite) westward, where they readily switch their host to the Western hive bee, *Apis mellifera*. In addition, these parasitoids attack that species in situ, within Asia, where the Western hive bee is often relatively defenceless (see Chapter 16). The other significant impact is Africanization of honey bees in the Neotropics. The ecology of this introduced bee species creates pervasive yet varied changes, and provides the first feral population of stinging honey bees in most of the Americas [22, 47–56, and the present publication]. Those bees are not amenable to crop pollination achieved by trucking (i.e. transporting over roadways) colonies in large numbers, because they are too dangerous. They can, however, be cultivated along with crops in a suitable setting, or their hives moved on a small scale.

Global agricultural intensification and the accompanying fungicide, herbicide, rodenticide, miticide, bacteriacide and insecticide (collectively called biocide or pesticide) treatments, plant growth regulators, fruit thinners, fertilizers and the ploughing of land, have had mostly predictable effects [46, 57–70]. When former pollinators are pushed out, other pollinators need to be brought in [69, 70]. In cases where those pollinators present problems or are not in abundant supply when needed, the cause and effect may be clear, but adequate solutions may be less obvious and seldom work out satisfactorily. Meanwhile, research and outreach continue to highlight important topical problems and needed additional research and management aimed at pollinators, as emphasized repeatedly in this publication. Pollinator wellbeing requires serious study and long-term commitment [16, 71–77, 101, 112], but more pollinators are needed *now* for agriculture.

In North America and Africa, in particular, pollinated fruit and vegetables are major crops both in net value to growers and in total tonnage [78, see also Chapter 7.1]. Generally, however, wind-pollinated wheat, rice, sugarcane, corn, barley, millets and other grains or tree crops, such as walnuts, remain the major world crops. Dense plantings ensure that pollen is transferred among individuals by wind. As long as the farmer stays ahead of the pests, parasites, soil depletion, temperature extremes and moisture deficits that such croplands experience, pollination seems guaranteed. And yet, until herbicide-resistant pollination units are invented [1–3, 66], or pesticide-resistant strains of honey bees are available (parasite and pathogen resistant varieties are known, see Chapter 16), no pollinator or pollination service should be taken for granted. While the attractive notion (for growers) persists that someday many crops will be pollination-free or parthenocarpic, or prompted to fruit uniformly by inexpensive commercial growth hormones or regulators, or that honey bees will resist whatever environmental or other obstacles are thrown at them, all such ideas ultimately *assume that no new economic factors, weather patterns, pathogens or natural enemies* will arise. Likewise, they assume that the flexibility and survival of pollinator populations, currently known simply as "health", will not decline from genetic or nutritional issues. Most biologists, growers and resource managers presumably know better. Furthermore, certain proven sustainable practices remain superior because of their economy, flexibility and durability. Pollinators are part of the sustainability equation, but which pollinators merit this status and which human inputs will maintain them is only now being established.

1.3 THE POLLINATION FACTOR IN CROPLANDS

1.3.1 Crop harvest constraints

What happens when numerous seeds and fruit are produced in a stand of animal-pollinated plants? Growers are generally content; however, the type of produce and its commercial sale largely determine final outcome and income. One result of a larger crop is that the fruit may be smaller and less attractive or, when regional production reaches a peak, the market price declines. Another is that, in the following year, the perennial fruit and nut trees will bear less fruit and seeds, an outcome known as alternate bearing (see glossary). A third consequence, although rare, is that the plant will die (this occurs in peaches and cacao, among others, when nearly every flower sets a fruit); however this situation is impossible in all but artificial pollination experiments. Nevertheless, the observation underscores the relationship between short-term and long-term production from a cultivated plant. The critical question of which level of pollination is most beneficial for both short and long-term productivity often remains poorly understood, at least for perennial plants under cultivation.

1.3.2 The nature of agricultural sustainability

A major consideration in attaining sustainability concerns slow fruit and seed production.[1] Fruit growers have been known to drive a stake into their trees (causing stress) to gain more profit from a season's blooming, and are actively seeking possible solutions to perceived underproduction. Can production rates or success be augmented and is this a sustainable solution to production shortfall? More study can provide evidence of pollinator decline and pollination shortcoming, versus a limitation related to plant physiology or farming practice. However, in agricultural plots – in contrast to natural mixed habitats of diverse species – the *relatively* sustainable (i.e. multiyear) value of any one season must be carefully assessed. Where there are fewer and fewer pollinators, questions arise as to which kinds are still available, which existed previously, how the performance and consistency of either group might be rated, and what it costs to replace them. Those are by no means new themes (see Chapters 2.2 and 3.2), but they have been the subject of considerable study since the first edition of this book was published (see Further reading).

[1] Short-term pollinator deficits are addressed in several chapters of this publication (e.g. Chapter 3.1).

At the population level, almost no studies have been made on the abundance (versus diversity or species richness) of pollinators over three or more successive years. This is an important subject because pollinators and their resources naturally vary between years. Such variation may be cyclical and predictable, difficult to predict or may indicate certain plants "take a break" due to their biology after producing a relatively large fruit or seed crop. Some of the great climatic drivers of bee and flower population cycles occur sporadically, and in cycles of a few to several years or even decades. Of these, there also are very few studies, for example, of the general flowering phenomenon in Southeast Asia. Nonetheless, yearly crop yield management involves attempts to optimize flowering and final fruit production in a relatively stable system, at least in the development of a particular management scheme (see Chapters 4 and 6 in particular). If the few population studies are sorted into "relatively stable and natural" habitats, versus those that are "human-induced and probably unstable", there is little to allow for a statistical comparison. Yields may be subject to fine-tuning and rational planning, or they may be beyond human control. In truth, a pollinator deficit may be remedied with more careful cultivation or management of pollinators. Obtaining more produce from a plant, in the case of a perennial, also means that its life expectancy is possibly shortened [32, 33]. Plants are replaced at an appreciable cost, thus having a bumper crop one year may result in an economic deficit the next, or later when those plants require removal and replacement, or more care.

1.3.3 A taxonomic impediment for crops

Local crop pollination requirements and pollinator performance vary considerably, as highlighted in this compendium. One reason involves the differing needs of botanical cultivars. A recognized cultivar has a certified name, enabling farmers to buy its seeds with confidence. But not every cultivar of a given crop has the same breeding system or pollination requirements. Among mango and apple with their thousands of cultivars, for example, some depend entirely on flies for pollination while bees are responsible elsewhere, and female flowers of certain cultivars produce fruit without pollination or pollen. Each of these is the same generic crop wherever it is grown, and has the same common and scientific name. However, in this case biology supersedes scientific nomenclature and necessitates a focus on the detailed knowledge and nomenclature of named cultivars. It is known that pollinator and pollination requirements differ among plants of the same genus or family. That this is sometimes true for individual populations within a given species should come as no surprise.

1.3.4 Crop pollination ecology

Pollen-free clonal crops are certainly used widely, along with many that self-pollinate within the flower (see Chapter 2.1 and Part V). Those apparently self-sufficient cultivars are developed by plant breeders, whenever possible, but so-called "hybrid vigour" remains a mainstay of many crops and their commercial seeds. Genetic inbreeding within any crop usually produces less and less adapted individuals. Because crops are biological entities, despite their modification and selective breeding, they need an adequate fund of genetic variation to adapt to challenges in their life and over generations. In addition, hybrid seeds cannot exist without cross-pollination, which is often impossible by wind or abiotic agent, or by agrochemical means. In the world's farms and plantations, aside from a few widely grown commercial species (banana, pistachio, seedless grape, date palm, oil palm, agave, olive, certain citrus, papaya), bees supply most of the necessary natural and managed pollination, and the means of producing abundant hybrid seeds via outcrossing – the movement of pollen between plants. In fact, many plants that do not necessarily need bees – those that self-pollinate – are nonetheless aided in their seed, fruit and fibre production when bee-pollinated or outcrossed. Field examples are given in the present book (e.g. Chapters 3 and 9.3) and additional outstanding examples include coffee and lettuce [54, 79]. Growers often appreciate this, and some have experimented and learn to make sure there are at least honey bees present. Even if inefficient by some standards, honey bees are almost never a waste of effort, unless better pollinators are found and propagated for their contribution to yield and vigour [70].

Pollination service providers (PSPs) design management schemes for large farms in a variety of settings that have evolved at a steady and sometimes rapid pace (e.g. see Chapter 4). Outstanding success in greenhouse or glasshouse production of tomatoes – among a few dozen crops – has made bumblebees star performers due to persistent study and management over the course of a century (Chapter 11). The alfalfa leafcutter bee, a lucerne pollinator, was imported to the Americas accidentally from Europe in the 1930s and later became the most intensely managed non-*Apis* bee in the world [41, 80]. *Osmia*, another megachilid bee known as a Mason bee – due to its plastering of nest cells with mud – is stored artificially in the resting or diapause stage during the cold season, then released en masse in extensive croplands during the spring bloom [19, 20, 41, 80, and Chapter 3.1]. Such benchmark events have been accompanied by the combined impetus of the Internet and World Wide Web, and the blossoming of detailed and original, comprehensive works on pollination, pollinators, the environment and food production over recent decades. Stingless bees, the foremost honey-making bees on the planet, are now receiving serious consideration as more than tropical curiosities [22, 81, 82 and Chapters 13–15]. In addition, international pollination initiatives and networks are now operational worldwide. New scientific journals are focusing on beekeeping in diverse settings, bees in general, applied pollination work, conservation, applied ecology, and the economics of crop and farming stability. The welfare of pollinators has finally been incorporated into the perception of human welfare.

However, it is not possible to be certain about the stability of pollinators. They are seldom under our control and often do not prefer or meet the needs of crops put before them. In at least two decades, one of the major pollinating species, *Apis mellifera*, has been markedly affected by a variety of stresses, yet they survive and maintain considerable diversity [83]. Recent information points to possible disease, primarily viral "spillover" from Western hive bees – and also bumblebees kept by growers largely for greenhouse operations – to a few other bee species [84, 85 and Chapter 11]. No pandemic involving bees in general has ever been found.

The view that agricultural pollinators are livestock is being replaced with a more realistic view towards maintaining habitat quality for pollinator populations (Chapter 3 and Part II). In the long run this seems desirable. Recognizing the general level of ignorance regarding pollinator conservation or restoration, most experts stress the importance of conserving nature as a whole, and trust that this foresight, fraught with ignorance though it is, will allow nature and its processes to conserve pollinators and correct some of the problems.

Much of the modern scramble to retain bees in the environment is tied to their honey production, as well as agricultural advantages. This rationale is founded on basic economics, and not necessarily the requirements of forestry, agronomy, conservation or sustainability [86–90]. Such "productive conservation" or the application of pollinators to multiple needs and desires occurs in habitats that are no longer natural or fully intact. The concept of a mature and diverse ecosystem versus a more disturbed environment is of importance for this general theme, but seems poorly understood. For instance, a large part of the tropics is thought to be pristine, although this is not the case [90, 91]. When a natural patch of wildlife or vegetation is present, it is often located in an area that has already been used and altered by humans, even in the recent past. There are secondary forest species that persist despite disturbances such as land clearing, burning, fragmentation and local climate change. Most species alive today have in fact experienced drastic changes during their evolutionary and ecological history, the largest driven by repeated periods of glaciation over the past few million years. Glacial conditions in these remote times created drier and cooler habitats, while forests retreated and open habitat increased. During such periods the landscape was populated with different groups of organisms. Today, the search for new pollinators to be managed requires both honey production and pollination by

bees adapted to change and manipulation (Part IV). An ice-age analogue is now being created by human activity [34, 92] and pollinators tolerant of such a disturbance will gradually predominate. The wild bees that persist under these conditions, most of them solitary but some of them social with perennial colonies, are likely to be those adapted to edge or open habitats, where their nesting resources and food plants are concentrated. Some social bees including the highly social honey-making species that form long-lived colonies will continue to hoard food or migrate between floral habitats, and thereby survive dearth periods. Agricultural lands, notwithstanding pollutants and pesticides, continually test and select for certain kinds of flower-visiting animals, largely by eliminating those that are ill adapted to abrupt or progressive habitat modification. The future has places for both colonial and other bees, and efforts to help them may occasionally prove decisive.

1.3.5 Prospects in pollination biology

Prominent worldwide habitat conditions include burgeoning human populations, not unlike human arrival in the Americas just 15 000 years ago. However, as the students of two decades in Central Amazonian experimental forest plots and elsewhere report, the present marks an unprecedented pace and scale of change [34, 89, 91]. Can biotic elements keep up and survive in the tropics and elsewhere? Will most native pollinators be stripped from the landscape by competition with invasive honey bees? Species that seem to be on the rise include Africanized honey bees, *Apis cerana, A. dorsata, A. florea* or *A. indica*, flies, small halictid bees, persistent populations of solitary and stingless honey bees, and long-range foragers such as *Xylocopa*, *Centris, Amegilla* and *Bombus*. Will flowering plants evolve self-pollination in response to pollinator loss or deficit? More importantly, is there any general restoration model available and can such restoration projects, which include pollinators, be cost-effective?

The tropics, particularly the Neotropics, are now repeating the temperate zone history of urbanization and retreat from smallholder agricultural plots and family farms. These abandoned lands may generate more native habitat – at a low successional stage – and eventually become biocide-free environments or be brought into large-scale development [92]. Conversely, traditional family farming is still the dominant practice in much of the tropics.[2] The world may "green up" a little as a result of land-use change, but an old-growth forest or natural prairie, even in relatively small areas, needs decades to centuries to form and perform its proper function. The concern is how to deal with the interim regarding the pollination of current crops.

Within secondary growth forest and other regenerating habitats, there is a good chance that more pollinator species may thrive, due to loss of their natural enemies after community simplification. Successional stages of natural communities seem to include a greater abundance of fewer pollinators, which thereby replace more species foraging and pollinating at lower rates, in the more advanced or complex communities. This scenario is now a factor in planning for pollination futures [89]. Certain generalists may replace specialists, to an extent, through their flexibility or evolutionary change.

Modelling pollination in natural habitats is a useful tool for realizing a sharper focus on crop and wildlife management, including pollinators and their resources [93, 94]. Concurrently, the practical experience of farmers who recognize the value and goal of pollination service provides abundant empirical data and insight presented in recent FAO publications (see the References and Chapter 7). Fortunately, such organizations motivate scientific extension work and promote cooperation across continents through a number of farsighted projects aligned with international pollinator initiatives.

Technicians and growers are currently more sensitized to the fact that pollination is just as important to their livelihoods as other kinds of farm management. Extension and outreach efforts confirm the concept and validity of pollination. As illustrated in the case studies presented in this publication,

[2] See www.fao.org/assets/infographics/FAO-Infographic-IYFF14-en.pdf

pollination is a broad theme with consistent and predictable features. Above all, if there is no provision for pollinators, then the management of farms or wildlands – in any real sense – is precarious and incomplete. Manuals or compilations such as this one can be used to inform and train those interested, who may, in turn, then present the facts to future farmers, pollination activists, professional pollination service providers, and officials or governments responsible for management and policy.

A noteworthy difference from the previous book, published in 1995, is that food, fuel and beverage crops are accorded greater emphasis, resulting in the removal of some content on timber, forage and medicinal cultivated plants. Because most plant names and a wealth of information are now easily accessible via the Internet, and the more credible sources follow international standards and norms, there seems little reason to repeat them here where a general online query will suffice. These are essential steps in an overall enterprise of providing information, cross-checking, and confirming trends and facts. Much is sure to change and will certainly improve. While the present scope of this compilation precludes discussion of wider themes, it reviews major advances in pollination biology, with some consideration of policy and management in the tropics, subtropics and the temperate zone. Commercial crops and certain techniques and tools are discussed in detail, along with general methods, experiments and theory. While this publication is not a husbandry manual for pollination service providers, or a set of guidelines for applications of chemical input to management questions, it does attempt to outline the practices and concerns of this vital human activity.

1.4 HOW TO USE THIS BOOK

The first part of the book reviews general issues, applied pollination, and makes suggestions or general recommendations on pollination for agriculture and conservation. More detailed information is then presented for particular crops, organized by geographic region and crop type. Pollination successes and challenges are identified and examined. Pollinator management is given its own chapter, followed by a chapter on research techniques, a further look at theory and the identification of pollen – the materia prima of cultivated plants – from a practical point of view. As formal or written agreements seem essential for crop pollination and professional pollination service providers, a first annex presents a basic pollination contract, and a second presents crop pollen species descriptions and documents the requisite voucher material and common and scientific names for pollen of cultivated plants depicted here for microscopic, taxonomic reference and pollinator study (Annex 2).

A number of relatively new and pertinent resources are available online. For example, Canada provides concise information for many animal pollinated crops at http://pollinator.ca/canpolin/ – a model that will hopefully motivate further work in this field.[3] The World Wide Web has truly permitted entry to an era of rapid enlightenment. It is of particular value for research, for example, with regard to establishing the scientific names of living things, and the publications and laboratory websites of authors. Caution should be exercised, however, when consulting "grey" literature and consulting websites offering services free of charge. Random searches for specific answers to crop cultivation or pollination needs are not encouraged. While these may be forthcoming or are sometimes available, the real tests and implementation take time, and are not assisted by quick or superficial answers. That biologists and other professionals will transform the current "Anthropocene" age into the needed "Biologicene", based on field tests and science, is a worthy goal, encapsulated in the following message: "When he [or she] enters a forest or meadow he [she] sees not merely what is there, but what is happening there" (Paul B. Sears, "Deserts on the March", 1935).

[3] Another promising example is a pollination report for passion fruit produced at the national level: www.iea.usp.br/pesquisa/grupos/servecossistemas/publicacoes/manejo-dos-polinizadores-e-polinizacao-de-flores-do-maracujazeiro (in Portuguese).

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Chapter 2

POLLINATION, POLLINATORS AND POLLINATION MODES: ECOLOGICAL AND ECONOMIC IMPORTANCE

2.1 POLLINATION: A GENERAL OVERVIEW

R.C. Sihag

Angiosperms are credited with the most beautiful gift of nature – they have flowers. The latter, though scientifically of reproductive relevance, have much greater significance in the ecosystem and for human society. As Richards remarks (1987, p. 66):

> An outstanding feature of Angiosperms is the amazing diversity in forms and colour that has been adopted by the inflorescence, sufficient to inspire great art, fuel a major industry and serve as a solace for suffering mankind. Yet the flower is merely a sex organ, and never has any function except to promote reproduction by seed, usually sexually. The beautiful, weird, sinister, astounding forms that flowers have acquired are strictly pragmatic, and have encouraged the ecological diversification, and dominance, of the flowering plants.

This quote underlines the ecological importance of flowers.[4] If the authentic paleontological and present ethological records can prove (and they do) that the evolution and perpetuation of this floral diversity is due to pollinators, this surely demonstrates their importance. Likewise, if it is also proved that pollinators help to increase the seed yield of many crops, this should underline their economic importance.

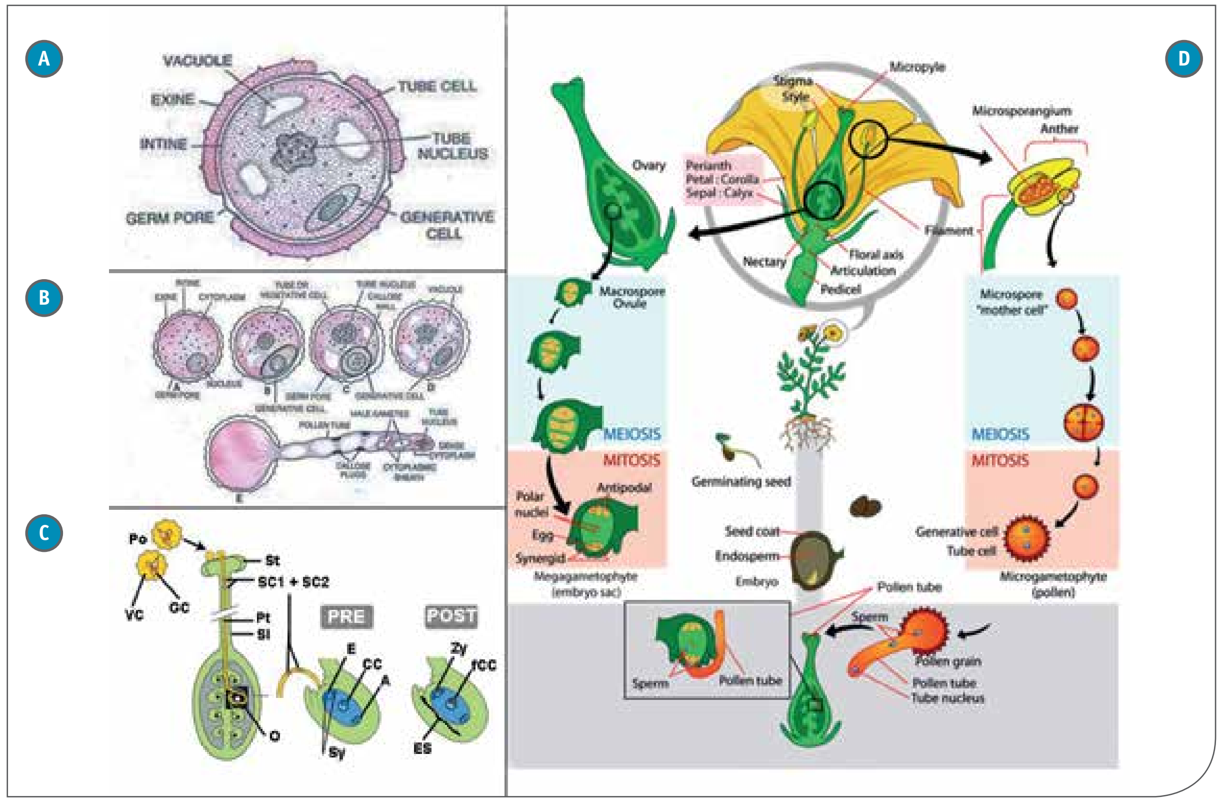
In angiosperms, pollination is an important event that acts as a prerequisite to sexual reproduction. Pollen performs the same function in plants that sperm does in animals. Successful pollen transfer is therefore very important. However, pollen is a non-motile spore: it must be transferred from anthers (the seat of their production) to the stigma (the seat of their germination) by a vector.

Different plant species exercise different pollination modes, and the benefits accrued depend upon the kind of pollen transferred. While self-pollination normally tends to increase homozygosity, pollen from other flowers, plants or genotypes should increase heterozygosity. Self-pollination generally sacrifices plant quality (particularly in outcrossers), while outcrossing helps to increase hybrid vigour, resulting in healthier and stronger plants (although this is not always the case). The type of pollination also determines the chances of gene recombination and exchange between individuals. In changing

[4] S.L. Buchmann. 2015. *The reason for flowers. Their history, culture, biology and how they change our lives.* Scribner, New York

Figure 2.1

SCHEMATIC REPRESENTATION OF POLLEN, FERTILIZATION AND REPRODUCTION IN THE ANGIOSPERM LIFE CYCLE



(A) eukaryotic pollen cell; (B) pollen grain and germination; (C) angiosperm fertilization (Po = pollen grain, VC = vegetative cell, GC = generative cell, St = stigma, Sl = style, Pt = pollen tube, SC1/SC2 = sperm cells, O = ovule, E = egg, ES = embryo sac, Sy = synergides, A = antipodal cells, CC = central cell, Zy = zygote, fCC = fertilized central cell, and PRE/POST = before and after fertilization; (D) complete angiosperm life cycle

environments, gene recombination (and therefore cross-pollination) should provide an opportunity to produce strains better suited to new conditions, and is therefore an ecological necessity. In changing pest scenarios with rapidly evolving resistance to pesticides, especially in the tropics, gene recombination and heterozygosity through cross-pollination are reliable means to increase crop yield. Literally, they provide certain crops with the opportunity to keep up with or escape their enemies.

This section reviews pollination modes and pollinators, along with their ecological and economic importance. The use of complex terminology for pollination ecology is avoided where possible, although such terms are used elsewhere in the present book (see also the Glossary). The discussion is limited to descriptions of the importance of pollinators and pollination modes in crops grown to produce seeds and fruit.

2.1.1 The flower

Before exploring the benefits of pollination it is important to first understand how flowers work and how they relate to pollination and pollination modes. These subjects are explored in more detail in Chapters 5–7.

A typical hermaphrodite (bisexual) flower has four parts:

- *Calyx*: The calyx (consisting of sepals) is normally green and provides protection to other floral parts during the bud stage.

Figure 2.2

FLIES POLLINATING A STRAWBERRY

Source: Drawing and design by F. Gattesco and D.W. Roubik

- *Corolla*: The corolla (consisting of flower petals) is the coloured part of the flower, which provides the primary attraction and stimulus for pollinators.
- *Androecium*: This is the male part of the flower. It consists of anthers that hold pollen and function as the seat of male spores.
- *Gynoecium*: This is the female part of the flower and carries the female gamete – the ovule – in the ovary. Pollen is received at the distal tip called the stigma, where the former germinates for fertilization.

2.1.2 Pollination modes and pollinators

Pollination is the process of transferring pollen from the anthers to the stigma. The agent provoking this transfer is called the pollinator. Normally, angiosperms exhibit two kinds of pollination mode:

- When pollination takes place within a flower it is called *self-pollination* or selfing (Figure 2.1). Self-pollination takes place if: (i) the flowers are bisexual and have stigmas and anthers at the same heights (the stamens and the style are of the same length); (ii) both sexes mature simultaneously (protandry or protogyny are absent); and (iii) contact of newly dehisced anthers (releasing fresh pollen) with the receptive stigma is imminent. Proximity of anthers to stigma under the above conditions should result into self-pollination. If selfing results in fertilization, this should indicate at least some occurrence of strict inbreeding.

- When pollen from one flower is carried to the stigma of another, the process is termed *cross-pollination* or outcrossing. Here an external agent is required to accomplish the pollen transfer.

There are two kinds of outcrossing: (i) when crossing occurs between flowers of the same plant (this process is genetically equal to selfing although a foreign pollen vector is required); and (ii) when crossing occurs between flowers of two different plants. Outcrossing is important in plants where either flowers or plants are unisexual; anthers and stigma of the same flower are at different heights (i.e. stamens and style are of different lengths); sexes mature at different times (presence of protandry or protogyny); there is no contact of dehisced anthers with stigma of the same flower during their functional phase; and, above all, plants are self-incompatible (i.e. pollen from a plant cannot be utilized by its own flowers).

Outcrossing is brought about by two kinds of agents: abiotic and biotic. Abiotic pollinating agents are inanimate physical forces. Thus, abiotic pollination is generally "random", or at least is not directed specifically between flowers. Different kinds of abiotic pollination have been recognized:

- Gravity pollination (*geophily*) is found in self-pollinated plants. Here, some pollen is expected to fall on the receptive stigmas of other flowers due to gravity and may pollinate the flowers. However, geophily is highly unreliable and is a rare and insignificant pollinating agent.
- Water pollination (*hydrophily*) is found only in some water plants where inflorescences float or are submerged. However, many freshwater plants produce aerial inflorescences.

Wind-pollination (*anemophily*) is found in many plant families including crop plants – especially grasses. Characteristics of plants using the wind-pollination method include: (i) a reduced leaf surface area; (ii) exposed flowers; (iii) reduced perianths; (iv) long stamens and sometimes explosive anther dehiscence; (v) smooth, dry pollen grains that may bear air sacs; (vi) lack of nectaries and nectar in flowers; and (vii) flowers having no colour or scent.

The relative disadvantages of the wind pollination method are: (i) low accuracy; (ii) pollen concentration declines with distance from the emitting source; (iii) pollen is intercepted by all surfaces in the line of dispersal; and (iv) pollen availability may diminish with height for flowers of wind-pollinated trees.

In the case of biotic pollinating agents, animals perform the task of pollination (zoophily). Biotic pollination is highly accurate, but has a higher cost: nectar in addition to pollen must be offered to pollinators by the plant, which often has large and colourful flowers. Pollen vectors such as bees are characterized by high floral constancy.

Characteristics of plants using the biotic pollination mode include: (i) the production of relatively small amounts of pollen; (ii) the existence of some kind of relationship between the pollen vector and pollination unit (see Sections 2.1.2-2.1.4); (iii) significant variation in size and external appearance of pollen, which is usually sticky; and (iv) flowers with attractive colours and odours that also produce nectar. Biotic pollination naturally falls into several distinct classes:

- pollination by insects (entomophily) such as beetles (cantharophily), flies (myophily), bees (melittophily), butterflies (psychophily) and moths (phalaenophily);
- pollination by invertebrates such as snails and slugs (malacophily);
- pollination by vertebrates such as birds (ornithophily) and bats (chiropterophily).

Entomophily has played a major role in the evolution of angiosperms. The other pollination modes are considered to be secondary derivatives of entomophily. Among these modes, bee pollination is the most effective primarily for two reasons: first, bees visit flowers to gather food and thus seek flowers at all times, and second, the flower constancy of bees (their persistence in seeking flowers of one species) is very high.

All these forms of pollination modes are present in nature, but are scattered in space and time. For example, ornithophily is best witnessed in Australian and Neotropical forests, with hummingbirds and large nectar-producing flowers the best example. Different pollinating animals are in fact associated with different sizes and shapes of flowers and are usually effective pollinators of these flowers, regardless of the species and their origin. These relationships vary from the most specialized to the least specialized types, as illustrated in much of the pollination literature and elsewhere in this book.

2.1.3 The ecological importance of pollinators and pollination modes

Pollination modes and pollinators strongly influence ecological relationships, genetic variation in the plant community, floral diversity, speciation, plant evolution and ecosystem conservation (see Section 2.2). Pollination modes (e.g. abiotic or biotic) have a very broad range of effects, some of which are discussed below.

The role of selfing: Because selfing provides no chance of gene recombination, successful inbreeding over generations leads to genetic impoverishment (i.e. loss of variability) and limited possibility for adaptation in new situations. Inbreeding may also become a starting point for the formation of a successful inbreeding species. The chances of the former remain larger than the latter. Obligate selfing is a rare event and is found in a small minority of plants. However, individual species may show high levels of selfing, which may exceed 99 percent of all fertilizations. Examples include wheat, barley, oats and beans. Selfing is normally found in opportunistic annual plants.

Repeated selfing renders the majority of species less vigorous, when measured in terms of height, weight or reproductive and survival capabilities. Inbreeding depression occurs in organisms that are normally "outcrossers" and much less in those that have evolved to be "selfers". Selfing is a secondary derivative of outcrossing. Environmental changes that resulted in the failure of self-incompatibility among outcrossers led to the evolution of selfing in plants.

The role of wind-pollination (anemophily): Like selfing, anemophily is considered a later derivative of a widespread, pre-existing condition – in this case, biotic pollination. Retention of floral colour and scent, a well-formed corolla, effective and simultaneous wind and insect pollination, and similar features in a wind-pollinated plant, indicate its recent development and a connecting link between biotic pollination and anemophily. Sudden environmental change resulting in failure of pollination is considered to be the fundamental cause of anemophily. However, unlike selfing, anemophily provides some chances of genetic recombination through outcrossing. Anemophily might be considered a highly wasteful pollination mode because the pollen falls randomly. However, a recent analysis shows that this is not the case, and it is precisely its greater economy that promotes the evolution of anemophily wherever possible. Nonetheless, large amounts of energy and material are used in the production of massive amounts of pollen and feathery styles on flowers. In compensation the perianths are highly reduced and rudimentary. Therefore, floral features are greatly restricted. As a consequence, anemophiles exhibit low floral diversity.

Effective anemophily requires dry weather and either low plant species richness or a large number of individuals in a relatively small area. The frequency of anemophily increases with both latitude and elevation. Wind pollination is generally uncommon in lowland tropical environments, especially in rain forests, and is dominant in temperate deciduous and boreal forests. These latter forests show low plant and floral diversity.

The role of animal pollinators (zoophily): The majority of extreme floral adaptations are directed towards animal visitors. Animals accurately transport a high proportion of the relatively small amount of pollen produced over large distances to a tiny stigmatic target. Accordingly, zoophily provides the best chances of gene recombination. Pollination by animals goes hand in hand with floral diversity and its perpetuation. In species-rich communities with a low level of ecological dominance by individual plant or animal species, biotic pollen dispersal predominates. This is why, for example, alpine grasslands and Mediterranean and tropical forests are populated by attractive flowers and show high floral diversity.

In more productive and stable communities, the proportion of specialist flowers is slightly higher, indicating the availability of more reproductive niches. Such communities will tend to have a greater number of species in each pollination syndrome. The diversity of reproductive niches available in a habitat is necessarily a major component in floristic richness.

Pollinating animals also play a highly important role in speciation (new species formation). Selfing and wind pollination are considered to have no role in this process and generalist animal pollinators play only minor roles. With regard to the interdependent relationships of pollination syndromes and pollinators, specialized associations, even if only temporary, are vital.

The mutual adaptation of flowers and pollinators and their interdependence are considered to be the result of long and intimate co-evolutionary relationships. Various paleontological records now clearly show that many flower forms evolved due to the selective pressure of pollinators over geological periods. Non-specialized, flower-visiting animals were followed by highly specialized visitors, ultimately culminating in the specialized blossom and pollinator classes found today (Chapter 5).

Pollinators and ecosystem conservation: As described above, there are several specialized pollinator and blossom classes. These classes and the existence of several pollination syndromes highlight the interdependence of pollinators and plants. In such systems, pollinators promote the perpetuation of plants by making their sexual reproduction a success. This is because successful reproduction is the major currency in the life of an organism, and failure to reproduce impairs individual fitness. Therefore, the conservation of pollinators should imply the conservation of plant species, and vice-versa. The conservation of plants and pollinators upholds species diversity in the ecosystem. A species-rich ecosystem with high species diversity is considered to be the most stable. This is the normal state of the tropics. Conservation of pollinators and their host plants should therefore imply the conservation of ecosystems.

2.1.4 The economic importance of pollinators

The economic importance of pollinators has now been fully recognized and realized in agriculture. The list of crop plants that either rely completely on pollinators or benefit from their pollinating visits is vast. By increasing their seed and fruit yield through cross-pollination and the fecundity and survival benefits that these bring, pollinators are also receiving benefits. The relationship is self-sustaining. Since human populations depend directly on agriculture for food, fibre and other articles, and population growth has heightened the need for these commodities, the importance of pollinators in modern times has increased several times over. Honey bees and some solitary bees can now be managed successfully and utilized for the pollination of crops. Their necessity is felt whenever it is established that they increase yield, especially in crops that are self-incompatible or otherwise in need of visitors to their flowers.

Table 2.1 presents a list of crops grown in the tropics – fruits, vegetables, oil seeds, forage, fibres and spices. The benefits accrued to these crop plants, and hence the importance of pollinators in agriculture, is indicated as the percentage increase in yield.

Table 2.1
COMMON WORLD CROPS, BREEDING SYSTEM AND BENEFITS FROM POLLINATORS

FRUIT CROPS		
Acerola	*Malpighia glabra*	1–3% (S), 6.7–55% (H), 6.7–74% (C)
Almond	*Prunus dulcis*	No bees, no fruit formation
Apricot	*Prunus armenica*	Benefited from BP
Blackberry	*Rubus*	Benefited from BP
Cashew	*Anacardium occidentale*	55.5% (S), need BP
Cherimoya	*Annona cherimola*	6% (OP), 44–60% (H)
Cherry	*Prunus*	20–35% (S), 49% (H)
Chestnut	*Castanea*	1.3% (S), 68%(OP), 34.9% C(H)
Kiwifruit	*Actinidia deliciosa*	CE
Citrus	*Citrus*	40–60% (H), 80-100% (OP)
Coconut	Cocos nucifera	CE
Date	*Phoenix dactylifera*	CE
Grape	*Vitis vinifera*	1.7 seeds/cage, 1.8 (BP), 1.8 (OP) (BE)
Guava	*Psidium guajava*	CE
Jamun	*Syzygium vulgare*	CE
Jujube	*Ziziphus jujuba*	CE
Litchi	*Nephelium chinensis*	0.01–0.03% (BE), 0.7–11.2% (BP)
Mango	*Mangifera indica*	C increases fruit set
Muskmelon	*Cucumis melo*	1.6 crates/A (BE), 242 crates/A (BP), CE
Pawpaw	*Asimina triloba*	CE
Papaya	*Carica papaya*	CE
Passion fruit	*Passiflora*	CE
Peach	*Prunus persica*	BP increases yield
Watermelon	*Citrullus lanatus*	CE

VEGETABLE CROPS		
Balsam pear	*Momordica charantis*	CE
Beet	*Beta vulgaris*	BP increases seed yield 14%
Cabbage	*Brassica oleracea*	CE
Carrot	*Daucus carota*	128 lb/A (IE), 435 lb/A (TI), 711 lb/A (OP), 840 lb/A (BP)
Chayote	*Sechium edule*	CE
Cucumber	*Cucumis sativus*	CE
Egg plant	*Solanum melongena*	C increases production
Lettuce	*Lactuca sativa*	C increases seed yield
Onion	*Allium cepa*	9.8% (BE), 93.4% (BP)
Pumpkin	*Cucurbita*	6.8% (BE), 61.2% (BP), CE
Radish	*Raphanus sativus*	CE
Tomato	*Solanum esculentum*	Buzz pollination essential
Turnip	*Brassica rapa*	CE
Loofah	*Luffa cylindrica*	CE
White Gourd	*Benincasa hispida*	CE
Bottlegourd	*Lagenaria siceraria*	CE

OILSEED CROPS		
Flax	*Linum usitatissimum*	BP increases seed yield 22.5–38.5%
Niger	*Guizotia abbyssinica*	BP increases yield
Rapeseed, Canola and Mustard	*Brassica*	64.7 seed set (BE), 95.3% (BP)
Oil palm	*Elaeis guineensis*	CE
Olive	*Olea europaea*	C increases fruit set
Peanut	*Arachis hypogaea*	BP increases seed yield 6–11%
Safflower	*Carthamus tinctorius*	32–47% (BE), 100% (BP)
Sesame	*Sesamum indicum*	BP increases seed yield
Sunflower	*Helianthus annuus*	311 lb/A (BE), 931 lb/A (OP)

"PULSE" CROPS		
Broad bean	*Vicia faba*	BP increases seed yield
Cicer milkvetch	*Astragalus cicer*	2.3% (S), 12.4%, (H), 23.1% (C)
Pigeon pea	*Cajanus cajan*	BP increases seed yield 10%

SPICES, CONDIMENTS AND BEVERAGES		
Black pepper	*Piper nigrum*	BP essential
Cacao	*Theobroma cacao*	CE
Carambola	*Averrhoa carambola*	C obligatory
Cardamom	*Elettaria cardamomum*	11% (BE), 67% (BP)
Chicory	*Cichorium intybus*	0% (S), 61% (OP)
Clove	*Syzygium aromaticum*	CE
Coffee	*Coffea*	61.7% [*within branch*] (BE),
Coriander	*Coriandrum sativum*	C obligatory
Fennel	*Foeniculum vulgare*	BP increases seed yield 7 times
Kolanut	*Cola acuminata*	CE
Methi	*Trigonella corniculata*	0.09 kg/plot (BE), 6.2 kg/plot (BP)
Pimento	*Pimenta dioica*	19 berries (BE), > 1 000 berries (BP)
Tea	*Camellia sinensis*	CE
Vanilla	*Vanilla*	*Pompona*
FORAGE CROPS		
Alfalfa	*Medicago sativa*	0.3 kg/A (BE), 20.3 kg/A (BP)
Berseem	*Trifolium alexandrinum*	0.27-0.64 seed/head (BP), 19.58–70.54 seed/head (BE)
Lespedeza	*Lespedeza*	C level 61.480.9%
Vetch	*Vicia*	BP increases seed production
FIBRE CROPS		
Cotton	*Gossypium*	2.3–3.4% (BE), 0–53% (BP)
Kenaf	*Hibiscus cannabinus*	C helpful in yield
Sisal	*Agave*	C necessary
Sunn hemp	*Crotalaria juncea*	2.6% (OP) 65% (BP)

Notes: BE = bees excluded; BP = bee pollination; C = cross-pollination; CE = cross-pollination essential; H = hand pollination; IE = all insects excluded; TI = tiny insects permitted; OP = open pollination; and S = self-pollination.

A companion table listing known pollinators for global crops grown for human consumption be found in A.M. Klein *et al*. 2007. Importance of pollinators in changing landscapes for world crops, *Proceedings of the Royal Society B*, 274(1608). doi: 10.1098/rspb.2006.3721.

2.1.5 Conclusion

Pollination involves the transfer of pollen from anthers to the stigma. Self-pollination is of little ecological or economic significance to many plant species, and when followed by self-fertilization it can cause inbreeding depression. This is a result of homozygosity, which provides no chance for gene recombination. Therefore, variability in the plant species is impoverished. The homozygous individuals have stunted growth and low yield in many of the wild and cultivated plant species. Cross-pollination, on the other hand, leads to heterozygosity and provides chances of gene recombination. This may increase variability in a plant population and provides opportunities for the evolution of new varieties, strains and even species. Heterozygosity in cultivated crops is expected to increase hybrid vigour, resulting in more healthy plants with higher seed yield. Aside from monospecific croplands of wind-pollinated species, cross-pollination by wind, water or gravity is of often of little importance due primarily to its random nature. However, pollination by insects can have great significance in the evolution of flowering plants and many floral, vegetative and genetic traits. All other biotic and abiotic pollination modes are secondary derivatives of zoophily – the animal transport of pollen grains. The presence of a wide variety of pollinators and pollination syndromes has contributed to present-day floral diversity in the tropics and subtropics. Among the animal pollinators, bee pollination (melittophily) is of great significance in agriculture, increasing seed production in many entomophilous and anemophilous crops. The conservation of pollinators and pollination services for plants is essential to preserve floral diversity in the ecosystem. Managed pollination should be accorded a high priority, in order to increase the crop yields of seed and fruit.

2.2 CONSERVING POLLINATORS FOR AGRICULTURE, FORESTRY AND NATURE

P.G. Kevan

Pollination is a pivotal, keystone process in almost all biotically productive terrestrial ecosystems. These include the most remote wildernesses of the Arctic to the most highly managed farming operations, such as hydroponics in greenhouses. Pollination is at the centre of a multi-spoked wheel that has human, livestock and wildlife consumers at its circumference. Other relationships of importance to maintaining the health of ecosystems include fungal and microbial interactions with roots affecting plant growth and nutrition, biophysical interactions in the soil, biophysical interactions between life and the atmosphere, plant propagule (seeds, etc.) dispersal by animals, the role of forests and multifarious pollution problems.

In recent years, conservation concerns over pollination have received increasing attention. This concern has been triggered in part by recognition of the value of pollination to agriculture. Figures calculated for Australia, Canada and the United States, mostly in regard to honey bees, show that the value of pollination far exceeds that of hive products such as honey. Recognition of this issue in Europe prompted several pioneering studies. However, the economics of animal pollination in agriculture within any one country are complex and difficult to assess. Regardless, agriculture and other equally vital economic ventures are dependent on a variety of pollinators, including the most generally important, honey bees. The total value of animal pollination to world agriculture has not been estimated, but the value to the global health of ecosystems is beyond measure.

The demise of pollinators is the consequence of four major human activities: (i) pesticide use, (ii) habitat destruction, (iii) diseases, and (iv) competition from introduced flower visitors. The majority of related information is drawn from temperate regions, but the same problems can be assumed to be equally or more severe in the tropics (see Chapter 3). The aim of this chapter is to review briefly the information available on each factor and place into perspective the potential consequences of ignoring the impacts to date.

Another issue in pollinator conservation is increasing recognition by scientists and others that "non-honey bees" are important as crop pollinators. However, the lack of general acceptance of the greater efficiency of other pollinators for certain crops, and the failure to recognize that some crops are poorly, if at all, pollinated by honey bees have hampered appropriate developments towards pollinator conservation for agricultural productivity.

2.2.1 Pesticides

The dangers associated with pesticides, especially insecticides, and pollinators are well documented and understood, especially with regard to European honey bees. Roubik et al. (2014) and other recent works have summarized the current available information (see Preface and Chapters 1 and 4). Johansen and Mayer (1990) wrote a highly informative book on the subject with an emphasis on the United States. Information has been published on most pesticides used worldwide regarding their toxicity to European honey bees, and sometimes other bees. In fact, many pesticide containers bear labels highlighting the associated dangers to pollinators.

Recent trends in many parts of the world towards reducing the use of pesticides in agriculture and forestry have lessened the overall incidence of pollinator poisonings. However, the problems are still severe in developing countries. It must also be remembered that pesticides constitute an integral part of integrated pest management practices (IPM) for crop protection in modern agriculture and forestry. The dangers must still be kept in mind and a constant vigilance maintained.

Many pesticide problems seem to stem from accidents, carelessness in application and deliberate misuse despite label warnings and recommendations (see Chapter 4). As pesticide application becomes increasingly regulated and users are required to take safety courses before certification, the problem should diminish. However, in many countries regulations are wanting, lax or ignored. General problems are exacerbated by the free availability in developing countries of pesticides that are outmoded or illegal elsewhere. In agricultural settings, pesticide use can be easily monitored and controlled by: (i) responsible agents of the agrochemical industries who manufacture and sell pesticides, (ii) diligent applicators who pay heed to labels, recommended application rates, and warnings about pollinator poisonings and human health, (iii) government extension agents, and (iv) other persons interested in agriculture and pollination services including the general public.

Issues in non-agricultural settings and agroforestry are more complex because of the importance of a wider diversity of pollinators, both wild and managed. One example of a well-understood situation occurred in eastern Canada where fenitrothion, sprayed against spruce budworms that were defoliating forest trees, had devastating side effects on wild, native pollinators of commercial blueberry fields. The effects were also immediately felt on the pollinators servicing the sexual reproductive needs of native vegetation. A number of different plant species of the forest and forest margins suffered reduced fruit and seed set, which in turn would be expected to impact wildlife by depriving them of natural quantities of food. The effects on pollinators resulting from extensive applications of pesticides against other major pests, such as forest defoliators, locusts and grassland herbivores, have received only minimal investigation.

2.2.2 Habitat destruction

Habitat destruction affects pollinator populations, as with populations of any organism, in three ways: (i) destruction of food sources; (ii) destruction of nesting or oviposition sites; and (iii) destruction of resting or mating sites.

The destruction of food sources is best illustrated by examples of the removal of vegetation, which provides pollinator with food when crops are not in bloom in agricultural areas. The vegetation removed is frequently regarded as unwanted, as weeds or as competition for the crop plants, yet is invaluable to pollinators and other beneficial insects. Kevan (1986) made special reference to these problems with respect to biological control, IPM and pollination in the tropics. The negative effects on pollinator populations in agricultural areas of removing "unwanted" vegetation have been documented, in particular, for Europe and North America (see Chapter 4).

The destruction of nesting and oviposition sites has been documented in central Canada for the demise of populations of leafcutter bees (Megachilidae), which were left without nesting sites in stumps and logs as fields of alfalfa expanded; in Europe for bumblebees as the amount of relatively undisturbed land in hedgerows and greenbelts declined; and in the tropics for the inadequate pollination of cacao by midges in plantations from which oviposition substrates or rotting vegetation had been too fastidiously removed.

Examples of the destruction of special mating or resting sites pertain to pollinators with rather special requirements and to those associated with rare plants. Although this problem is suspected to be real, documentation is not available and evidence would be difficult to obtain without specialized research.

The general issue of habitat destruction for pollinators has evoked concern on a broad scale. Janzen's 1974 article "The deflowering of Central America" exemplifies the problem. He points to a vicious cycle of reduced vegetation for pollinator resources, reduced pollination of vegetation, the demise of plant reproductive success, and reductions in seed and fruit set. These result in the failure of re-vegetation with the expected level of biodiversity. This cycle applies to all parts of the world where pollination by animals forms an integral part of the ecosystem. Nevertheless, recent publications on the conservation of insects and other animals give short shrift to pollinators and all but ignore the consequences of their demise. In the context of the present publication, this attitude is very difficult to understand.

2.2.3 Pollinator diseases

Mite diseases of honey bees have evoked major concern, as trachael mites and *Varroa* have spread at alarming rates. The impact of such diseases on honey bee colonies is well documented, but little information is available on the effects on pollination. It has been suggested that many amateur and small-scale beekeepers will abandon their activities because of the additional complexities of bee management associated with monitoring for mite diseases and controlling them once detected. Furthermore, chemical control of mites may not be acceptable to producers of pure honey.

The necessary changes to beekeeping, which is mostly in the hands of small-scale operators widely dispersed over the agricultural landscape, seem to be resulting in fewer beekeepers and lower distribution of free pollination from bees in their hives. There are already complaints from parts of the United States about inadequate numbers of honey bees for pollination of pome, stone and small, soft fruit crops. Pollination services may come to be provided by commercial beekeepers at an additional cost to the grower and consumer (see Chapter 10).

This scenario would apply to beekeeping operations in other parts of the world where non-native diseases have invaded the native stocks of honey bees. In India, the possible transfer of diseases from European honey bees to the Asiatic hive bee (*Apis cerana*) was suggested as the cause of the demise of the latter to the detriment of honey production.

Great care is needed for the introduction of honey bees from one part of the world to another. The spread of honey bee diseases from place to place and between species is mostly attributable to human activity (e.g. *Varroa* in western Asia, Europe, and North and South America, and trachael mites in North America, etc.). Quarantine protocols are well established in some countries, but are unfortunately lacking in others. Bailey and Ball (1991) provided a key work on bee pathology worldwide, and the subject is advancing with new information and protocols (see Chapter 16).

Leafcutter bees also suffer from diseases. The most important are the many chalk brood fungal varieties, such as that affecting the alfalfa leafcutter bee, *Megachile rotundata*. This disease has a major impact on the culture of the bees, and diagnosis facilities have been established in certain places (e.g. western Canada) where these bees are highly important to pollination in agriculture. Research on diseases affecting other managed pollinators, such as orchard bees (*Osmia*) and bumblebees (*Bombus*), is assuming importance as these pollinators take on a role in agricultural crop production.

The importance of disease in the regulation of populations of native pollinators is unknown. The same can be said regarding the roles of other natural enemies, such as the many parasitic wasps that attack natural populations of all kinds of bees, but are much more concentrated and capable of creating adverse effects in commercially established populations of solitary bees. However, a wide variety of pathogens, parasites, parsitoids and predators attack native bees and other pollinators in nature.

2.2.4 Pollinator competition

The most studied of the competitive interactions between pollinators as they relate to pollination is that of the effect of the Africanized (naturalized hybrid African x European) honey bees on native pollinators and European honey bees in South and Central America. The apparent reductions in abundance of native bees in the Neotropics after the invasion of Africanized bees was first pointed out by Roubik (1978), who subsequently placed the phenomenon in a broader context (2009). However, the issue of the competitive interactions of African bees with native pollinators in South and Central America seems complex.

In Australia, there has been debate recently over the effects of the introduced European honey bee on the native flora and fauna of pollinators. Some conclude that there is justification for the concern that European honey bees have caused reduction in the pollination of some native plants, especially those pollinated by birds, by removing the sought-after nectar and causing changes in their populations and foraging habits. The issue of effects on native pollinating insects is less clear from the botanical side, but the same trends are evident with respect to the native bees.

2.2.5 Diversification of pollinators

Although it must be conceded that honey bees are the most valuable pollinators in agriculture, they are not the sum total of crop pollination. Numerous examples illustrate this point including the greater efficiencies of orchard bees for pome fruit pollination, alfalfa leafcutter bees for alfalfa pollination, bumblebees for pollination of tomatoes and other solanaceous crops in greenhouses, blueberry bees for blueberries and carpenter bees for passion fruit. The lack of pollination brought about by honey bees for oil palm, various Annonaceous fruit crops, red clover and other crops with flowers too deep for honey bees to access, as well as bat-pollinated durian, provide further evidence of the need to consider alternative pollinators for many crops. This issue is particularly important for the tropics because the natural pollination mechanisms of a large proportion of plants (crops and others) are not understood.

2.2.6 Conclusion

The conservation of honey bees, other domesticated bees, wild bees and other pollinators raises an important issue in the global context of agricultural and natural sustainable productivity. It is extremely important that apiculturists expand their horizons to embrace the culture of alternative species and the importance of other pollinators in agriculture. The significance of pollinators and the adverse affects that habitat destruction, poisoning, disease and competitive interactions with alien species have on pollination processes, need to be fully acknowledged by biologists, ecologists, agriculturalists and the general public, within the new spirit of global, environmental sustainability and conservation of biodiversity.

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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

L.A. Garibaldi, S.A. Cunningham, M.A. Aizen, L. Packer and L.D. Harder

3.1.1 Introduction

Land use has changed at an unprecedented rate over 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

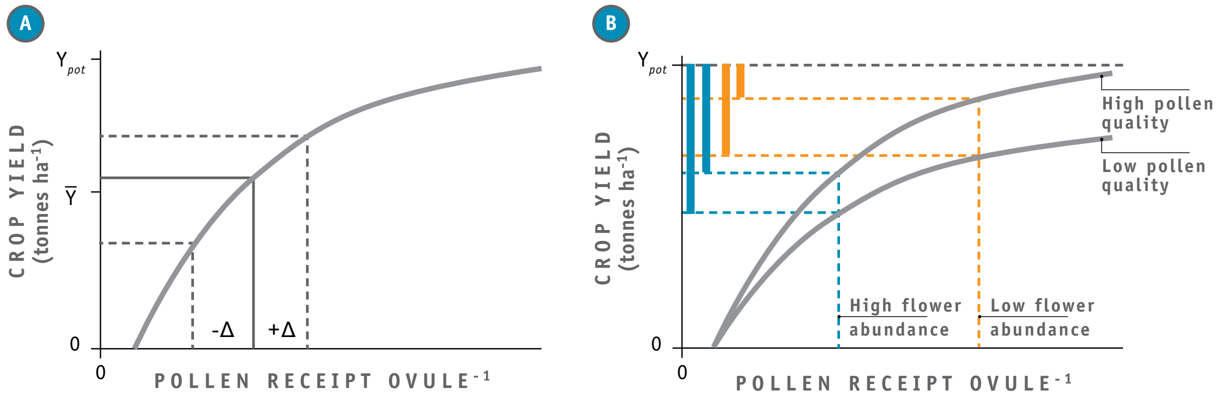
Crop yield (tonnes h^{a-1}) [ca. 2.25 tonnes = 1 ton] increases asymptotically with the delivery of resources in general, and for most fruit or seed crops, with the pollen delivered to the stigmas [4–10]. The relation can be summarized generally as

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

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, 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 (+Δ in Figure 3.1a) is smaller than the yield decrease, with Δ units of pollen receipt below the average, during a bad year (–Δ 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 (Y bar), where *Ypot* 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

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-pollination and reduced inbreeding depression [8, 12], can increase both potential yield *Ypot* 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 (% dependence) compared to potential yield (Figure 3.1). Previously, the contribution of animal pollination to global agriculture was 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 found 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.

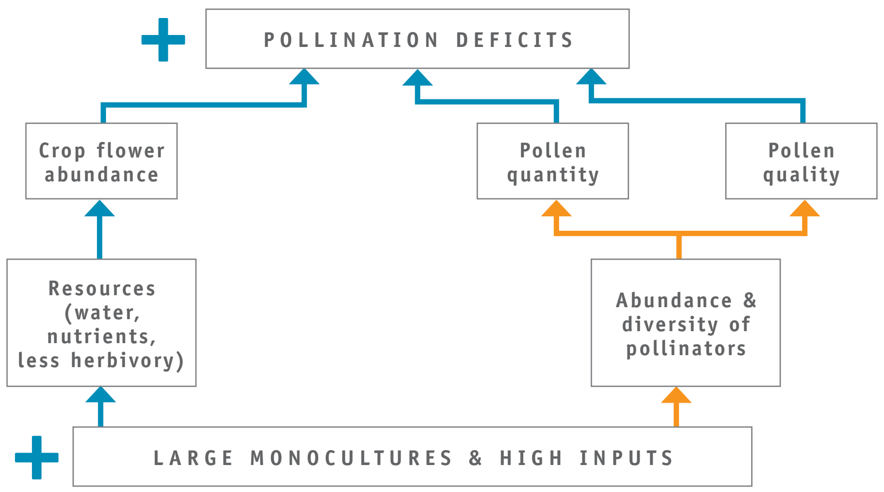
3.1.4 Are pollination deficits common?

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

CONSEQUENCES OF STANDARD AGRICULTURAL PRACTICES FOR POLLINATION DEFICITS



Agricultural landscapes have been increasingly (blue +) transformed into homogeneous environments with large crop monocultures and high inputs, both of which aggravate (blue +) pollination deficits. Blue lines indicate ameliorating effects on the feature indicated by the arrow, whereas orange lines indicate aggravating effects.

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]. The 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 proportion 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 as 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 varies positively with flower visitation by honey bees in only 14 percent of the sampled crops. In contrast, flower visitation by wild insects increases 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 over 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 further 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 and 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.

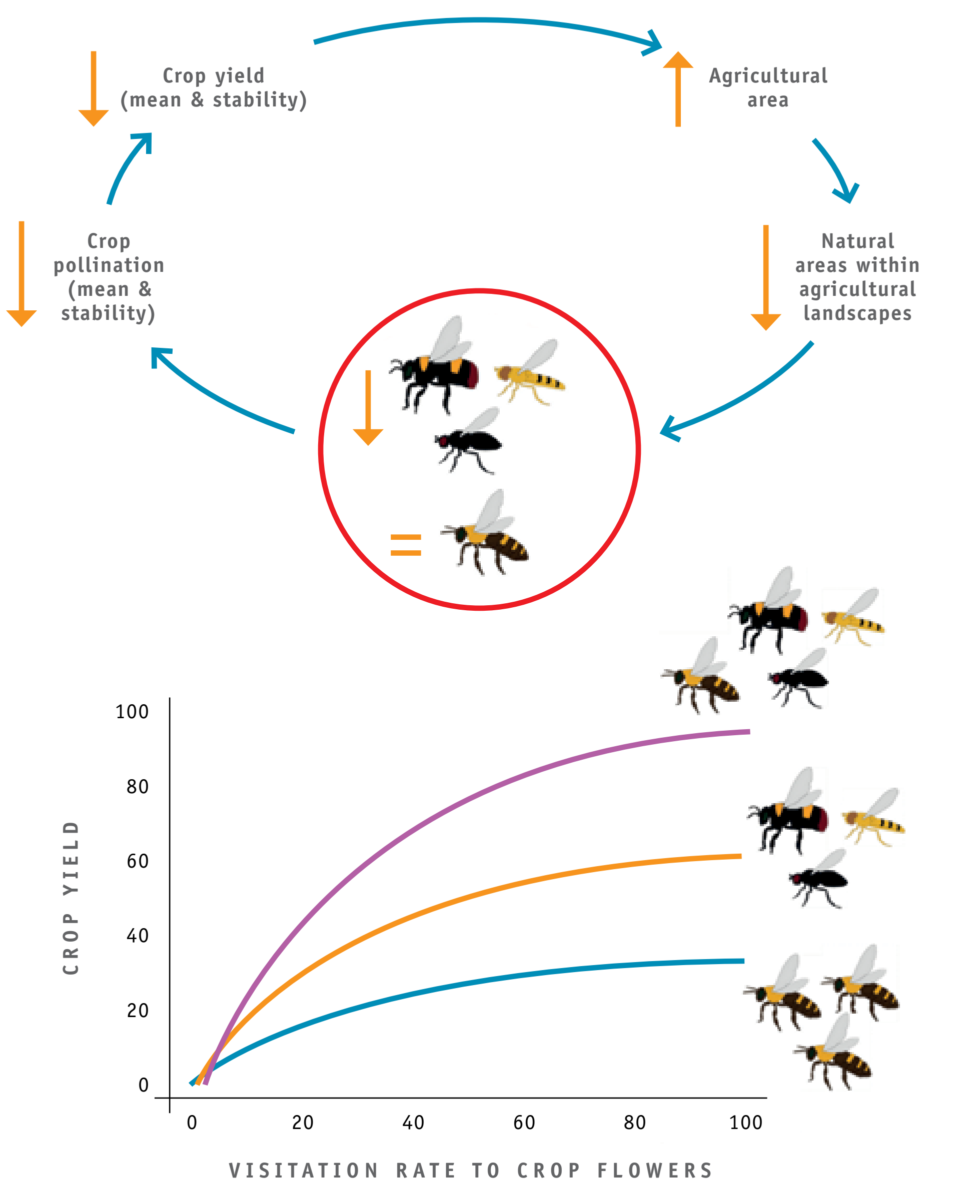
3.1.7 Sound practices that reduce pollination deficits

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



(A) and its expected consequences for crop yield (B). (A) 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). (B) 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.

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 an 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.

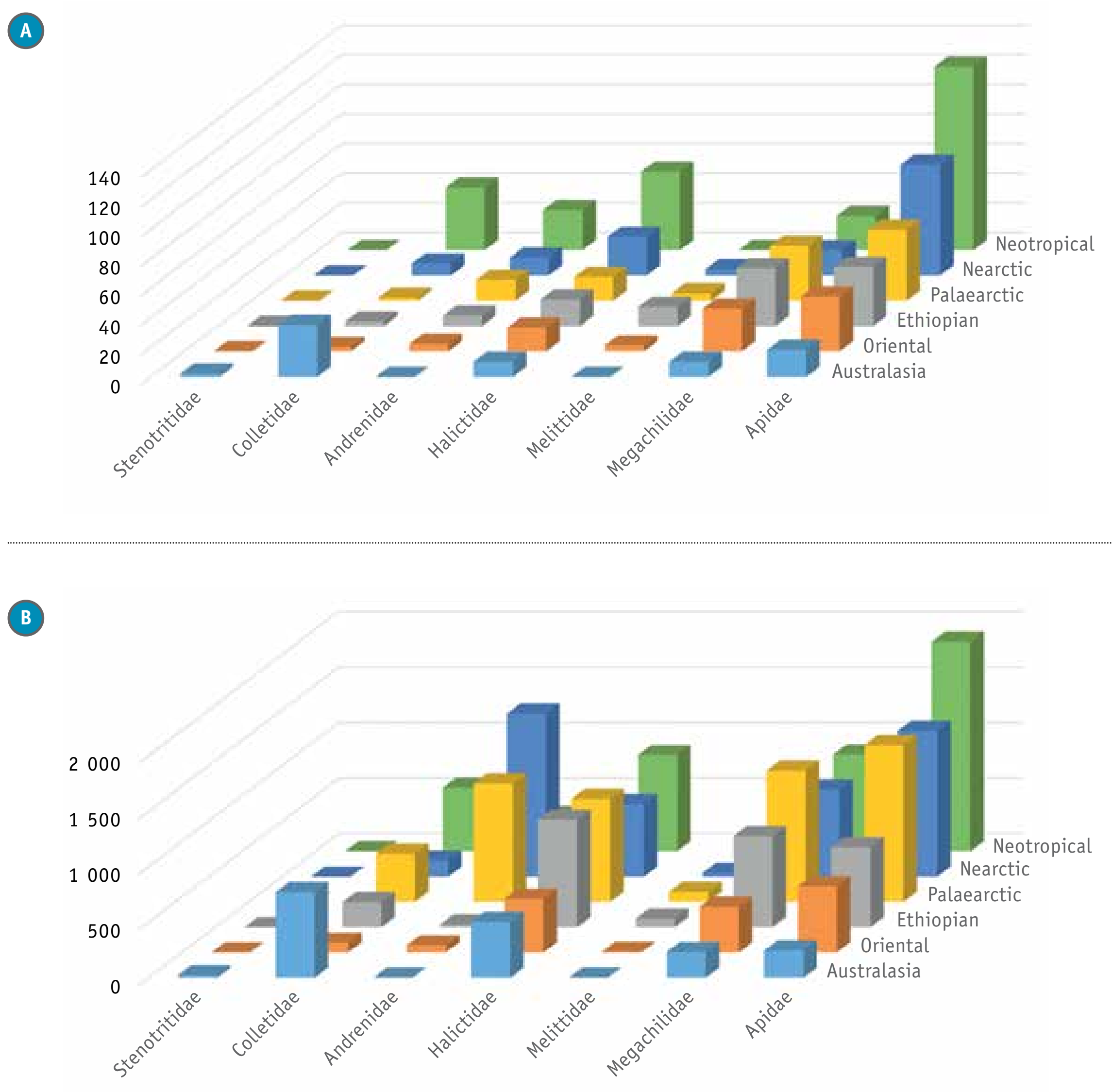
Bees are not equally spread geographically, but instead are most diverse in arid and semi-arid habitats, perhaps as a consequence of their purported evolutionary origin in drier parts of Gondwana [74, 75]. The preponderance of different bee taxonomic groups also varies with habitat and continent. Some 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

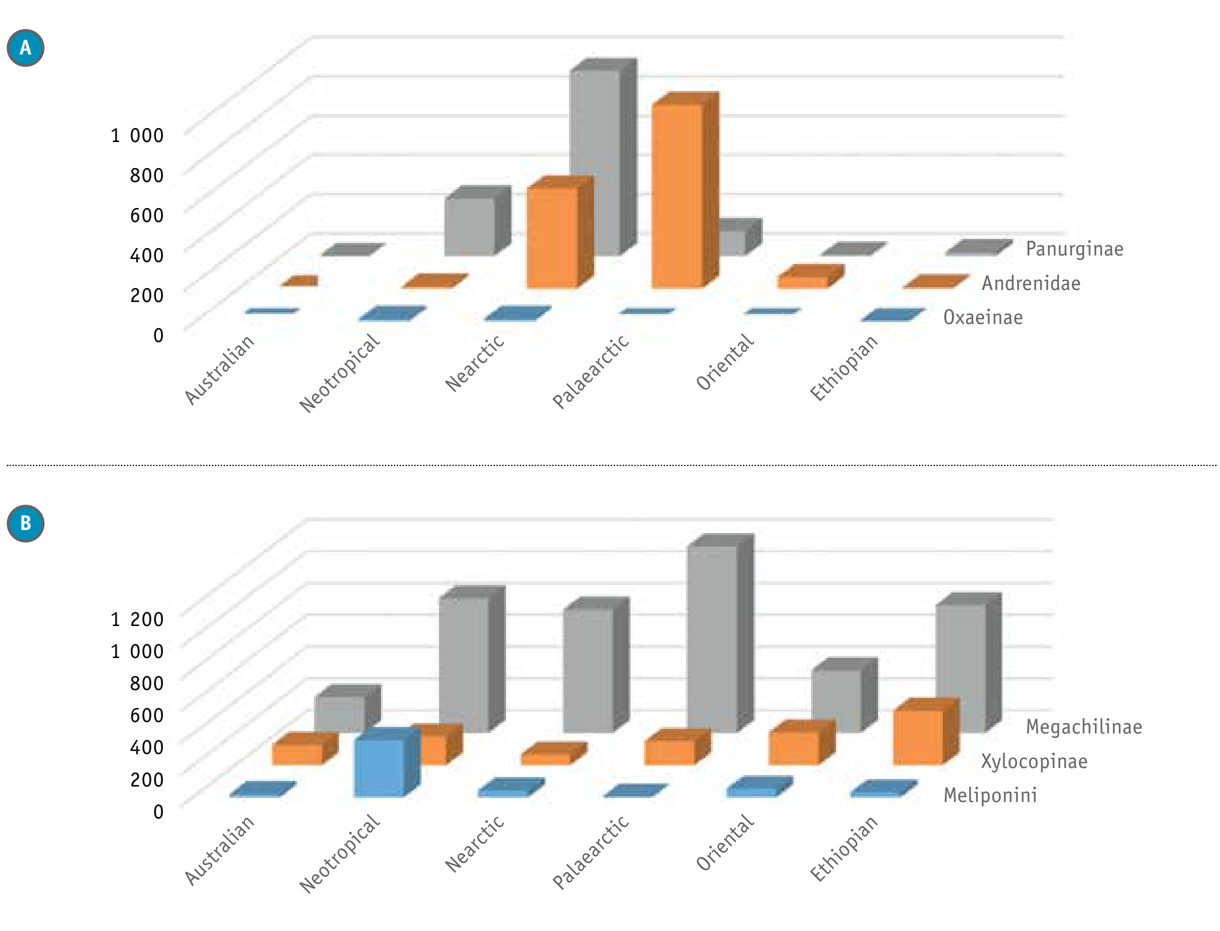
NUMBERS OF GENERA (A) AND SPECIES (B) OF BEES OF DIFFERENT FAMILIES FROM DIFFERENT ZOOGEOGRAPHICAL REALMS



These data were obtained from [128] 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

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



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 a handful 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 impact [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 though 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* over 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 beehives 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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3.2 ALTERNATIVES TO ARTIFICIAL POLLINATOR POPULATIONS

R. Krell

3.2.1 Introduction[5]

Agricultural practices have undergone drastic changes over the last 100 years. The push towards mechanization in recent decades has seen ever-larger areas devoted to the cultivation of single crops with the aim of maximizing profit, alongside increased use of chemical fertilizers, herbicides and pesticides. Higher and higher production goals ignored the long-term effects on pollinators, with the pollination requirements of many crops taken into consideration only once changes in cultivation practices demonstrated new production limits. In the meantime, numerous natural pollinator populations were diminished or lost. Until very recently, honey bees were still considered dangerous and damaging to fruit orchards, and while the tremendous progress made in understanding the beneficial interactions of insects and plants has given rise to many potential applications, these have yet to be implemented.

Although exploitative agricultural practices similar to those described above have long been promoted in both tropical and subtropical developing countries, many regions are still undergoing the process of transformation. Other areas have come under pressures such as population growth or desertification, which also result in drastic changes to habitats.

This section presents ideas related to pollinator needs and for improving degraded habitats and those still to be transformed. Such a discussion cannot neglect social, technical and other environmental concerns. At the same time it is beyond the scope of this book to consider all possible aspects. Therefore, emphasis is placed on ideas and principles that should be considered by planners, technicians and others involved in making sustainable agriculture and multiple, sustained, non-destructive use of forests a reality. The concepts necessarily include subjects such as biological pest control and the promotion of less capital-intensive farming practices (e.g. intercropping, rotation and cover-crop plantings). These ideas require a new but not necessarily more difficult approach to improving agricultural efficiency. They also depend on a better understanding of the biological, physical and social interactions underlying all agricultural production.

Suggesting practices such as the foregoing examples to village communities and countries which have much more pressing problems may seem idealistic, particularly when such practices are not employed in other more stable industrialized countries not facing continuous emergency situations. However, traditional agriculture often resembles closely modern approaches that minimize dependence on agricultural chemicals and destructive land-use practices, albeit at a reduced scale. The goal is to highlight alternatives to increased agricultural production at any cost. Fortunately, methods exist that can be employed without the need for large-scale, long-term scientific studies, huge investments or loss of productivity, and rely instead on common sense.

It seems unreasonable to place an additional burden on the shoulders of the weakest link in the chain, the primary producer. Instead, a communal or concerted effort could be promoted by providing other benefits, such as better prices, greater access to markets and privileged access to the omnipresent subsidies. This also requires a change in the attitude of local politicians, bankers and merchants, as well as those countries and organizations that function as the primary source of finance, buyers, teaching and technology transfers. In this way, improvement in pollinator availability becomes a "global" problem in the purest sense. As with all global problems, the solution necessarily begins with the smallest details and changes in the attitudes of each and every one of us.

The following sections present a range of ideas which can be tested, improved upon and transferred to relevant stakeholders for active implementation, as well as to others for inclusion in a more global, complete plan of development.

[5] For ease of reading, principal and general references are included at the end of the section.

3.2.2 Mechanical pollination and chemical pollination

Pollination by hand may be feasible under a certain limited circumstances and for small-scale production such as home gardens. On a larger production scale it is not profitable. Traditional date palm pollination or sometimes passion fruit and special hybrid seed production, as well as orchid propagation, including *Vanilla*, is done by hand. Increasing use is made of insect pollinators, even for greenhouse production. Mechanical pollination of fruit trees (apples and peaches) with large blowers has been attempted, but never incorporated into commercial enterprises. Thus, hand or mechanical pollination will remain restricted in application and cannot replace pollinators in agriculture on a large scale.

3.2.3 Habitat management for wild pollinators

The natural pollinators of wild plants and agricultural crops include a wide variety of organisms, not just bees and certainly not just honey bees. But aside from the pollinators whose populations can be manipulated or managed in large numbers, there exist a wide array of bee and non-bee pollinators capable of pollinating agricultural crops. Not the least important among theses are a variety of flies. Over a hundred different insect species can be observed on the flowers of certain fruit trees, although not all contribute significantly to their pollination. Maintaining such a diverse insect fauna increases the chance of sufficient pollination without the need for additional pollinator populations.

In order to ensure a sufficient number of wild pollinators, their habitats must be preserved and maintained. This means that the adult and larval stages of the pollinators need to locate food (often highly specific flowers, leaves, other insects, etc.). For many pollinators, nesting sites are also required. Some insects require certain soil conditions to survive during one of their life stages. For migratory species such as certain varieties of hummingbird or Asian and African honey bees, the habitats needed at each extreme of the migratory range must be preserved to ensure that sufficient numbers return during the next migratory season. In short, it is crucial to know the life history and requirements of species to ensure their conservation and multiplication. This is a demanding task even for the much less diverse fauna of the better-studied temperate climates. Fortunately, as long as the original plant cover of wildlands is preserved, much of the diversity will maintain itself.

What is the best way to determine the correct size of habitat for these purposes? Opinions are divided on this matter. Because few definitive scientific studies will be completed in the available time, the only safe approach is to conserve the largest possible area. Minimum requirements for some of the better-studied larger animals and ecosystems are known. For example, insect populations probably do not need the same size of habitat as certain mammalian predators. However, since many insects depend on other plant and animal species, they likely need somewhat extensive habitats for their survival. As more information is amassed about beneficial insects and other animals, the capacity of experts to prepare smaller habitats for them will increase.

In the event that only small islands of non-cultivated land can be maintained, it may be necessary to selectively plant and control species in those habitats to maintain pollinator populations that better suit the needs of these special environments (see also Part IV). If the more important natural pollinators for the crops are known, plant species used by these pollinators can be planted or maintained selectively. This approach would ensure the availability of flowers at the correct time. These selected habitats need more advanced planning in land use and also require more management, as they are less stable, being largely artificial. The lower the level of management possible in an area, the larger the area will have to be in order to maintain the required species diversity and abundance.

The composition of reserves or protected habitats will differ across regions and climates, but all should share a few common characteristics:

- a large diversity (to the extent possible) of local or locally adapted plants;
- freedom from exposure to pesticides;
- connection between habitat "patches" to enable species exchange, migration, etc.;
- sufficient numbers and distribution of such habitats in order to provide benefits to many agricultural producers.

The economic benefit of protected habitats cannot be justified only by the provision of pollinators and resulting production increase, particularly if only a few crops planted benefit from abundant pollinators. Additional values have to be found and a plausible intrinsic value for the local population, since monetary values are often of less importance. In order to make the additional effort worthwhile for the farmer, these small pieces of "unused" or "unaesthetic" land should preferably have another direct benefit, such as the provision of water, firewood, fruits, fodder, windbreaks, soil improvement or erosion control. If sustainable habitats are to be created or preserved, intrinsic values might include:

- traditional use of plants and forest for hunting
- food reserves for years in which crops fail
- medicinal resources
- ceremonial or religious uses.

Thus, the reserve size or species composition of such habitats might also be determined by intended alternative uses and established values.

While large reserves, such as biosphere reserves and World Heritage reserves, can and must conserve entire ecosystems, many small habitats can also preserve natural, beneficial pollinator species where they are needed. The smallest such habitats are field boundaries, hedges between fields and forest edges with various stages of successional plant growth. Following in size are fallow fields, planted forest patches for firewood and other communal or private uses, forests along river edges (riparian forests) and other pockets of more or less managed natural forests, preferably all connected to each other.

Hedges: Hedges play important roles in traditional agricultural systems in extreme climatic or geographical conditions, such as steep slopes or windswept plains. Their benefits can also be enjoyed in tropical climates. Apart from possible aesthetic values, hedges act as food and nesting resources for a large variety of animals, including pollinators such as birds, bats and insects. They also include windbreaks and livestock fences, provide erosion control, may stabilize dunes and water runoff, and produce firewood, fodder, fruits and medicinal plants.

Hedge communities can be chosen by observing local habitats and selecting those species most closely matching the desired hedge environment. The woody or shrubby hedge species should be chosen according to the major benefits expected from the hedge. Among suitable plant species, those that improve soil, provide rich nectar and pollen sources or have the most diverse use, may be preferred. Orientation of the hedgerows may follow land contours, property boundaries or be positioned to avoid (or enhance) the shading of cultivated plants.

Companion species should be planted or seeded according to the shade the mature hedge will provide. Naturally, shade-tolerant species should be in the centre of the hedge and on the side receiving more shade during the hottest part of the day. Some maintenance may be required to prevent one species from dominating and eliminating all others. But it is important to avoid weeding by completely destroying any plant cover, so common in tropical countries. The possible creation of natural hazards by providing new sites for poisonous snakes or stinging insects should also be taken into consideration. Sensible control by the elimination of such hazards is usually feasible.

Single or multiple-species hedges are frequently used for erosion control where they directly contribute to increased agricultural production, not only through feeding and protecting beneficial insects, including pollinators, but also through maintaining or improving soil and providing additional crops or food.

Fast-growing species that are easy to establish are preferred, especially if they are nitrogen-fixing legumes such as *Gliricidia sepium, Calliandra calothyrsus, Acacia decurrens* or *Desmodium rezonii*. These species give nectar and are actively sought by important pollinators like *Xylocopa* and *Apis*. The trees also can be pruned for mulching, animal fodder and firewood. Hedge pruning often determines whether species come to flower and provide nectar for bees. Selecting woody plants that act as pollinator food sources is sensible, as long as management of the hedges allows for flowering. The width of the hedge may vary with its overall function from a single row of planted sticks to a couple of metres.

Field boundaries: Field boundaries, in contrast to hedges, may or may not consist of perennial or woody species. They can be cultivated as boundaries by ploughing, cutting or spraying to maintain selected beneficial plant species for weed, pest and soil control, as well as to provide alternative food sources for pollinator species. Their width and maintenance may change more frequently with the rotation of crops.

Roadsides may cover considerable areas in some countries. These surfaces can be managed by cutting, which is fairly expensive, or by seeding and selective planting in order to maintain growth in certain successional stages. This allows them to serve functions similar to those of field boundaries, hedges or even small forest patches.

Home gardens: Due to their size, home gardens do not usually contribute much to feeding large pollinator populations. However, when entire villages plant flowering hedges around their homes, as well as fruit trees and bushes, and cultivate other flowers and certain vegetables, these habitats provide limited support for pollinator populations. Most of all, they constitute a source of food when there are few or no wild flowers nearby. This can be particularly helpful for beekeeping with species such as the Asia *Apis*, stingless bees and many non-*Apis* pollinators.

Riparian forests: Riparian forests grow in the immediate vicinity of a creek or river and perform an important ecological function by preventing soil runoff into the creeks, thus keeping water clear and less contaminated by agrochemicals.

Soil runoff not only constitutes a loss to the farmer, but also a threat to fish and other aquatic fauna. The soil changes the river bottom and the river course, and fills up reservoirs and lakes. Accordingly, trees on steep slopes or ravines should never be removed, and borders of 30 m to 100 m should be maintained, even on level riverbanks. Local conditions relating to flooding, aquatic life, river changes, land orientation and rainfall patterns must be considered. In addition, possible alternative uses of these areas, as described below for small forest patches, must be taken into consideration when planning the size of these borders.

Thus, leaving riparian forests untouched brings many ecological benefits, including the provision of unusually rich sources of nectariferous plant species and nesting sites for many kinds of pollinators. Where these habitats have already been destroyed, it is worthwhile replanting water edges with native tree and shrub species. Selecting the right species constitutes an active area of new research in much of the world.

Small forest patches: Forest vegetation can also be planted near agricultural fields. As is the case with natural forest, these patches can present a multitude of uses in addition to maintaining pollinators. Selecting only the fastest growing species used for firewood or timber production produces results similar to the planting of highly selective monocultures for agricultural production. Conversely, the application of sustained yield concepts considers the benefits of selected species for the soil, alternative uses, and the habitats provided by the forest patches for other crops and healthy populations of plants and animals. Mixed plantings should allow some undergrowth management. Future crop breeding might select for forest undergrowth conditions, thus simulating multilevel natural forests.

The classic eucalypt or pine groves do not present the best solution in most situations (either over the short term or long term), as these plants are selected for maximum rate of biomass production, which is only one among many important criteria. Even though most *Eucalyptus* species provide abundant nectar, their pollen is deficient in nutrients and very few companion plants can grow in the understory of these trees. As such, they provide no sources of cover, forage or alternative food for many kinds of animals. Soil quality and the water table are often negatively influenced and no other benefits can be obtained from the barren ground until many years after cutting.

In contrast, many fast-growing indigenous tree species permit various other uses of the land and the tree crop. Carefully selected species can even improve soil conditions through nitrogen fixation and organic matter deposition. More information on species selection, characteristics and requirements is available from a variety of information centres and networks.[6] The directory of world honey plants by Crane, Walker and Day (1984) allows cross-referencing of some species also known to be good producers of nectar or pollen.

A variety of experimental approaches have been employed for the establishment of small forest patches, mostly with an emphasis on multiple use of existing forests, forest conservation, community forestry, agroforestry, watershed management and sustained natural forest resource management. Few have considered the conservation of beneficial animals such as pollinators.

The multiple use of tree plantations should be included in any planting scheme. Selecting highly nectariferous tree species or those that allow nectariferous undergrowth brings additional income sources (beekeeping or native pollinator management) until the tree crop can be harvested. Therefore, higher diversity contributes to the sustainability of future crops and a higher quality of environmental conditions in general. Wise planning of multiple uses can help avoid loss of income and may instead become an attractive alternative.

Successional growth (second-growth habitat): While forests provide a large diversity of resources to nectar and pollen-feeding animals, this need is also met by certain savannahs and successional re-growth of fields and forests. The latter, in some tropical areas, can sometimes produce more nectar than mature forests. They also form an essential part of natural and "mature" ecosystems, harbouring many animal species and forming essential habitats for many pollinators and other beneficial insects.

Traditional slash-and-burn agriculture continuously creates areas of successional growth. If small enough and not too dense, these plots might maintain the desired pollinator species. In regions adhering only to slash and burn agriculture, there should be no pollinator shortages. This is due to the lack of vast monocultures. The principle of cutting only small areas and letting them regenerate, or replanting them with forest species, might be practised even in larger forest plantations. The same may be true in intermediate forest-agriculture zones or some park boundary zones where restricted exploitation is permitted. Forest edges provide a narrower, yet similar, habitat that should not be neglected. A rich flora and beneficial fauna can be maintained through minimal maintenance such as periodic cutting and selective clearing. Fallow fields in crop rotation or land regeneration (dunes, strip mines or eroded soils), like field boundaries, may be left to the natural succession of plant growth. They can also be planted with nectariferous, soil-improving species or receive minimum management, such as no-tillage, additional seeding and periodic cutting, to maintain successional growth at a preferred stage.

Nectar plants cultivated to benefit pollinators: Under most circumstances it is not common practice or economically feasible to plant crops solely for the purpose of providing nectar to pollinators. The value of honey or the resulting colony population of pollinators is always considered negligible in comparison to the value of the planted crop or the planting cost. For well-planned land use this may still be true in immediately recoverable monetary terms. But over the long term, the gap between planting costs and benefits from honey harvests, better pollination, increased natural pest control, lower fertilizer needs and other secondary benefits will become narrower.

[6] Please see the first edition of this publication, entitled *Pollination of Cultivated Plants in the Tropics* (1995), available online: https://books.google.fr/books?id=A1O8Ow6wDDUC&printsec=frontcover&dq=pollination+cultivate+plants&hl=en&sa=X&redir_esc=y#v=onepage&q=pollination%20cultivate%20plants&f=true.

Eventually, such planting costs may become negligible in comparison to all other benefits (when these are properly appreciated).

Pollinator populations can be enhanced through proper selection of flower species for their flowering times. This approach has been advocated for the maintenance of bumblebees in England, where they are very important pollinators. Thus early-flowering species serve to augment social bee populations or increase solitary bee populations or next year's population. Late-flowering species may increase the number of reproductive bees for the following season or year. Methods for studying the requirements and the preferred food plants of bumblebees on a countrywide scale were developed for England. Accordingly, groups of school children and volunteers were organized to make many of the basic observations. This worthwhile and affordable effort proved educational for the participants, increasing their environmental awareness, and was also very useful for researchers and farmers.

Abundance of attractive alternative food sources may in some cases reduce the efficiency of artificial and natural pollinator populations, if flowering occurs simultaneously with crop flowering. It is important to test, whenever possible, whether controlling such competing flora will decrease the following year's pollinator populations more than it will increase this year's pollination efficiency. This assessment should take into account alternative choices in pollinator species, crop varieties or timing of planting and pollinator introduction.

Cover crops: The practice of crop rotation enables the planting of cover crops during the fallow period. While the soil is recuperating the cover crop may provide flowers to pollinators needed in neighbouring fields. Self-seeding plants such as *Mellilotus* or other nitrogen-fixing legumes enrich the soil and may also provide a commercial honey crop, very rich fodder to livestock and/or "green manure". A combination of *Mellilotus* varieties can provide flowers over six months even on poor soils (at <40 °C). Some of these varieties have developed in Argentina for extreme subtropical climates.

Some problems do arise, similar to those stemming from highly nectariferous successional growth or forests. Attractive nectar-producing, non-crop flowers can compete with crop flowers for pollinators. In the case of natural pollinators, planting schedules and flowering periods must be synchronized as much as possible. The same problem with artificially enhanced pollinator populations can also be solved by placing colonies directly in the middle of the crop area, by providing more pollinators than are usually recommended, and/or by introducing the pollinator populations at a time when already 20 percent to 30 percent of crop flowers have opened. In extreme cases, competing floral resources may have to be temporarily reduced or eliminated during the crop flowering period.

3.2.4 Crop selection

It may be possible (as seen for many crops) to select additional varieties that do not require external pollination agents such as insects. Those varieties that continue to require pollinating insects, however, need to be made more attractive to pollinators (see Section 19.1). This means that more attention needs to be paid to flowering times and duration, nectar secretion and/or pollen attractiveness.

More emphasis on indigenous crops will reduce the need for exotic pollinators such as *Apis mellifera* in most of the world. Certain pollinators may prove less difficult to manage and propagate than imported honey bees, under local conditions. For example, it is generally well appreciated that *Apis cerana* is superior to *Apis mellifera* in much of the Asian tropics, due to better resistance to natural enemies and greater tolerance of environmental and resource conditions.[7]

The planting of *Mellilotus* in Northern Argentina, in a crop rotation system alternating with the cultivation of rice and cattle grazing, shows promise for profitable honey production (Krell, pers. obs.). A study by Accorti (1992) for Italy also demonstrates substantial savings in fertilizer expenses and petroleum resources for honey production under improved environmental conditions, rather than using sugar from sugar beets to feed the bee colonies. Further studies on similar subjects will likely show that conversion to environmentally "friendlier" cultivation methods can ultimately be more profitable. Maintaining wild pollinators and sustaining imported ones requires careful selection of crop and non-crop (cover crop) species.

Good management practices include cover crops and perennial crop varieties. Timber species should be selected among other criteria for their high nectar secretion. Unfortunately, this subject has not been sufficiently considered in the past, nor been given due importance by plant breeders. This is particularly relevant in forest plantations where harvest and therefore income are realized many years after the initial investment, as nectariferous species can provide a "balancing income" (cash flow) and provide for natural as well as managed pollinator species. The selection of nectariferous tree crops is relatively easy because many, if not most, tropical tree species are naturally good producers of nectar. Their indiscriminate cutting also drastically reduces the nectar sources available to all pollinator species, not just honey bees.

The creation or conservation of large wildlands for honey production can have strong secondary effects on pollinator availability in distant agricultural areas. This is demonstrated by an example from Sri Lanka. After the disappearance of most of the natural forest suitable for honey production, rubber plantations (*Hevea brasiliensis*) have become the principal sites for beekeeping. Recent improvements in bee management techniques are only now starting to permit beekeeping on a larger semi-commercial scale. However, the new varieties of rubber slowly replacing those of old plantations are said to produce little or no nectar. If this proves true, the developing beekeeping industry will have no future. The need for moveable pollinator populations is also simultaneously growing, in part due to the same environmental degradation, deforestation and increased pesticide use. They are needed for increasing seed production requirements and exotic cash crops such as gherkins (i.e. pickling cucumbers). Thus, eliminating profitable beekeeping on a commercial scale also eliminates manageable pollinator populations. The latter can only be made available in sufficient numbers through migratory beekeeping (i.e. moving hives into areas where pollinator enhancement is required). In effect, the selection of the new rubber variety might restrict agricultural cultivation possibilities in parts of the country far removed from rubber-growing areas. This example demonstrates the far-reaching consequences a slight change in cultivar or crop can have on the agricultural productivity of apparently unrelated, distant regions.

3.2.5 Pesticides

Aside from habitat destruction, the application of pesticides in large quantities and over large areas is the primary reason that wild pollinator populations have been reduced or completely destroyed. Large aerial applications over hundreds of thousands of hectares of Central American and African tropical forests to control the Mediterranean fruit fly, tsetse fly and malaria mosquito have undoubtedly had an impact on the pollinator fauna. Documentation of agricultural chemical effects, however, is incomplete (see Chapter 20 for recent evaluations regarding bees and beneficial insects). Farm applications are more frequent and widespread, also covering very large areas. Agricultural pesticides are often misapplied and have highly toxic effects on local animals (see Chapter 4).

Along the northwest coast of Sri Lanka, pesticides may have led to a production loss involving cucumber cultivation. Initial production during the first and second year was fairly high. During the third and fourth year production strongly declined, and after five years had dropped to only 30 percent of the first year's output, despite increased fertilizer and pesticide use. During the same period more land was cleared

[7] For more information see Section 2.5.4 in *Pollination of Cultivated Plants in the Tropics* (1995): https://books.google.fr/books?id=A1O8Ow6wDDUC&printsec=frontcover&dq=pollination+cultivate+plants&hl=en&sa=X&redir_esc=y#v=onepage&q=pollination%20cultivate%20plants&f=true.

in the dry forest zone and pesticides were applied, including by other farmers. The cucumbers are now deformed and of uneven growth – a clear indication of insufficient pollination. Unfortunately there is little that can be done. Together with increased pesticide use, the habitat was destroyed which otherwise could have allowed the re-establishment of honey bee colonies. Years of replanting will be necessary before the native pollinator population can increase its numbers.

Over the last decades, pesticides have become more potent, and only recently more specific. The broader a spectrum of pest species a pesticide potentially controls, the more devastating its effect will be on the total fauna, both pests and beneficial species alike. Its longevity in the environment and application timing and methods may further contribute to its destructiveness.

Although many broad-spectrum pesticides have been banned from the markets of industrialized countries for health and environmental safety reasons, many if not most of them are still being used in tropical and subtropical countries. Low levels of farmer and consumer education and strong political and economic interests permit the continued use of these often cheaper but more dangerous toxins. The newer, sometimes less toxic or more specific pesticides are usually much more expensive and therefore less accessible to the rural poor.[8]

Integrated pest management methods that will reduce pesticide use require very disciplined and well-educated farmers with more technical assistance than is available in most rural areas. Organic farming without the use of artificial or toxic chemicals requires traditional methods and even more education with new crops or at least a different kind of education than that commonly taught.

3.2.6 Cultivation practices

Studies of pollinator distribution in crop fields seem to indicate very limited foraging ranges of honey bees in situations with many more flowers than foragers. Similarly unsaturated conditions would occur with low natural pollinator populations or exceedingly large surfaces planted with one crop. If the overabundance of food (nectar) cannot be exploited, pollinators will concentrate on the areas closest to their natural habitat or nest. Uneven or incomplete pollination is often the result. Smaller field sizes and shapes following the contours of forest edges are therefore very important for pollination with "unenhanced" or natural pollinator populations.

Intercropping, or the planting of different crops in alternating rows or mixed rows, breaks up the uniform surfaces, reduces the overabundance of one food source and thus increases fruit set across the field. Although the number of plants to produce a crop is lower, production per plant is increased and the mixture of crops maintains or improves farmer income. Intercropping may also reduce relative production costs due to lessened pesticide and fertilizer requirements.

The most pressing change to be made to preserve natural pollinator populations is the adoption of less toxic and more balanced cultivation practices. Many of the alternatives have already been mentioned, such as reduced and more focused pesticide application (within integrated pest management programmes where pesticide-free cultivation is impossible), selection of more resistant locally adapted or indigenous crops, a larger variety of crops, multicropping systems, crop rotation, less tillage and more manuring. Last but not least, the soil must be monitored and taken care of as a highly complex living organism – a concept firmly established in many traditional cultures, but utterly disregarded by most of this century's agricultural development.

Initially, some of the suggested changes may result in lower yields than those heralded by the so-called "green revolution", but over the short term they save foreign exchange (pesticides and fertilizers) and farmer's lives (poisoning), and over the long term they preserve and likely increase yields for the future and reduce health costs, due to healthier food and water. The modern meaning of the "green revolution" is no longer equated with "highest output of biomass by any available means", but instead with the healthiest, least destructive, sufficient output of food.

3.2.7 Conclusion

To solve pollination-related problems in general, the easiest solution would be to switch to crop varieties that do not need pollinators, or to pollinator species that are easily manipulated and multiplied, such as some honey bees. This quick fix, often demanding a large investment, may be the remedy for some circumstances, but is unlikely to provide a long-term or sustainable solution. Fundamentally, it does not address the need for hybrid seed production, or for outcrossing in the many plant species that must be cross-pollinated to produce seed or fruit. Unless sufficient natural, non-cultivated flora are available, even the ubiquitous Western honey bee cannot provide the solution to pollination needs. Only a few highly specialized pollinator species with relatively short life spans, such as the alfalfa leaf cutter bee, may be maintained with one or a few crop species alone.

The next most efficient change would be to increase natural pollinator populations through reduced pesticide use. Alternative cultivation methods, conservation and selective planting will further increase natural pollinator populations and improve environmental conditions, as well as reduce farming costs.

Knowing the requirements, deficiencies and the costs, certain pollinator-limited crops may simply be poor choices for the economics of a given area. This is particularly true for some exotic or export crops which have to meet very specific standards of fruit shape or quality. Taken into account early enough, these conditions can prevent disappointing results, failed projects and farmers' losses.

For any sustainable and affordable solution to succeed, less destructive cultivation methods are necessary. Conservation efforts and sound agricultural practices are central to this goal. Creation or preservation of diverse environments, not only in national parks, is also required. This is true to the same extent for natural and managed pollinator populations.

[8] See the IPM PRIME database (https://ipmprime.org/pesticides/Home#), the Xerces Society and the Global Pollination Project for lists on known toxicity of pesticides to bees and other pollinators. University-based IPM extension agencies are among the most valuable of the numerous available online resources.

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