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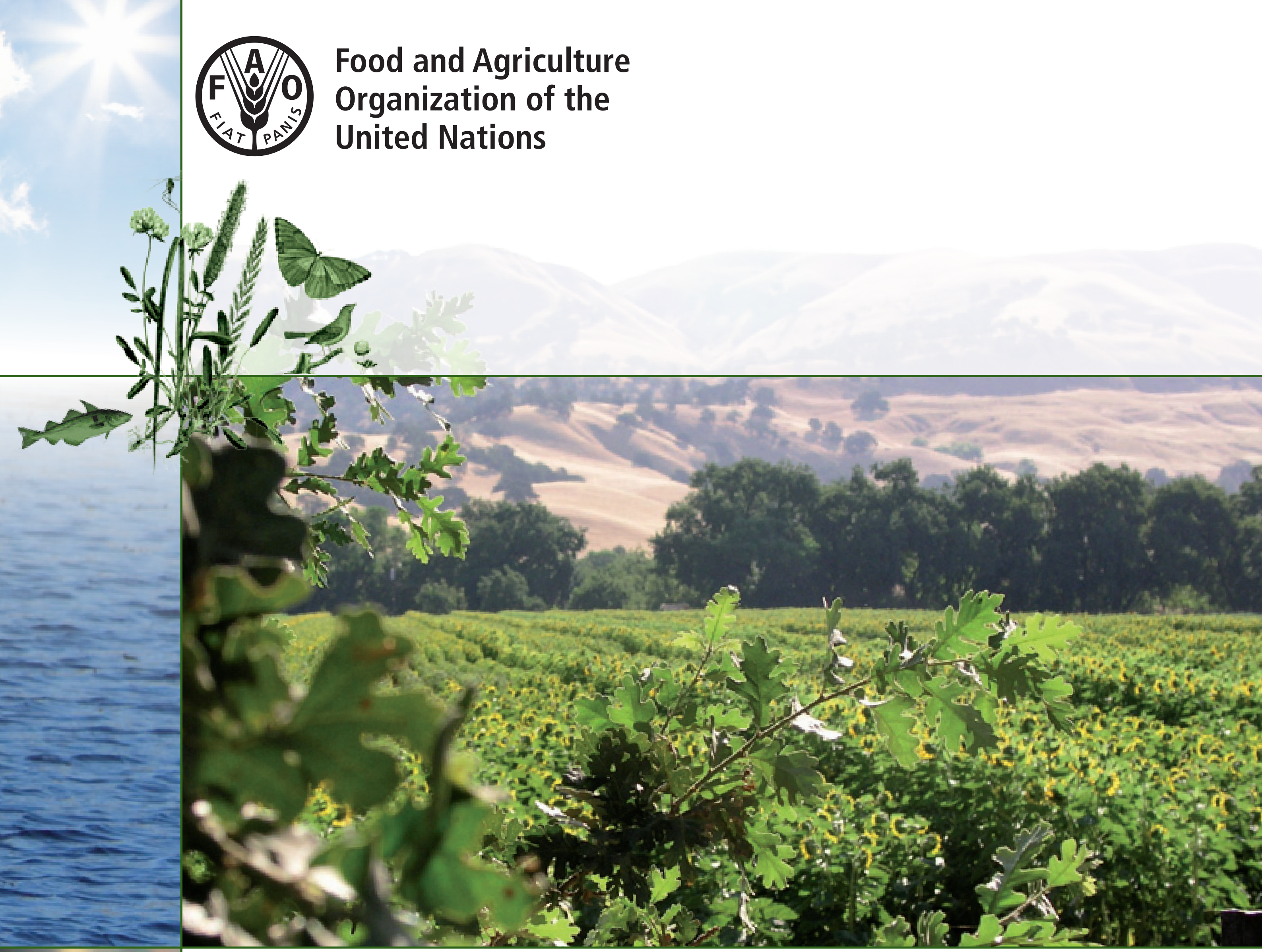

CROPS, WEEDS AND POLLINATORS

UNDERSTANDING ECOLOGICAL INTERACTION FOR BETTER MANAGEMENT

BIODIVERSITY & ECOSYSTEM SERVICES IN AGRICULTURAL PRODUCTION SYSTEMS

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UNDERSTANDING ECOLOGICAL INTERACTION FOR BETTER MANAGEMENT

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Lipotriches *bee gathering pollen from Buffel grass.*

PREFACE

It is increasingly recognized that it is both possible and highly advantageous to address future needs by transitioning to systems of food production that are based on an effective use of ecosystem services, in ways that are regenerative and minimize negative impacts. In managing agricultural systems through an ecological approach, it is often possible to build on beneficial biological interactions and find positive synergies. FAO's Strategic Framework, through it Strategic Objective 2 – to *increase and improve provision of goods and services from agriculture, forestry and fisheries in a sustainable manner* – recognizes that production systems can be managed to provide multiple benefits.

One area of synergy that merits closer investigation is that of weed and pollination management. These two aspects of agriculture consist of a multitude of interactions, both beneficial and harmful for the farmer and agriculture in general. If the practices applied to effectively control weeds can also benefit pollinators, there may be multiple benefits.

Another area of positive synergy is related to the practices enhancing populations of pollinators and favouring natural enemies. Under ecological management, some aspects of the farming system that are conventionally seen as problems, can become assets. Animal waste, for example, is a tremendous problem in intensive animal production systems, but becomes a valuable asset when crops and livestock are better integrated. Similarly, weeds in agricultural fields do provide resources to both pollinators and natural enemies, and in this respect can be better managed to provide such resources, while still managed to ensure that they do not impact on crop yields.

This review forms part of a multi-level approach to address pollination management and conservation, by the Food and Agriculture Organization of the United Nations (FAO). Recognizing the urgent need to address the issue of worldwide decline in pollinator diversity, in 2000 the Fifth Conference of the Parties to the Convention on Biological Diversity established an International Initiative for the Conservation and Sustainable Use of Pollinators (also known as the International Pollinators Initiative-IPI) and requested FAO to facilitate and coordinate the initiative. As part of this initiative, FAO has established a “Global Action on Pollination Services for Sustainable Agriculture” to expand global understanding, capacity and awareness of the conservation and sustainable use of pollinators for agriculture, including identification of best practices to sustain both agricultural production and natural pollination services.

The overarching aim of this review is therefore to develop sound advice aimed at a wide range of countries to sustainably promote the twin goals of weed and pollinator management, including the enhancement of other non-crop plant species into an agroecosystem with particular pollinator-friendly aspects.

These twin goals suggest that with a foundation in science, production practices designed by farmers and strategic policy makers exist, and they can address all parts of sustainable food systems including ecological, economic and social components, if an innovative, complex, and integrated way to address food security and environmental challenges of the 21st century is adopted.

Caterina Batello

Senior Programme Officer
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1

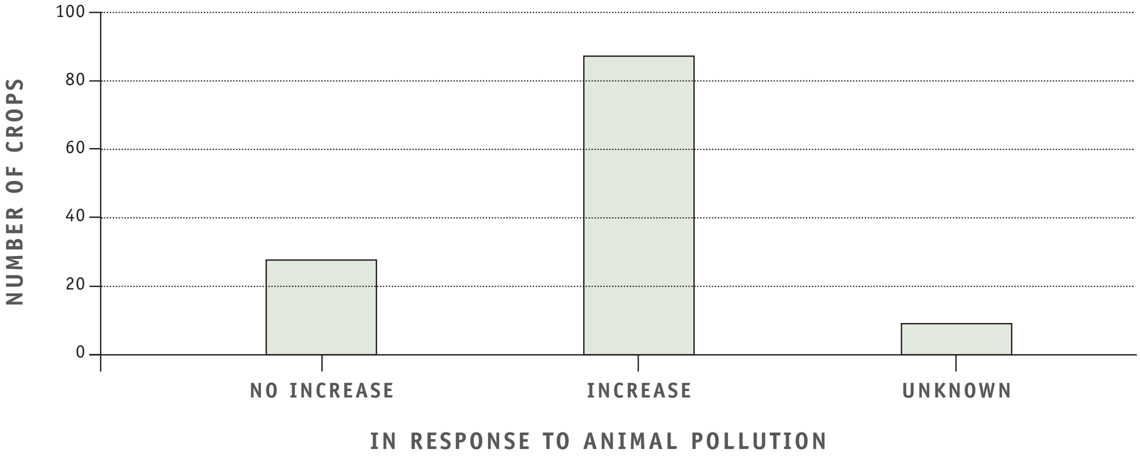
WEEDS AND POLLINATORS
IN AGRICULTURAL PRODUCTION SYSTEMS

Lycaenid butterfly and cuckoo wasp on coriander flowers.

1.1 THE IMPORTANCE OF POLLINATION AS A BIODIVERSE ECOSYSTEM SERVICE

The interactions between plants and pollinators are many and complex. The global number of described Angiosperm plants – those that flower and produce seed – is thought to be over 250 000 (Wilson, 1992). The transfer of pollen and subsequent fertilization of the plant is a fundamental necessity in the reproduction of these species, and while some plants can self-pollinate, the majority are reliant on, or experience greater reproductive rates through, cross-pollination (Buchmann and Nabhan, 1996). Between 78 percent and 94 percent of these angiosperm species rely on the cross-pollination services provided by some 300 000 animal species (Buchmann and Nabhan, 1996; Ollerton *et al.*, 2011), and 87 percent of crops benefit from insect pollination to some degree (Klein *et al.*, 2007) (Figure 1). Economically, the services provided by animal pollinators were conservatively valued at US$216 billion in 2005, or 9.5 percent of the value of global food production (Gallai *et al.*, 2009).

FIGURE 1. RESPONSE OF LEADING CROPS AND COMMODITIES TO ANNUAL POLLINATION



Source: Klein *et al.* (2007).

While animal pollinators include bees, wasps, butterflies, moths, flies, beetles, birds, bats and lizards, which are anatomically or behaviourally adapted for efficient and accurate pollen delivery (Faegri and van der Pijl, 1979; Proctor *et al.*, 1996), many of them vary in effectiveness of pollen transfer. A recent review by Klein *et al.* (2007) noted that a total of 63 animal species (60 insects, two birds and one bat) have been identified down to the species level as true pollinators of 107 of the world’s leading staple food crops. The authors acknowledge, however, that this number refers to the number of pollinators whose effectiveness has been documented through scientific evidence; the number of actual species involved is thought to be much greater.

There is now strong evidence that populations of both wild and managed insect pollinators are declining in both abundance and diversity (Biesmeijer *et al.*, 2006; Goulson *et al.*, 2008b; van Engelsdorp *et al.*, 2008; Patiny *et al.*, 2009; Potts *et al.*, 2010; Cameron *et al.*, 2011). For example, landscape scale declines in native bee species richness have been recorded in the Netherlands and the United Kingdom (Biesmeijer *et al.*, 2006), and hoverfly diversity is declining locally in the United Kingdom (Keil *et al.*, 2011). Across their range in temperate zones, bumble bee (*Bombus* spp.) species are also in decline (Goulson *et al.*, 2008b; Kleijn and Raemakers, 2008; Cameron *et al.*, 2011), and substantial losses in wild and managed honey bee colonies are becoming widely acknowledged (van Engelsdorp *et al.*, 2008; Jaffe *et al.*, 2010; Potts *et al.*, 2010).

The abundance and richness of wild pollination communities have been shown to decrease significantly in highly modified, intensive agricultural landscapes (Ricketts *et al.*, 2008; Winfree *et al.*, 2009), strongly affecting the levels of service provided to crops (Garibaldi *et al.*, 2011).

1.2 THREATS FACING CROP POLLINATORS

It is recognized that multiple and interacting pressures on pollinator species threaten to economically and ecologically disrupt a major ecosystem service and a keystone species interaction of all ecological communities (Potts *et al., 2010)*.

Much of the documentation on threats to pollinators has come from developed countries where strong historical datasets are held, but such data are not available for other regions such as the tropics and the southern hemisphere. Despite this, declines may be inferred from studies of the main threats to abundance and diversity of pollinators. These pressures are multiple and interlinked, and often stem from the need to increase land productivity to feed a rapidly increasing global population. Intensive agricultural practices such as pasture improvement, the creation of large and homogenous fields, and intensive grazing can lead directly to habitat loss and fragmentation (Kremen *et al.*, 2002; Ricketts *et al.*, 2008; Winfree *et al.*, 2009), destroying pollinator nest sites and refuges. Also, the widespread use of insecticides to control insect pests can have a direct effect on insect pollinators (Rortais *et al.*, 2005; Brittain *et al.*, 2010a). Intensive practices also reduce foraging habitats such as flower-rich set-aside land and field margins, grasslands and heathlands with which many pollinators are associated (Carvell *et al.*, 2006; Kleijn and Raemakers, 2008). Furthermore, more effective weed control is thought to have a significant impact on the availability of floral resources (Gabriel and Tscharntke, 2007). The application of chemical fertilizers alters weed communities in agroecosystems, providing conditions more suited to less rewarding annual species than to preferred perennial species (Pywell *et al.*, 2005). Similarly, weed control measures such as calendar herbicide application and intensive tillage methods, and the intensive management of simple landscapes, create hostile environments in which pollinators need to travel further to find rewarding forage plants (Gabriel and Tscharntke, 2007). Some plants associated with agroecosystems have become rare plants themselves (Roschewitz *et al.*, 2005), while parallel declines in many animal-pollinated plants (Biesmeijer *et al.*, 2006; Carvell *et al.*, 2006) suggest that the losses of both groups may be causally linked.

These factors combine with each other and other important drivers, such as the spread of pests and diseases affecting pollinators and climate change, to varying degrees for different species in different geographical regions. For example, the microsporidian infections thought to be partly associated with honey bee Colony Collapse Disorder (Cox-Foster *et al.*, 2007; Bromenshenk *et al.*, 2010) increase energetic stress on infected worker bees, raising their hunger level (Mayack and Naug, 2009). The subsequent need for more food is exacerbated by the lack of non-crop forage resources in intensive landscapes (Mayack and Naug, 2009; Naug, 2009), and additional foraging may increase the probability of an individual worker coming into contact with chemical pesticides, further affecting bee health (Cresswell, 2011). The impacts of climate change on land use, the spread of invasive species, and the perceived need to increase application of chemicals are not yet fully understood, but are likely to further compound contributory factors (Kjøhl, *et al.*, 2011).

Overall, a lack of available nutrition in non-crop floral resources found in simplified agricultural landscapes leaves many pollinators susceptible to other pressures, particularly those with narrow diet breadths (Goulson *et al.*, 2008b), low levels of ecological trait plasticity (Schweiger *et al.*, 2010), or those at the edges of their climatic ranges (Williams *et al.*, 2009) While more dominant species may be less affected, pollination, like other ecological functions, is more likely to be stable in ecosystems with high biodiversity. A more diverse community of pollinators is better able to withstand environmental changes than a simple community, because if one or more important species become locally extinct, other species are able to fill the vacated niche through the operation of species redundancy (Hooper *et al.*, 2005).

Widespread declines in important species can lead to concomitant declines in plant diversity (Kaiser-Bunbury *et al.*, 2010). As plants provide the building blocks of most terrestrial ecosystems, disruption or collapse of pollinator networks could be calamitous (Memmott, 1999; Potts *et al.*, 2010), and have knock-on effects for other ecosystem services (Mittelbach *et al.*, 2001; MEA, 2005; Balvanera *et al.*, 2006). These consequences may be most significantly felt among the world's rural poor and subsistence farmers who rely most on wild pollinators for crop production and on other ecosystem services (Allen-Wardell *et al.*, 1998; MEA, 2005; Diaz *et al.*, 2007).

1.3 HABITAT MANAGEMENT TO PROMOTE POLLINATORS IN FARMLAND: THE POTENTIAL ROLE OF WEEDS

While it is uncertain whether declines in flower abundance are driving declines in pollinators or vice versa (Biesmeijer *et al.*, 2006), increasing evidence suggests that providing floral resources within farmland ecosystems improves pollinator diversity or abundance or both (Carvell *et al.*, 2004; Pywell *et al.*, 2005; Carvell *et al.*, 2007; Gemmill-Herren and Ochieng, 2008; Carvalheiro *et al.*, 2010). However, planting non-crop flowers and restricting chemical applications and other agricultural prescriptions designed to benefit insect pollinators may conflict with farmers' interests because of the withdrawal of land from production and the need for extra labour to control potentially enhanced weed populations. Weeds may compete with crops, reduce crop quality and quantity, and create a substantial cost to farmers at a range of scales, a point highlighted by the fact that, globally, more money is spent by growers on weed control than on other inputs (Marshall *et al.*, 2003). In this review, the literature on pollinators and non-crop flowering species is comprehensively explored to identify areas where compromise between the need to enhance pollinator populations and the need to control weeds may be effectively pursued. The most effective alternative forage plants for certain pollinator groups are considered first in Section 2. Section 3 then introduces the important aspects of weed ecology in relation to pollination. Section 4 considers the effects of specific agronomic practices that contribute to managing weeds in ways that also benefit pollinators. Section 5 applies this focus at the level of impacts of farming systems on pollinator populations and weeds. Finally, Section 6 examines the costs and benefits of promoting pollinator-friendly non-crop flowers.

1.4 THE INTERNATIONAL RESPONSE

This review forms part of a multi-level approach to address pollination management and conservation, by the Food and Agriculture Organization of the United Nations (FAO). Recognizing the urgent need to address the issue of worldwide decline in pollinator diversity, in 2000 the Fifth Conference of the Parties to the Convention on Biological Diversity established an International Initiative for the Conservation and Sustainable Use of Pollinators (also known as the International Pollinators Initiative-IPI)[1] and requested FAO to facilitate and coordinate the initiative. As part of this initiative, FAO has established a “Global Action on Pollination Services for Sustainable Agriculture” to expand global understanding, capacity and awareness of the conservation and sustainable use of pollinators for agriculture, including identification of best practices to sustain both agricultural production and natural pollination services. One area of best practice that requires investigation is that of weed and pollination management. As described above, these two areas of agriculture consist of a multitude of interactions, both beneficial and harmful for the farmer and agriculture in general. The overarching aim of this review is therefore to develop sound advice aimed at a wide range of countries to sustainably promote the twin goals of weed and pollinator management, including the enhancement of other non-crop plant species into an agroecosystem with particular pollinator-enhancement traits.

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[1] CBD Decision V/5, Section II.

2

THE IMPORTANCE OF WEEDS TO POLLINATORS

Blueberries in bloom.

2.1 MAPPING THE LINKAGES BETWEEN WEEDS AND POLLINATORS

2.1.1 Key systems of interaction between "weeds" and pollinators

Although a comprehensive review of non-crop flowers and pollinators would cover thousands of species of pollinators, in the interests of relevance this review will focus on the small subset of pollinators that have been scientifically documented to contribute to the increase in yields through pollination of leading crops, as detailed by Klein *et al*. (2007). Some of those are omitted, however, due to obligate mutualism. For example, the fig wasp (*Blastophaga psenes*) is vital to the reproduction of the common fig (*Ficus carica*), and both plant and insect are specialized around this single interaction (Galil and Neeman, 1977). Also omitted are the nitidulid beetle species (*Carpophilus hemipterus* and *Carpophilus mutilatus*), which are essential pollinators of *Annona squamosa* (Atemoya or custard apple) in tropical climates and are thought to be attracted to the flowers by the odour of the nectar that resembles their usual food of rotting fruit (Nadel and Pena, 1994; Klein *et al*., 2007). However, the interaction is not fully understood, as the beetles do not appear to feed on any floral resource or use the flowers for mating or oviposition, but remain in the flowers for many hours and emerge covered in pollen (Podoler *et al*., 1985).

Such true specialization, as in the fig wasp and common fig, tends to represent the exception rather than the rule in plant-pollinator interactions (Waser *et al*., 1996; Memmott, 1999), as many pollinators are opportunistic and generalist (Olesen and Jordano, 2002; Bascompte *et al*., 2003). They are generally not "perfectly matched" to crop species, as in the case of the fig wasp life cycle mentioned above. Pollinator life cycles are often longer than the flowering periods of individual plant species, particularly mass-flowering crops. Pollinating insects therefore often require numerous additional flower sources to complete their life cycle and contribute to subsequent generations. Similarly, many plants are also generalists in that they can be visited by a large number of different pollinators (e.g. Memmott *et al*., 2004). This complexity and the high degree of multi-species interactions indicates the difficulty in understanding the importance of different alternative forage species to both pollinators and the ecosystem service of crop pollination.

With this level of complexity in mind, as well as temporal and spatial variation in interactions, a comprehensive review of all non-crop plant-pollinator interactions involving the above focal pollinator species would be voluminous. This section therefore focuses on a few key model interactions between flowering non-crop plants, flowering crops and pollinators, then reviews recent work advancing current understanding of complex pollinator networks. A consideration of these complexities is required if appropriate pollination service management strategies are to be designed (Kearns *et al*., 1998). In addition, an appreciation of interaction networks demonstrates that reliance on a few species for pollination is not sustainable, and that pollinators require more resources than a monocultural and limited flowering crop plant in order to persist from generation to generation.

2.1.2 The importance of floral resources to pollinators

Pollination is a mutually beneficial interaction. In return for pollen transfer services, animals are "rewarded" with a nutritional plant product such as nectar, pollen, oils and resins (Buchmann, 1987; Roulston and Cane, 2000; Roulston *et al.*, 2000). Pollen is an important source of protein for animal visitors such as bees and flies (Roulston and Cane, 2000). Many plants must produce vast amounts of pollen to enable pollination. For example, Schlindwein *et al.* (2005) observed that only 3.7 percent of the pollen of *Campanula rapunculus* contributed to pollination, with 95.5 percent removed and consumed by bees.

An increase in local availability of floral rewards is expected to result in greater fitness benefits such as longevity and fecundity of pollinators (e.g. Kim, 1999; Goodell, 2003). However, the effects of food quality are less well understood (Burkle and Irwin, 2009), and this is undoubtedly a factor behind the importance of different forage plants. The protein content of pollen affects bee colony growth as well as the development of the individual (Schmidt *et al.*, 1987; Roulston and Cane, 2000; Genissel *et al.*, 2002), and recent evidence demonstrates that insects are attracted to plants with high-quality pollen (Hanley *et al.*, 2008). For example, members of the *Fabaceae* family produce pollen with a higher protein content than plants that can also be self or wind-pollinated, and are visited most often by pollinators (Hanley *et al.*, 2008). Thus, for obligate pollen feeders such as bees, accessible non-crop flowers producing a high quality of pollen are likely to enhance survival and growth.

Food quality and diversity may have important implications for pollinator health. Few studies have investigated the relationship between protein nutrition and immunity in insects, but a recent investigation showed that bees fed with monofloral pollen (even that containing the highest protein levels) produced fewer antiseptics (secreted in the food for larvae and in honey) than those fed with multiflower pollen. As a result, the colony became more susceptible to disease (Alaux *et al.*, 2010). In another experiment, aged honey bees fed a mixed pollen diet lived significantly longer than those fed on pollen from a single plant species in a series of studies (Schmidt, 1984; Schmidt *et al.*, 1987; Schmidt *et al.*, 1995). This underlines the importance of a diverse diet to ensuring bee and colony health.

Nectar quality is also important as flower nectars may be specialized to suit different pollinator groups (Faegri and van der Pijl, 1979; Alm *et al.*, 1990). Flowers pollinated by long-tongued bees tend to produce sucrose-rich nectar, unlike those pollinated by short-tongued species (Baker and Baker, 1983). These latter species favour flowers with a lower amino acid nectar concentration and are likely to supplement their amino acid intake from alternative sources such as pollen (Baker and Baker, 1983). Baker and Baker (1973, 1986) also demonstrated a correlation between the concentration of amino acids in nectar and pollinator type, indicating that nectar plays a role in pollinator nutrition as well as acting as an energy source.

The importance of floral resources to biodiversity can be also inferred from studies that have reported a positive correlation between the diversity of animals and the diversity of flower species. Such correlations have been demonstrated for bees (Ostler and Harper, 1978; Dramstad and Fry, 1995; Steffan-Dewenter and Tscharntke, 2001; Kleijn *et al*., 2004; Albrecht *et al*., 2007; Frund *et al*., 2010), hoverflies (Albrecht *et al*., 2007; Frund *et al*., 2010) and many other insect species (e.g. Clausen *et al*., 2001; Pywell *et al*., 2004; Albrecht *et al*., 2007; Gillespie and Wratten, 2012; reviewed by Haaland *et al*., 2011). A positive correlation also occurs between pollinator diversity and flower abundance (Hagen and Kraemer, 2010) and between pollinator abundance and plant diversity (Potts *et al*., 2003; Ghazoul, 2006; Ebeling *et al*., 2008).

The decline in wildflower abundance in arable landscapes since the nineteenth century as a result of agricultural intensification (Robinson and Sutherland, 2002) has coincided with a decline in several animal species (Biesmeijer *et al*., 2006). In the British countryside, the decline of preferred forage plants of long-tongued *Bombus* spp. is suggested to be a principal cause of the rarity of these bee species (Goulson *et al*., 2005; Williams, 2005). Conversely, an increase in non-crop flowering species improves biodiversity. Field margins sown with a range of different annual and perennial flowering species result in variable improvements in the diversity and abundance of bumble bees, depending on plant composition, seasonal flowering patterns and bee forage preferences (Carvell *et al*., 2007). There is also a long-standing theory that co-flowering plants may facilitate pollination rather than compete for it (Brown and Kodric-Brown, 1979; Rathcke, 1983; Callaway, 1995; Moeller, 2004; Ghazoul, 2006). A species-rich sward of flowering plants may have greater pollination rates and reproductive success over less diverse swards through improved pollinator attraction or stability of populations, even among morphologically dissimilar flowering plant communities (Ghazoul, 2006). However, some plant species are better facilitators of pollination than others (Ghazoul, 2006), and more work is required before these interactions can be exploited for agriculture.

While there is ample evidence of the importance of different floral species for pollinator attraction, and of floral biodiversity for pollinator diversity, there has been much less work undertaken on the importance of non-crop flowers to agricultural pollinators, and on the indirect effects of improving farmland biodiversity on crop yield. Mass flowering monocultural crops, which produce floral resources simultaneously, may only flower for a fraction of the active season of many pollinators. For the remainder of their lives, they therefore rely on alternative foraging resources, often including, but not limited to, non-crop flowering plants occurring throughout the agro-ecosystem or in other semi-natural habitats in the vicinity. The availability of these “weeds” is therefore potentially important to the persistence of pollinators in agroecosystems throughout the year, and for the continued conservation of these species from one year to the next. The relative importance of non-crop flowering resources to different pollinator groups is considered in the following sections.

2.2 THE IMPORTANCE OF NON-CROP FLOWERS TO HONEY BEES (*APIS* SPP.)

2.2.1 General ecology of honey bees

Although the most common and well-known honey bee species (*Apis mellifera*) is native to or has been introduced to almost every country for the purposes of both pollination and honey production (Goulson, 2003b; Goulson *et al.*, 2008a), there are eight other honey bee species, most of which occur in tropical regions. For example, the Eastern hive bee, *Apis cerana*, is the most widespread honey bee in the Oriental taxonomic region (Hepburn *et al.*, 2001) and fulfils the roles of pollination and honey-making, although with fewer and smaller workers and a shorter foraging range than *A. mellifera*. The red dwarf honey bee, *Apis florea,* is also an important pollinator of field and orchard crops in Asia (Rehman *et al.*, 1990; Sihag, 2000; Corlett, 2004), and is expanding its range into the Middle East (Mossagegh, 1993). The giant honey bee, *Apis dorsata*, is considered to be an important pollinator of durian, cashewnuts and, to a certain extent, coffee in Asia (Klein *et al.*, 2007), making foraging flights within a 3 km radius of the nest and often covering vast distances to track large sources of nectar and pollen (Corlett, 2004), including those of many crop species (Koeniger and Koeniger, 1980). However, much of the literature concerning *Apis* species other than *A. mellifera* tends to focus around nesting sites as a limiting factor, rather than floral resources, with the conversion of primary forest to short-cycle plantations and agriculture being of particular concern (Oldroyd and Nanork, 2009).

The focus of the literature on *A. mellifera* is perhaps justified by the economic value of the species as a pollinator, with many commentators observing that the domesticated honey bee pollinates most crops. However, recent criticism of the reliance on this species has reported that it is responsible for only 18 percent of crop pollination worldwide (Westerkamp, 1991; Westerkamp and Gottsberger, 2000), or 35 of the 107 important global crops (Klein *et al.*, 2007). For some crops like blueberry and cranberry (*Vaccinum* spp.) and tomatoes and potatoes (*Solanum* spp.), which have anthers that are poricidally dehiscent (pollen released through pores), access to pollen is restricted to those bees capable of "buzz" pollination – the use of flight muscles to vibrate the pollen free from the apical pores of the anthers (Buchmann, 1985). The honey bee is ineffective at this form of pollination (Stubbs and Drummond, 2001), despite possessing the musculature to do so (Buchmann, 1985). Nevertheless, farmers rent thousands of hives during the blooming period of these crops for pollination (Winfree *et al.*, 2008). Native pollinators are often considered more effective pollinators of both crops and native flowers (Parker *et al.*, 1987; Torchio, 1990; Westerkamp, 1991; Batra, 1995; Westerkamp, 1996; Westerkamp and Gottsberger, 2000), and communities of native bees can provide effective replacement of honey bee services in appropriate conditions (Kremen *et al.*, 2002). The presence of *A. mellifera* among native pollinator communities has been thought to carry a number of negative impacts including displacement (Walther-Hellwig *et al.*, 2006), impacts on foraging rates and reproductive success (Thomson, 2006), assisted spread of bumble bee natural enemies (Ruiz-Gonzalez and Brown, 2006) and pathogens (Genersch *et al.*, 2006). However, more recent research suggests that interactions between honey bees and other bee species may improve the pollination effectiveness of honey bees (Greenleaf and Kremen, 2006b; Carvalheiro *et al.*, 2011)

This is not to say that the honey bee is an ineffective crop pollinator, however. Like many successful species, *A. mellifera* is adapted to colonizing new habitats due to a generalist diet breadth, enabling bees to forage from a wide range of plants in different habitats and throughout the year, ensuring overlap with many other species (Goulson, 2003a). Honey bees are also able to forage over relatively large distances from their nests, with some foraging trips of over 10 km (Schwarz and Hurst, 1997). This generalist ecology contributes to the recognition of the honey bee as an effective pollinator of a number crops (Klein *et al.*, 2007), even if it is not usually the sole pollinator. Honey bees, by virtue of being able to be managed, may make up in sheer numbers what they make lack in terms of the effectiveness of single floral visits.

2.2.2 Honey bee nutrition

Adult honey bees use pollen as the main source of protein, minerals, sterols, lipids and vitamins (Herbert and Shimanuki, 1978), and nectar as the main source of carbohydrates. Pollen also stimulates glandular secretions that are fed to larvae (Haydak, 1970). A lack of pollen, or pollen of a low nutritional value, leads to lower brood-rearing activity and shorter longevity (Knox *et al.*, 1971). Poorly nourished honey bees are also more susceptible to the microsporidian *Nosema ceranae* (Bromenshenk *et al.*, 2010), a contributory factor to Colony Collapse Disorder (CCD) thought to have caused a 30–40 percent decline in bee colonies in 2006 (Oldroyd, 2007). Nutritional stress resulting from increasing pollen transportation distances may also contribute to CCD, and pathogen-induced stress can further lead to additional nutritional requirements (Mayack and Naug, 2009; Naug, 2009).

Honey bees tend to choose flowers and inflorescences based on size (Martin, 2004), sex phase (Greco *et al.*, 1996), age (Higginson *et al.*, 2006) and number of flowers (Duffield *et al.*, 1993); features that often correlate with nectar production and accessibility (e.g. Kay *et al.*, 1984; Duffield *et al.*, 1993; Torres and Galetto, 1998). They have shorter proboscises and visit smaller open flowers compared to *Bombus* spp. (Corbet, 1995; Kells *et al.*, 2001). For honey bee keepers and farmers, non-crop flowers may cause concern due to the undesirable trait of honey bees of foraging on flowers other than the crop (Jay, 1986). In most managed honey bee crops, this migratory tendency of the honey bee when food is lacking is managed by providing an energetic diet (Brighenti *et al.*, 2010), moving hives to floral rich areas, using attractants and sprays, and removing alternative forage with herbicides or even repellents used on non-target flowering plants (Jay, 1986). In particular, dandelion (*Taraxacum* spp.), white clover (*Trifolium repens*) and mustard (*Sinapis alba*) are thought to attract bees away from orchards (Mayer *et al*., 1991), and are often removed.

2.2.3 Non-crop flowers and honey bee conservation

The majority of recent studies focus more on providing forage for alternative pollinators due to recent population declines and increasing recognition of the problems associated with reliance on the honey bee (Goulson, 2003a). Conserving alternative pollinators is likely to act as an insurance or buffer against significant declines such as those experienced recently (Greenleaf and Kremen, 2006b), and may even facilitate honey bee pollination efficiency (Carvalheiro *et al*., 2011). This diversity approach is reflected in the number of studies that include *A. mellifera* in investigations of bumble bee forage preferences rather than focusing on providing forage for *A. mellifera per se*. For example, in annual plant seed mixtures commercially available to attract beneficial insects to farm habitats, *A. mellifera* was overwhelmingly attracted to borage (*Borago officianalis*) (Carreck and Williams, 2002; Carvell *et al*., 2006) and phacelia (*Phacelia tanacetifolia*) (Williams and Christian, 1991; Carreck *et al*., 1999; Walther-Hellwig and Frankl, 2000; Carreck and Williams, 2002). Such species are agronomically and biologically suitable for use in field margins to attract bees, smothering the growth of pernicious weeds without themselves becoming weeds (Carreck and Williams, 2002) and providing a long succession of flowers, in European conditions (Engels *et al*., 1994). Other commercially available mixes include early spring flowering perennial species, although the importance of these mixes to honey bee species has not been studied in depth.

Studies that have examined forage preferences of honey bees have reported a wide range of flower species. In their survey of British farmland, Fussel and Corbet (1991) recorded frequent visits by honey bees to *Rubus fruticosus* agg., *Cirsium vulgare*, *Epilobium hirsutum*, *Heracleum sphondylium* and *Brassica napus*, in particular. Kells *et al*. (2001) reported that honey bees used *Matricaria* species, *Lamium purpureum* and *Persicaria maculosa*, as well as the biennial *Dipsacus fullonum* and perennial *Chamerion augustifolium* to a lesser extent. These species were mainly confined to naturally regenerating field margins compared to conservation headlands, and were not utilized extensively while oil seed rape was flowering nearby. As such, they may fulfil the requirement of not providing forage preferable to the crop. This is supported by Carvalheiro *et al*. (2011), who reported that the presence of weeds in sunflower fields increased pollinator diversity and crop productivity, which consequently enhanced honey bee movement. Conversely, pollen of sweet clover (*Melilotis officinalis*) dominated the pollen catch in honey bee hives over oil seed rape in a study by Lagerlof *et al*. (1992), suggesting that sweet clover may be an inappropriate alternative forage species. A similar finding was reported by Abrol (2006), where *A. mellifera*, *A. cerana*, *A. florea* and *A. dorsata* all preferred to forage on the weed *Lepidogathus incurva* over peach flowers due to greater quantities of sugar and energy per flower. These findings may affect decisions to include non-crop forage plants in farmland ecosystems by managers, particularly if they lead to greater seed set and population increases of weeds.

For the eastern honey bee species, there is even less information about non-crop floral species. Instead, there has been much work into the effects of the distance of crops from areas of natural habitat. For example, a study in Thailand demonstrated a high correlation between visits of *A. cerana*, *A. dorsata* and *A. florea* to crops of pear, plum and longan and the proximity of forest sites (Boonithee *et al.*, 1991). Klein *et al.* (2003a, 2003b) have shown in a series of studies that the diversity of social bees decreases with distance to forest in coffee-growing agro-forestry systems and attributed this to the preference of *Apis* species to nest in the cavities of tall trees. This system also demonstrated the importance of a pollinator community. When coffee plants bloomed, social bees were the main visitors to coffee flowers, at which point solitary bee species foraged on the ground vegetation of open habitats (Klein *et al.*, 2002). Outside this mass flowering period, although coffee plants flowered occasionally, social bees were absent but solitary bees visited the flowers, ensuring maximum seed set (Klein *et al.*, 2003a). A flower-rich ground layer of herbs flowering throughout the year was therefore recommended, particularly when social bees displaced the solitary bees.

An additional requirement of honey bees may also explain the importance of local semi-natural habitats. It is becoming increasingly apparent that feral honey bee species require plant resins, thought to be essential to *A. florea* in preventing the invasion of ants to the hive (Simone-Finstrom and Spivak, 2010). Other species also use propolis to narrow hive entrances and cover unwanted holes to maintain homeostasis in the nest, to provide waterproofing and protect against bacterial growth (Simone-Finstrom and Spivak, 2010). Such plant products are collected from *Clusia* spp. flowers (Pereira *et al.*, 2003) or the leguminous *Dalbergia* sp. (Silva *et al.*, 2008) in tropical regions, and species of poplar (*Populus* spp.), elm (*Ulmus* spp.), alder (*Alnus* spp.), beech (*Fagus* spp.) and horse chestnut (*Aesculus hippocastanum*) in temperate climes (Crane, 1990; Markham *et al.*, 1996; Salatino *et al.*, 2005). The proximity of natural habitats is clearly important to feral honey bee populations, and the ability of the ecosystem to provide plant materials such as resins, diet diversity and season-long forage may be important to honey bee health. But the moveable nature of domestic honey bee hives may mask these relationships.

2.3 THE IMPORTANCE OF NON-CROP FLOWERS TO BUMBLE BEES (*BOMBUS* SPP.)

2.3.1 General ecology of bumble bees

Due to the abundance (*c.* 400 species worldwide) and behavioural adaptations of bumble bees, they are often regarded as the most important of insect pollinators (Williams, 2002), although they are largely restricted to temperate, alpine and arctic regions, including areas where they have been introduced such as Australasia (Delaplane and Mayer, 2000). Bumble bees are generalists and pollinate a wide range of crops from broad bean and red clover to cucumber and blueberry (Klein *et al.*, 2007). As eusocial species, the annual life cycle of bumble bees begins with a solitary phase as a young mated queen overwinters and emerges in spring to find a nest site and forage for energy reserves for brood production (Delphane and Mayer, 2000). The resultant colony will produce a new queen during mid to late summer, and the success of this process depends largely on floral resource abundance throughout the active season (Bowers, 1986).

It is well established that the primary trait in which bumble bee species vary is tongue length (e.g. Brian 1957, Hobbs *et al.* 1961, 1962). Differences in corolla length of the plants they pollinate are thought to ensure coexistence, although this has been occasionally disputed because bees with a short tongue can still collect pollen from flowers with a long corolla (Kleijn and Raemakers, 2008). Shorter-tongued species also tend to have a broader diet breadth and are less susceptible to decline than longer-tongued species (Goulson, 2003a; Goulson *et al.*, 2005; Kleijn and Raemakers, 2008), apparently coping with agricultural intensification (Goulson *et al.*, 2008b), possibly due to the adaptability of their preferred forage plants (Kleijn and Raemakers, 2008). The bumble bee species in decline across Europe and North America tend to have narrower diet breadths and are particularly likely to be affected by agricultural intensification (Goulson, 2003a, 2003b). While their rarity does not necessarily make them effective pollinators for today's crops, conserving populations of rare species, and therefore diversity, is likely to be beneficial to common species, other wildlife and crop pollination services in general (Westerkamp and Gottsberger, 2000). This is because, in theory, a diverse community of pollinators is better equipped to buffer the effects of environmental changes than a simple community. If one or more important species become locally extinct within a diverse community, for example, other species are able to fill the vacated niche (Hooper *et al.*, 2005).

2.3.2 Bumble bee nutrition

Bumble bees may use different plants for different rewards (Ghazoul, 2006). Longer tongued than honey bees, they can visit flowers with deeper corolla tubes. Unlike honey bees, they are also effective both at "tripping" leguminous flowers such as lucerne and buzz pollination (vibration of flight muscles to eject pollen of certain species) of flowers and crops such as cranberry and blueberry (Delaplane and Mayer, 2000). Bumble bees select diverse foraging patches based on the ability to fulfil many resource requirements (Ghazoul, 2006). Worker bees, in particular, require protein from pollen to ensure ovary development (Duchateau, 1989), but also to form glandular secretions that they add to the food they deliver to larvae (Pereboom, 2000). Pollen deprivation experiments have shown that pollen deficits significantly increase mortality of worker bees (Smeets and Duchateau, 2003). Fertilized colony founding queens emerge in spring and require nutrition for brood production in the form of nectar and pollen, and are unlikely to have energy for long foraging bouts (Delaplane and Meyer, 2000, Cresswell *et al*., 2000), so will locate nests close to floral resources in grass tussocks or underground in existing holes (Proctor *et al*., 1996). Following colony foundation, worker offspring tend to be few early in the year, but increase as emerging workers bring additional resources enabling the queen to spend more time on egg-laying (Delaplane and Meyer, 2000). The success of the colony from its foundation to the production of workers and healthy new queens depends largely on the availability of good floral resources (Bowers, 1986). Food shortage, particularly in mid-summer, can reduce the probability of producing a successful queen for the subsequent season (Delaplane and Meyer, 2000).

2.3.3 Non-crop flowers and bumble bee conservation

In the United Kingdom alone, 76 percent of the 97 preferred forage plants of bumble bees have declined in the last 80 years (Carvell *et al*., 2006), a pattern reflected across Europe (Kleijn and Raemakers, 2008). Although many bumble bee species can take advantage of mass flowering crops such as oil seed rape (*Brassica napus* ssp. *Oleifera*) (Westphal *et al*., 2003), these resources are only temporarily available and may support only a small proportion of the species assemblage. For example, flowering crops are usually unavailable in the early spring when queens are attempting to establish colonies, or in late autumn when foraging is required to build winter food stores.

In much of Europe, the conversion of species-rich hay-meadows, the reduction of legume-rich set-aside land, the degradation of mid-successional vegetation in field margins, and the removal of hedgerows are all factors resulting from management changes associated with intensive agriculture that impact all *Bombus* spp. and their forage sources (Goulson *et al*., 2005; Pywell *et al*., 2005). In a study using pollen grains still attached to the corbiculae of museum specimens of European bees, Kleijn and Raemakers (2008) found that, prior to 1950, *Trifolium pratense* was the primary pollen species of five of the seven bee species considered, three that declined and two that had stable populations. Pollen of other abundant plant species associated with traditional land use types, such as heathland and legume-rich set-aside land, were also found in large numbers, but their importance decreased in bee specimens caught more recently. Plant species such as *T. repens*, a common feature of modern farmland, and invasive plants like

Impatiens glandulifera, had increased in importance, illustrating the potential breadth of diet of more common bee species. Crop pollen was not an important part of the diet of bumble bee species, indicating that if protein is to be obtained it should be provided by alternative sources. Members of the Fabaceae, *T. pratense* in particular, also provided the largest sources of pollen collected by bumble bees in the traditional mountain farming landscapes of southern Poland, where horse-drawn ploughs are still used (Goulson *et al.*, 2008b), supporting similar findings from a range of other European studies in more intensive settings (Teras, 1985; Fussell and Corbet, 1992; Carvell, 2002; Goulson and Darvill, 2004; Goulson and Hanley, 2004; Goulson *et al.*, 2005; Carvell *et al.*, 2006).

In Europe, agri-environment schemes that provide a mixture of annual and perennial grassland species have been well studied (Carreck and Williams, 2002; Meek *et al.*, 2002; Carvell *et al.*, 2004; Pywell *et al.*, 2005; Pywell *et al.*, 2006). For example, in the United Kingdom, the flora of arable land tends to comprise species that can tolerate modern agricultural operations, including the use of herbicides and fertilizers (Robinson and Sutherland, 2002). Such species include cleavers (*Galium aparine*), common knotweed (*Polygonum aviculare*) and twitch (*Alopecurus myosuroides*). These are also species that cannot be used for forage by bumble bees or butterflies (Pywell *et al.*, 2004). However, field margins sown with agricultural legume species (for food) and perennial grass species (for nesting) attract more bumble bee species and individuals than conservation headlands, consisting mainly of annual plants, and naturally generating field margins (Carvell *et al.*, 2007).

Carvell *et al.* (2006) argued for the inclusion of annuals such as *Borago officinalis* in wildflower mixes and stated that most species in both annual and perennial mixtures contribute little and can be replaced with suitable forage plants for long-tongued *Bombus* spp., such as *Centaurea cyanus* or *Vicia sativa*. Pywell *et al.* (2005) suggested that preferred forage species, such as *Trifolium pratense*, *Lotus corniculatus, Phacelia tanacetifolia* and *Borago officianalis*, should be included in sown mixtures, but also that species already present in many field margins such as *Viola arvensis* Murray should be maintained. Lye *et al.* (2009) suggested that early flowering plants such as *Lamium album, L. purpureum, Symphytum officinale, Silene dioica* and *Ulex europaeus* be encouraged close to potential nesting sites as spring queens have limited energy to forage far and wide (Cresswell *et al.*, 2000). The sowing of field margin mixtures can also help to suppress pernicious weed species such as *Cirsium arvense*, *C. vulgare* and *Sonchus arvensis* to a manageable level, although they are also favoured by bees (Pywell *et al.*, 2005).

Some farmers can also selectively target bumble bee species. For example, a farmer growing field beans will benefit from encouraging long-tongued bumble bee species like *B. pascuorum* and *B. hortorum* by planting field margins with white deadnettle (*Lamium album*), red clover (*Trifolium pratense*), woundworts (*Stachys* spp.), foxgloves (*Digitalis* spp.) and teasel (*Dipsacus* spp.). Such plants would encourage the target species without enhancing numbers of *B. terrestris*, which competes for nectar by robbing the flowers without coming into contact with the pollen of the crop (Fussell and Corbet, 1992). The alternative forage plants should be placed within 1000 m of the crop for *B. pascuorum* due to its relatively short foraging range (Knight *et al.*, 2009).

In North America, bumble bees are less well studied and declines are not thought to be as severe (Winfree, 2010). For the few species that are declining, parasite infection is thought to be a main driver (Evans *et al.*, 2008), although in some regions agricultural intensification is also considered an important factor (Grixti *et al.*, 2009). In the few North American studies that have considered using non-crop flowers as aids to the conservation of bumble bees, findings are specific to regions. For example, in a study of cranberry farms in Washington state, western USA, the most attractive plants for the important short-tongued species (*B. mixtus, B. occidentalis* and *B. sitkensis*) include *Agastache ruposa*, *A. foeniculum* and *Lotus corniculatus*, and for the long-tongued bumble bees (*B. caliginosus* and *B. californicus*), *Nepeta mussinii, Borago officinalis, Phacelia tanacetifolia* and *A. foeniculum* (Patten *et al.*, 1993). Alternatively, in blueberry crops in Michigan, eastern USA, the *Bombus* spp. were dominated by *B. impatiens*, which were attracted to *Silphium perforatum*, *Liatris aspera, Solidago speciosa, Lobelia siphilitica* and *Agastache nepitoides*. Such regional considerations are important in identifying the best mix of alternative forage species, and make generalization especially difficult for the majority of species groups (Tuell *et al.*, 2008).

2.4 THE IMPORTANCE OF NON-CROP FLOWERS TO STINGLESS BEES

2.4.1 General ecology of stingless bees

Stingless bees, also known as *Meliponines* (tribe: Meliponini), are social, honey-producing bees occurring mainly in tropical and sub-tropical regions (Heard, 1999; Freitas *et al.*, 2009). There are around 600 species in 56 genera worldwide (Cortopassi-Laurino *et al.*, 2006) with broad differences in colony size, body size and foraging strategy, although due to their tropical habitats they are able to forage year round and form perennial colonies (Slaa *et al.*, 2006). Despite their apparent importance to the pollination of 18 crop species, including coffee (Klein *et al.*, 2003a, 2003b), and their contribution to the pollination of a further 60, including avocado, sweet pepper, tomato, cucumber, macadamia and strawberry (Heard, 1999; Slaa *et al.*, 2006; Klein *et al.*, 2007), they remain understudied in many parts of the world (Freitas *et al.*, 2009), probably because they produce much less honey than *Apis* spp. and are therefore less economically appealing (Roubik, 2006). However, there is potential for stingless bees to act as an alternative to honey bees because they are generalists at the colony level, but exhibit flower constancy (repeated visits to the same plant species) at the individual level, which is thought to lead to more efficient pollination (Slaa *et al.*, 2006). They are also capable of buzz pollination, can be domesticated and commercially reared, and their diversity allows the selection of the most appropriate species for certain crops and plant-breeding systems (Cortopassi-Laurino *et al.*, 2006; Slaa *et al.*, 2006).

2.4.2. Stingless bee nutrition

Stingless bees are similar to honey bees in that they use both nectar and pollen. While pollen is often the sole resource collected and consumed by adults, nectar is also collected as an energy source and an adhesive for pollen transportation (Roubik, 1989), with individual bees using substantial amounts of stored nectar from the nest to provide energy for the foraging trip and to assist with pollen collection (Leonhardt *et al.*, 2007). Stingless worker bees also provide larvae with pollen and honey combined with glandular secretions, which is stored in cells prior to oviposition by the queen (Gilliam *et al.*, 1985). Stingless bees also collect resin, water, sap, wax, honeydew, extrafloral nectar, mud, salts, dead animal material and fungal spores for nutrition and the building of elaborate and varied nests (Roubik, 1989; Heard, 1999; Eltz *et al.*, 2001).

While it is not possible to generalize on plant preferences, Wille (1983) has suggested a preference for small flowers and other reports have identified dense inflorescences (Roubik and Moreno, 1990), trees (Wille, 1983; Kleinert-Giovannini and Imperatriz-Fonseca, 1987; Ramalho *et al.*, 1990) and white or yellow flowers (Cortopassi-Laurino and Gelli, 1991). Plants from the families *Myrtaceae, Melastomataceae, Solanaceae* and *Leguminosae* are important for all *Melipona* species, and the preferred species are mainly trees or shrubs (Ramalho *et al.*, 1990).

As with many other bee groups, stingless bees are affected by deforestation and agricultural intensification. These broad drivers have a significant impact on conservation, directly decreasing floral resources and nesting sites (Freitas *et al.*, 2009).

2.4.3 Non-crop flowers and stingless bee conservation

In terms of management, literature sources have highlighted the importance of proximity of primary or secondary forest to stingless bee nesting, and therefore pollination ability and crop yield (Heard and Exley, 1994; Ricketts *et al.*, 2004; Blanche *et al.* 2006; Brosi *et al.*, 2007; Brosi *et al.*, 2008). These studies have been conducted in relation to cropping systems involving macadamia (Heard, 1993), grapefruit (Chacoff and Aizen, 2006), tomato (Slaa *et al.*, 2006), chayote, longan and cupuassu (Heard, 1999), and coffee (Klein *et al.*, 2003a, 2003b). For example, in Argentina, 22 bee species from six families of bees were found to pollinate grapefruit crops, but the frequency of visits and diversity of visitors decreased with increasing distance from forest habitats (Chacoff and Aizen, 2006). The effect of deforestation on alternative forage plants is sometimes made explicit (e.g. Melendez *et al.*, 2004; Klein, 2009), although data have not yet been collected on the loss of specific floral species or conservation through floral resource management. The effect of deforestation is usually demonstrated in terms of the direct effects of logging on stingless bee nests (Eltz *et al.*, 2002; Cortopassi-Laurino *et al.*, 2006) or on suitable, unoccupied sites for nests (Villanueva-Gutierrez *et al.*, 2005). A review by Slaa *et al.* (2006) on the practicalities of stingless bee pollination services indicated that the main management measures for local farmers to increase bee diversity and abundance included preservation of forests and forest fragments and the reduction of agro-chemical use. This is because many stingless bees nest in tree cavities (Roubik, 1989).

Other studies have demonstrated and reported the absence of a relationship between stingless bee richness and abundance and blooming plant richness and abundance (Brown and Albrecht, 2001; Brosi, 2009, although see Brosi *et al.*, 2008). However, measuring floral resources in species-rich tropical forests is a daunting task (Brosi, 2009), which may in part explain the dearth of studies examining floral resource preferences. Some stingless bees are adapted to utilize mass-blooming tropical trees, because they adopt the recruitment foraging strategy whereby a small number of "scouts" locate resources and recruit large numbers of forager bees to aggressively monopolize intense tree blooms that may last only a few days (Brosi, 2009). This makes them important pollinators for crops such as coffee, which exhibit similar blooming periods (Ricketts *et al.*, 2004; Slaa *et al.*, 2006; Brosi *et al.*, 2008). A number of stingless bee species also forage individually like bumble bees, behaviour adapted to low-density, low-reward species (Johnson and Hubbell, 1975), and can exploit resources and nest sites in human-dominated habitats (Klein *et al*. 2002; Ricketts *et al.*, 2004; Brosi *et al.*, 2008). Such species are likely to be more prevalent in deforested areas and more important for crop pollination in disturbed habitats (Brosi, 2009). The same is true for facultative recruiter species, such as *Trigona fulviventris*, which have been observed in the field foraging as individuals, but can also recruit nest mates to high-density resources (Hubbell and Johnson, 1978; Slaa *et al.*, 2003).

The provision of additional forage plants is likely to help enhance the populations and longevity of certain stingless bees in similar ways to other bee species. For example, Melendez-Ramirez *et al*. (2004) suggested that while *A. mellifera* are effective pollinators in coconut plantations in Mexico, stingless bees do not contribute to pollination because the coconut monocultures do not provide a diverse range of flowering plants. The provision of additional sources of forage may help to ease the reliance on honey bees, but on the basis of current evidence such management may be ineffective without consideration of nesting habitat provision.

2.5 THE IMPORTANCE OF NON-CROP FLOWERS TO SOLITARY AND OTHER BEES

2.5.1 General ecology of solitary bees

Solitary bees construct nests and provide food for their own larvae without the help of other female bees; in contrast, social bees include worker females that provide food for the larvae of the queen (Michener, 2007). This section also deals briefly with the "primitively eusocial" bees, including sweat bees (*Halictinae*) and carpenter bees and related species (*Xylocopinae*), which may start out as solitary females until the emergence of daughters when colonial activities temporally begin (Michener, 2007). This crude definition merely scratches the surface of the many forms of sociality and solitary lifestyles in bees, and the interested reader should consult Michener (2007). Where reference is made below to "solitary bees", "wild bees" or "native bees", this often refers to solitary and primitively eusocial species.

Solitary bees occur in every region around the globe and visit a wide range of plants and crops (Wcislo and Cane, 1996; Freitas and Pereira, 2004; Klein *et al.*, 2007). Nest building may occur in the soil, in standing or rotting wood, in construction timbers or plant stems, in earth walls and sandstone, or even in cavities made by other insects (Michener, 1964; Roubik, 1989). Nests usually consist of a number of cells provisioned with pollen, nectar and oils onto which an egg is laid (Wcislo and Cane, 1996). Cells and nests can also be lined with a number of different chemical secretions that are thought to help to repel invasive and parasitic enemies (Wcislo and Cane, 1996).

While the scope of potential plant-bee interactions is huge, the importance and use of solitary bees as pollinators has only recently begun to gather pace. They are considered to be efficient or contributing pollinators of fruit tree crops (Abel and Wilson, 1998; Klein *et al.*, 2007), almonds (Bosch and Blas, 1994), coffee (Klein *et al.*, 2003a), watermelon (Kremen *et al.*, 2002; Njoroge *et al.*, 2004), tomato (Greenleaf and Kremen, 2006a), sunflower (Greenleaf and Kremen, 2006b), blueberry (Cane, 1997), canola (Morandin and Winston, 2005), eggplant (Gemmill-Herren *et al.*, 2008) and squash (Klein *et al.*, 2007). For some crops they can provide additional pollination services alongside honey bees, particularly during honey bee population fluctuations (Winfree *et al.*, 2008). However, it is increasingly recognized that solitary bees can be important pollinators in their own right, offering a potentially more effective alternative to honey bees (Bosch and Blas, 1994; Canto-Aguilar and Parra-Tabla, 2000; Kraemer and Favi, 2005; Bosch *et al.*, 2006) and can be managed commercially (e.g. *Osmia cornifrons*, Abel and Wilson, 1998; *Osmia cornuta*, Bosch and Blas, 1994; *Osmia lignaria*, Bosch *et al.*, 2006; and *Megachile rotundata*, O'Neill and O'Neill, 2011).

2.5.2 Solitary bee nutrition

While colonies of eusocial bees tend to be relatively long lived, making specialization difficult to maintain, most solitary bees have short adult flight seasons lasting a matter of weeks (Pitts-Singer and James, 2008), and can therefore afford to be floral specialists (Michener, 2007) or oligolectic (Wcislo and Cane, 1996). Polylecty does occur among solitary bees, but in the short term they are often constant visitors to particular plant species (Wcislo and Cane, 1996). These strategies can be beneficial to the plant species as they enhance the probability of the pollinator visiting another plant of the same species (Michener, 2007). As a result, it can be expected that the needs of solitary bees may not correspond precisely to crop flowering periods. However, the gregarious nesting nature of some solitary bees permits management strategies in agriculture through the provision of nest sites (Pitts-Singer and James, 2008), and even the production and installation of artificial nests (Delaplane and Mayer, 2000).

Both sexes exploit flowers for nectar, although in some species the female may have more specialized pollen requirements (Wcislo and Cane, 1996). Reproduction is significantly improved when bees feed on preferred floral species (Abel and Wilson, 1998). A lack of nectar in the diet can reduce the ability of *Osmia lignaria propincua* to provision nests with larval food and to attach eggs properly to the "pollen dough", affecting neonate eclosion (Torchio, 1985). Resource shortage and/or competition for resources can also lead to longer foraging trips or less time spent in the nest, which can increase the probability of parasitic attack on the nest (Goodell, 2003). Solitary species can be formidable collectors: a female *Megachile parietina* requires the entire pollen content of 1 139 individual flowers of the preferred species *Onobrychis viciifolia* (4.3 plants) to rear a single offspring (Müller *et al.*, 2006) – a factor that may have contributed to the decline of the bee in central Europe (Amiet *et al.*, 2004).

2.5.3 Non-crop flowers and solitary bee conservation

Overall, the resource requirements of many solitary bee species are poorly understood (Kremen *et al.*, 2002; Watson *et al.*, 2011). There is a body of research that seeks to identify candidate solitary bee species as additional or alternative manageable pollinators to honey bees (Bosch and Blas, 1994; Canto-Aguilar and Parra-Tabla, 2000; Vicens and Bosch, 2000; Shuler *et al.*, 2005; Bosch *et al.*, 2006; Gruber *et al.*, 2011). However, frameworks for developing solitary bees for commercial pollination services do not often consider alternative forage as an important factor in their management (Bosch and Kemp, 2002; Gruber *et al.*, 2011). Despite this, there is empirical evidence highlighting the impact of alternative forage. For example, Gruber *et al.* (2011) found a relationship between the occurrence of *Osmia* spp. and the amount of fallow land and small settlements with diverse flowering gardens surrounding apple orchards. Cover of other orchard tree species was also an important factor in the number of brood cells produced, which the authors suggested was probably due to this alternative forage (Gruber *et al.*, 2011). This is supported by other studies. In Canada, the use of big-leaf lupine (*Lupinus polyphyllus*) as an alternative forage plant within 600 m of orchards improves population recovery rates of *Osmia lignaria* (Sheffield *et al.*, 2008). In northern Utah, USA, the establishment of *O. lignaria* females in artificial nests was thought to be enhanced by the presence of orchard tree species, such as apricot and plum trees, blooming earlier than the target cherry and peach trees (Bosch *et al.*, 2006). While in Virginia, USA, the bee fed on wild radish, members of the *Brassicaeae* family and winter honeysuckle when orchard species were not in bloom (Kraemer and Favi, 2005).

Megachile rotundata, the alfalfa leafcutting bee, can be used domestically through the provision of artificial and moveable nest shelters within alfalfa fields (O'Neill *et al.*, 2004). Additionally, they can be used for carrot (Tepedino and Parker, 1988), blueberry (Stubbs and Drummond, 1997) and canola (Holm *et al.*, 1985). The main concern with this system, however, is that the bee may be preferentially attracted away from alfalfa by other species such as white sweetclover (*Melilotus alba*), purple loosestrife (*Lythrum salicaria*), crown vetch (*Coronilla varia*), bird's foot trefoil (*Lotus corniculatus*) and members of the *Rosaceae* family (Stubbs *et al.*, 1994; Horne, 1995; O'Neill *et al.*, 2004). While this preference may in part result from the decline in untripped alfalfa flowers during the course of the season (O'Neill and O'Neill, 2011), farmers are advised to move nests to closely track the blooming of the main crop (MacKenzie *et al.*, 1997). However, other studies have shown that the proximity of alfalfa fields to sources of alternative forage actually increased visitation to alfalfa due to "spill-over" of pollinators at certain scales (Brookes *et al.*, 1994), and has been demonstrated for other solitary bee species (Winfree *et al.*, 2008).

The importance of diversity – often due to the presence of solitary bee species – to attenuate temporal fluctuation in pollinator abundance has been shown in studies of watermelon (Kremen, *et al,* 2002), coffee (Klein *et al.*, 2003b) and orchard crops (Tepedino *et al.*, 2007). In turn, the diversity of wild bees visiting crops has been shown to be improved by the abundance of "weedy" flowers in farm fields in vegetable crops in Pennsylvania and New Jersey, USA, with the majority of species being those with longer flight seasons and therefore requiring floral resources after the blooming of the crop (Winfree *et al.*, 2008).

The conservation of solitary bees on agricultural land often requires suitable nesting sites due to a short dispersal range (Bosch and Kemp, 2002; Gathmann and Tscharntke, 2002) and, in some cases, the targeting of the right species for the crop grown so that the phenology of the crop and insects are matched (see Westerkamp and Gottsberger, 2000). For example, while "buzz pollination" of species such as *Xylocopa cafra* and *Macronomia rufipes* leads to more effective pollination of crops like aubergine (*Solanum melongena*), these bees rely on other flowers for nectar sources as *S. melongena* produces only pollen (Free, 1993). In a study in Kenya, the distance of the crops to the nearest riverine *Acacia tortilis* forest was important to visitation levels, and native non-crop flowering species played an important role for the wild bee community, particularly the flowers of *Commicarpus helenae*, *Justica flava* and *Duospermum kilimandscharium*, located alongside farm paths (Gemmill-Herren and Ochieng, 2008). Elsewhere, pollinators sought out flowers such as *Leucas massaiensis* in nearby grassy sward habitats, while *A. tortilis*, located within forests, also provided forage at the start of the rainy season (Gemmill-Herren and Ochieng, 2008). The continuous and relatively dense cover of floral resources in most months throughout farmland ensures pollinator visitation to crop plants, and the local forest provides important shade and refuge during the hot, dry season when floral resources became scarce (Gemmill-Herren and Ochieng, 2008). The importance of floral resources and natural habitat remnants has been repeatedly found in studies of other species (e.g. Franzén and Nilsson, 2004, 2008; Carvalheirho *et al.*, 2010).

The proximity of natural habitats to crops and the heterogeneity of the landscape appear to be particularly important for solitary bee diversity and abundance in farmland. Relationships between bee abundance and local natural habitats have been reported among watermelon (Kremen *et al.*, 2002; Winfree *et al.*, 2007b), tomatoes (Greenleaf and Kremen, 2006a), apples (Watson *et al.*, 2011), blueberries (Tuell *et al.*, 2009), cranberries (Ratti *et al.*, 2008), pumpkins (Julier and Roulston, 2009) and sunflowers (Greenleaf and Kremen, 2006b), although some species are also associated with more disturbed areas (Klein *et al.*, 2002; Westphal *et al.*, 2003; Winfree *et al.*, 2007b). Isolation of the nest site of *Osmia lignaria* from semi-natural habitat decreased both nest establishment and offspring reproduction (Williams and Kremen, 2007). While pollen was collected from a range of habitat types, four native plant species groups (*Cercis occidentalism*, *Salix* spp., *Quercus lobata* and *Lupinus* spp.) from semi-natural areas formed the majority of collected resources in a farmland mosaic, although at more isolated farms, pollen from plum (*Prunus domesticus*) and strawberry (*Fragaria ananassa*), and pollen from plants in restored farmland habitats such as hedgerows was important. The cover of natural habitat in the landscape may also play an important role (Kremen *et al.*, 2004). For example, total deciduous forest area within 2 km of apple orchards significantly affects spring active solitary bee abundance (Watson *et al.*, 2011). In general, a mix of natural habitats and diverse field margins are likely to be optimal for a diverse community of solitary and other wild bees (Watson *et al.*, 2011).

2.6 THE IMPORTANCE OF NON-CROP FLOWERS TO HOVERFLIES

2.6.1 General ecology of hoverflies

There are nearly 6 000 species of hoverfly worldwide, but the only hoverflies considered by Klein *et al.* (2007) to provide an important service to crops are *Eristalis cerealis* and *E. tenax*, two closely related and common non-aphidophagous species that lay eggs in liquefied manure or stagnant water (Bugg, 1994). They are active throughout most of the year (Irvin *et al.*, 1999) and provide pollination services to apples, pears, strawberry, *Rosa* spp., *Rubus* spp., canola/oil seed rape (Klein *et al.*, 2007) and greenhouse sweet pepper (Jarlan *et al.*, 1997a, 1997b). Despite this, hoverflies and Diptera in general are considered to be a group that have been relatively poorly investigated as pollinators (Kearns, 2001; Larson *et al.*, 2001), despite suggestions that they are pollinators or regular visitors of over 500 species of flowering plant (Larson *et al.*, 2001), including over 100 crop plants (Kearns, 2001). Jauker and Wolters (2008) found that *Episyrphus balteaus* increased seed set and yield of oil seed rape in caged environments. This species may also provide a biological control service as the larvae are aphidophagous (Hickman and Wratten, 1996). In Himachal Pradesh, India, *Episyrphus* sp., and the group of syrphid flies visiting apples have been shown to have multiple benefits, in addition to being highly effective apple pollinators (Gupta, 2013). Their aphid-eating larvae may be important for the control of aphids on fruit trees (Sharma, 2001), and the adults may also pollinate other crops, such as cauliflower, for seed production (Kapatia, 1987). Hoverflies may be more effective pollinators in landscapes that may lack aspects of landscape structure and distance to semi-natural habitat favourable for a diversity of bee species (Jauker *et al.*, 2009).

2.6.2 Hoverfly nutrition

Hoverflies feed on nectar and pollen and/or aphid honeydew, which provide carbohydrates and sugars required for high-energy hovering flight, and pollen, which provides essential protein for sexual maturation and egg development (Schneider, 1948; Chambers *et al.*, 1986). Species may vary on the mixture of these substances taken; however, *E. balteatus* is principally a pollen feeder, *E. tenax* tends to feed more on nectar and some species take an equal mixture of the two (e.g. *Playcheirus albimanus*) (Gilbert, 1981). There is also a correlation between tongue length and flower visited for nectar, with long-tongued species (e.g. *E. tenax*) favouring *Melilotus* spp., *Trifolium* spp., *Stachys* spp., *Armeria* spp., *Knautia arvensis*, *Centaurea* spp. and *Cirsium* spp. (Gilbert, 1981). Generally, though, most hoverfly species are considered to be generalist pollinators (Gilbert, 1981; Branquart and Hemptinne, 2000), and recent evidence suggests this is true of *E. tenax*. Irvin *et al.* (1999) showed that in New Zealand, *E. tenax* consumed 15 different pollen species belonging to a wide range of plant families throughout the year. Seasonal availability of pollen was important to the hoverfly, with winter and spring flowering *Salix*, *Erica* and *Pinus* spp. being consumed, although interestingly, the hoverfly avoided *P. tanacetifolia*, a plant species attractive to many aphidophagous species (Lovei *et al.*, 1993; White *et al.*, 1995; Hickman and Wratten, 1996).

2.6.3 Non-crop flowers and hoverfly conservation

Hoverflies appear to be less affected by many aspects of land use than other pollinators. Biesmeijer *et al.* (2006) reported that hoverfly populations experienced only localized declines in the Netherlands and the United Kingdom. Inconsistent findings have also been reported on the effect of landscape on hoverflies. Species richness did not differ with distance from semi-natural habitat in an agricultural matrix in central Hesse, Germany (Jauker *et al.*, 2009), and Australia (Arthur *et al.*, 2010), but did so in the Netherlands (Kleijn and van Langevelde, 2006) and in Lower Saxony, Germany (Meyer *et al.*, 2009). Flower abundance is sometimes (Meyer *et al.*, 2009), but not always positively associated with hoverfly diversity (Hegland and Boeke, 2006; Arthur *et al.*, 2010), despite clear evidence that flowering weeds and sown floral strips are attractive to hoverflies (Schneider 1948; Gilbert, 1981; Frank, 1999; Bianchi *et al.*, 2006; Haenke *et al.*, 2009). However, diverse landscapes are likely to provide for the ecological needs of hoverflies (Rader *et al.*, 2009; Arthur *et al.*, 2010). The aphidophagous species *E. balteatus* uses forest habitats as hibernation sites (Salveter, 1998) and *E. tenax* may feed and reproduce during autumn and winter, where the pollen of *Salix*, *Erica* and *Pinus* may be consumed and when stagnant water is available for egg-laying (Irvin *et al.*, 1999). A range of habitats is therefore likely to be important to maintaining populations of this species throughout the year (Meyer *et al.*, 2009).

Nevertheless, studies have considered alternative forage for *E. tenax*. In a Swiss arable landscape, this species was abundant in weed strips and oil seed rape fields, while aphidophagous hoverflies were more evenly distributed among crops in which aphids could be found (Frank, 1999). The most attractive plants were considered to be *Tripleurospermum inodorum*, *Daucus carota* and *Anthemis tintoria*. Frund *et al.* (2010) also noted a preference of *E. tenax* on *Leontodon autumnalis*, and in comparisons of different insectary plants, *Eristalis* spp. visited coriander flowers more frequently than buckwheat or phacelia (Ambrosino *et al.*, 2006). In general, however, the accessibility of diverse habitat types is essential for hoverflies to meet the nutritional and overwintering needs of adults and larvae. These needs are highly diverse for many species, and may be lacking in monocultural agricultural landscapes (Meyer *et al.*, 2009), even for those associated with crop pests because suitable adult feeding habitats become the limiting factor (Jervis and Heimpel, 1996).

2.7 OTHER IMPORTANT FACTORS OF POLLINATOR CONSERVATION

As highlighted in a number of the examples above, providing alternative forage for many pollinators is not always simply a case of increasing floral resources. Many arable “weed” species that proliferate under conventional agriculture are annual and self-compatible and are unlikely to present considerable rewards to insect pollinators, whereas those more abundant under organic management are adapted to insect pollination and thus can be expected to provide resources for pollinators (Gabriel and Tscharntke, 2007). Similarly, some alien wildflowers may not be present within the range of their co-evolved pollinators, limiting their usefulness to native pollinator species (Corbet *et al.*, 2001). This is particularly true of many garden ornamentals that often do not produce nectar (Comba *et al.*, 1999; Corbet *et al.*, 2001), but is unlikely for aliens with similar floral morphologies to natives (Bjerknes *et al.*, 2007; Morales and Traveset, 2009). A range of other considerations should be taken into account when attempting to match target pollinators to crops via weed or non-crop floral resource provision. Certain flowers may be toxic or unrewarding to some important species, for example, some Asteraceae to *Bombus* (Praz *et al.*, 2008), *Cucumis* spp. and coriander to *Osmia cornifrons* (Abel and Wilson, 1998).

Therefore, a thorough ecological understanding of the pollination system is recommended for each cropping scenario in different regions. Only when clear information of the most efficient pollinators, their resource requirements (Greenleaf and Kremen, 2006a), foraging range and behaviour (Knight *et al.*, 2009), and phenology is available, can pollinators be effectively matched to crops via conservation measures.

It is also important to note that food resources are just one factor of any animal's essential requirements. In a number of the examples above where wild bees are the main pollinators, researchers have pointed out the importance of landscape heterogeneity (Hagen and Kraemer, 2010), the proximity of natural habitat (Greenleaf and Kremen, 2006a; Heard *et al*., 2007; Knight *et al*., 2009), and the presence of abundant nesting sites and nest-making materials (Potts *et al*., 2005). Hoverflies are also unlikely to occur in large numbers where there is an absence of larval food resources (Schweiger *et al*., 2007), or where there are barriers to movement (Wratten *et al*., 2003). Similarly, a number of studies have argued that the reliance on a single pollinating species is unlikely to be as efficient or effective as maintaining a diverse community of pollinators. Although intensive agriculture will rely on commercially available pollinators, the dependence on and intensive management of honey bees has led to the development of density-dependent pathogens that are thought to contribute to the current Colony Collapse Disorder problems. Conversely, functional guilds of pollinating species can increase the yield of pollinator-dependent crops and facilitate the movement of honey bees (e.g. Kremen *et al*., 2004; Greenleaf and Kremen, 2006b; Winfree *et al*., 2008; Carvalheiro *et al*., 2011).

There has been much focus in recent literature on conserving pollinator communities, with a number of studies taking a food web approach to the issue through pollinator networks. For example, Memmott (1999) highlighted the interconnectivity of many pollinator interactions and demonstrated that specialization is more likely to be the exception than the rule. In parallel to food web theory, if an important pollinator species is removed from a network, plant biodiversity decline can follow (Memmott *et al*., 2004; Larsen *et al*., 2005; Pauw, 2007), although such networks are likely to be relatively tolerant to extinction (Memmott *et al*., 2004). Work elsewhere along this theme has been used to demonstrate the tight linkage between pollinator and plant communities and levels of specialization, to improve the understanding of species coexistence and to evaluate the degree of vulnerability to extinction of certain communities or sections of communities (e.g. Frund *et al*., 2010). While high levels of specialization are unlikely to occur in agricultural ecosystems, such work also serves to highlight the importance of floral diversity to pollinator communities.

The clear importance of the community in crop and wildflower pollination has led to the application of recommendations often put forward for many other aspects of biodiversity. The fragmented nature of many current agricultural ecosystems and the isolation of semi-natural habitats is a much-quoted driver in the decline of a large number of species in the wider countryside, particularly in Western countries. The enhancement of land use heterogeneity on a number of scales is likely to be beneficial to pollinator communities in that a variety of nesting and foraging niches (Kells and Goulson, 2003; Fenster *et al*., 2004; Lye *et al*., 2009; Murray *et al*., 2009) and aids to movement, such as hedgerows, green lanes, improved road verges and floral strips (Kleijn and van Langevelde, 2006; Marshall and Moonen, 2002; Moonen and Marshall, 2001), are provided. In diverse landscapes, these resources are also likely to be closer to crops, enhancing pollinator populations and diversity (Steffan-Dewenter *et al.*, 2002; Heard *et al.*, 2007; Knight *et al.*, 2009) and flower visitation. This is particularly important for those species with short foraging ranges, and central range foragers such as bees where the location of the nest and the forage range determines the availability of floral resources (Murray *et al.*, 2009). In the long term, a multi-functional agricultural landscape is the aim of such recommendations, although much research is still required to ensure that the right kind of biodiversity is encouraged without enhancing the spread of weeds and animal pest species. In the shorter term, enhancement of pollinator populations and communities is likely to be possible through the targeting of adult and larval food resources and nesting resources. However, much research is also required on which resources to improve. While the information presented here is likely to aid many cropping systems, researchers, outreach workers and farmers themselves are encouraged to investigate pollinator food preferences throughout the growing season in their own biogeographic regions, so as to identify important species and their foraging ranges and to share this knowledge widely. It will then be possible to design appropriate strategies for conservation (Knight *et al.*, 2009).

3

ECOLOGICAL INTERACTIONS AMONG CROPS, WEEDS AND BENEFICIAL INSECTS

An Amegilla bee foraging on cleome flowers in Tarangire, Tanzania.

3.1 WEED VEGETATION MANAGEMENT AS A TOOL TO ENHANCE POLLINATION SERVICES

Among the many threats that agriculture poses to pollinators (changes in land use, loss and fragmentation of habitat, introduction of exotic organisms, modern agricultural practices, pesticide use, etc.), removal of weeds that provide forage for pollinators has been suggested as an important factor in the decline of native pollinators in agroecosystems (Richards, 2001; Steffan-Dewenter *et al.*, 2005). A pioneering study by Benedek (1972) was among the first to report a dramatic change in the structure of Alfalfa leafcutter wild bee populations between the 1950s and 1960s, linked with a rapid increase in field size and the increased use of mechanical weed control along the field’s road sides associated with enhanced use of herbicides within crop fields.

Because of the ecological link between plant resources and insect biology, entomologists have long noted the positive role of weeds in enhancing beneficial insect survivorship in crop ecosystems (van Emden, 1963; 1965). For more than 45 years, biological control practitioners have been aware that the manipulation of specific weed species and/or the use of a particular weed control practice in a cropping system can affect the ecology of insect pests and associated natural enemies (Altieri *et al.*, 1977; Altieri and Whitcomb, 1979a; Thresh, 1981; William, 1981; Norris, 1982). These studies helped establish the foundations for strategies to manipulate natural enemies via weed management (Altieri *et al.*, 1977; Altieri and Whitcomb, 1979a).

Despite the fact that pollinators share similar habitat and resource requirements provided by flowers as arthropod natural enemies, very few studies have explored the potential to utilize weed vegetation management as a tool to enhance pollinator diversity and abundance in agroecosystems. In an attempt to fill this gap in knowledge, this section explores the multiple interactions among crops, weeds and insect pollinators and, in particular, examines how weed ecology and management can affect the dynamics of insect pollinators as well as natural enemies, and hence benefit both crop health and yields. A challenging task addressed here is to define a habitat management strategy in which weed manipulation plays a key role in enhancing key pollinator and natural enemy species, thus simultaneously achieving pollination and biological control services, while not detracting from crop production.

In this section it is suggested that the “pollination crisis” manifested as declines of honey bees and native bees may be ameliorated by changes in agricultural practices that restore habitats for beneficial arthropods (pollinators and natural enemies) by properly managing weeds within and around cropping systems.

3.2 WEEDS AS HABITATS FOR POLLINATORS

3.2.1 Ecological interactions between weeds and beneficial insects

Agricultural intensification has led to a more homogenous landscape characterized by large crop fields and fewer non-cultivated habitats. In this context, many weed species within and around fields offer many important requisites for beneficial insects, such as pollen or nectar, as well as microhabitats that are not available in weed-free monocultures (Landis *et al.*, 2005). In the case of natural enemies, weeds also provide alternative prey/hosts; this is important because many insect pests are not continuously present in annual crops, and their predators and parasitoids must survive during their absence (Altieri and Letourneau, 1982). Non-crop forage plants, often regarded as weeds, are of significant value to pollinators and farmers. In situations where such alternative forage, which would normally be available before, during or after the bloom of the crop, has been eliminated or reduced in abundance, the natural assemblages of pollinators suffer (Kearns and Inouye, 1997).

Weeds usually provide alternative food resources (e.g. pollen or nectar and alternate prey/ host) thus aiding in the survival of viable populations of pollinators and natural enemies. The beneficial entomofauna associated with weeds has been surveyed for many species, including the perennial stinging nettle (*Urtica dioica*), Mexican tea (*Chenopodium ambrosioides*), camphorweed (*Heterotheca subaxillaris*) and a number of ragweed species (Altieri and Nicholls, 2004). Perhaps the most exhaustive study of the fauna associated with various weeds is the work of Nentwig (1998) in Berne, Switzerland, where they monitored the insects associated with 80 plant species sown as monocultures in a total of 360 plots. According to this survey, weed species are insect habitats of widely differing quality. Plants such as chervil (*Anthriscus cerefolium*), comfrey (*Symphytum officinale*) and gallant soldier (*Galinsoga ciliata*) have extremely low arthropod populations of less than 15 individuals/m^2, whereas most plants have 100–300 arthropods/m^2 according to the D-vac sampling method used by these researchers. Five hundred or more arthropods were found per square metre on poppy (*Papaver rhoeas*) and tansy (*Tanacetum vulgare*), and the crops rape (*Brassica napus*) and buckwheat (*Fagopyrum esculentum*), which may grow adventitiously in areas previously sown to these plants. Considering the trophic structure of the arthropod communities, results were even more striking. Of all arthropods, phytophagous insects constituted about 65 percent of the species (most values between 45 percent and 80 percent) but the composition of the remaining arthropods varied greatly among pollinators, predators and parasitoids. In the former USSR, Naumkin (1992) found 83 species of insect pollinators from five orders associated with buckwheat. The various orders included Hymenoptera (32 species), Diptera and Coleoptera (30 and 11 species, respectively) and Lepidoptera and Neuroptera (with 7 and 3 species, each). The main family groups included *Syrphidae* (19 species), *Bombinae* (15), *Apoidea* (13), *Coccinellidae* (16), *Stratiomyidae*, *Vespidae* and *Chrysopidae* with 3 to 4 species each.

It is well known that Hymenopteran parasitoids require food in the form of pollen and nectar to ensure effective reproduction and longevity. Van Emden (1965) demonstrated that certain Ichneumonidae, such as *Mesochorus* spp., must feed on nectar for egg maturation, and Leius (1967) reported that carbohydrates from the nectar of certain *Unbelliferae* are essential for normal fecundity and longevity in three Ichneumonid species. In studies of the parasitoids of the European pine shoot moth, *Rhyacionia buoliana*, Syme (1975) showed that fecundity and longevity of the wasps *Exeristes comstockii* and *Hyssopus thymus* significantly increased with the presence of several flowering weeds.

Wildflowers such as *Brassica kaber*, *Barbarea vulgaris* and wild carrot (*Daucus carota*) provided nectar flowers to female parasitoids of *Diadema insulare*, an ichneumonid parasitoid of the diamondback moth in North America (Idris and Grafius, 1995). An increased fecundity and longevity of the wasp was correlated with flower corolla opening diameter and shading provided to the parasitoid by the plants. Because of its long flowering period over the summer, *Phacelia tanacetifolia* has been used as a pollen source to enhance Syrphid fly populations in cereal fields in the United Kingdom (Wratten and van Emden, 1995).

Spectacular parasitism increase has been observed in annual crops and orchards with a rich undergrowth of wild flowers. In studies in Ontario, Canada (Leius, 1967), parasitism of tent caterpillar eggs and larvae and codling moth larvae was 18 times greater in apple orchards with floral undergrowth than in those with sparse floral undergrowth.

Soviet researchers at the Tashkent Laboratory in present-day Uzbekistan (Telenga, 1958) cited lack of adult food supply in deciduous fruit orchards as a reason for the inability of *Aphytis proclia* to control its host, the San Jose scale (*Quadraspidiotus perniciosus*). The effectiveness of the parasitoid improved as a result of planting a *Phacelia* sp. cover crop in the orchards. Three successive plantings of *Phacelia* increased scale parasitization from 5 percent in clean cultivated orchards to 75 percent where these nectar producing plants were grown. Russian researchers also noted that *Apanteles glomeratus*, a parasite of two cabbage worm species (*Pieris* spp.) on crucifer crops, obtained nectar from wild mustard flowers. The parasites lived longer and laid more eggs when these weeds were present. When quick-flowering mustards were planted in the fields with Cole crops, parasitization of the host increased from 10 percent to 60 percent (Telenga, 1958).

3.2.2 Pollinators and flowering weeds

Although the above studies report on dependence on flowers specifically by a number of Hymenoptera parasitoids of pests, this dependency is a universal phenomenon among a great variety of pollinators (Kevan, 1983).

Most Lepidoptera feed extensively on floral nectar as adults. Butterflies are frequent diurnal visitors to flowers. The flowers they visit are often brightly coloured, may or may not be strongly scented, and have long tubular corollas that are frequently equipped with extended petal lobes forming a landing platform (e.g. *Phlox*, *Primula*). A platform is also provided by the capitulum in *Compositae* (Free, 1993). Butterflies generally land to feed on flowers that have proboscis guides or other structures designed to ensure that the proboscis touches the sexual parts of the flower so that pollination may be effected (Shepherd *et al.*, 2003).

Adult Hymenoptera are the most important order of anthophiles among which the Apoidea are most prevalent. Flowers that appear particularly attractive to Apoidea often have zygomorphic flowers, that is, bilaterally symmetrical flowers with hidden rewards (usually nectar or pollen). But many plant families with readily available resources are also well-frequented by Apoidea such as those that produce simple bowl-shaped flowers, like buttercups, and others that produce fluffy flower heads of massed florets. These broad flower types are the basis of pollination syndromes – the flowers have converged on certain morphologies and reward patterns because they exploit the abilities and preferences of particular kinds of visitors (Willmer, 2011). The provision of nectar is in accord with the energy needs of the pollinator visitors. Thus, the flowers influence the extent of interfloral movements by their visitors (Kraemer and Favi, 2005). A delicate balance is maintained: a visitor must not become satiated before making the required number of visits that will ensure the amount of pollination necessary for the plant's reproduction; yet it must receive sufficient reward to maintain its interest in visitation. The effectiveness of pollination is determined by floral structure, nectar volume, concentration and constituents, as well as the distribution of nectar among flowers, resource partitioning among visitors, and intraspesific competition. Anthophilous insects are finely attuned to their habitat in vision, olfaction and taste, tactile sense and appreciation of time (Goulson, 2003).

The colour of flowers is key to the attraction of pollinators, as bees locate potential floral hosts from a distance by the saturated colours of blossoms against the green foliage background, and are aided by scents as they get closer (Shepherd *et al.*, 2003). Dipteran pollinators seem most attracted to blues and purples and blind to red, whereas beetles, butterflies and moths are attracted to all colours (Ellis, 1995). Although nocturnal moths may locate flowers by their fragrances, they seem to prefer white, cream or pale green night-blooming plants. Colouring patterns of radiating lines in concentric circles on the petals direct the insect to the nectar after it has landed. The nectar guides on some flowers are ultraviolet. Bees do not see red but see ultraviolet (UV), which is invisible to human vision (Kevan, 1983). Guldberg and Atsatt (1975) reported the UV reflectance of 300 flower species looking for patterns found in UV. They found a positive patterning with flower size, and an increase in such patterns in yellow and purple flowers.

3.3 EFFECTS OF AGRICULTURAL PRACTICES ON WILD POLLINATORS

Natural pollination systems are characterized by broad flower types that exhibit particular reward patterns to attract certain kinds of pollinators. Different kinds of flowers of varying phenologies attract different visitors cementing the mutualisms and, by implication, tending to make flowers increasingly specialist and visitors more and more selective (Willmer, 2011). Such co-evolutionary processes have been interrupted in modern agroecosystems dominated by a uniformity of flowers with similar sizes, shapes and colours. These flowers usually bloom massively in synchronous periods only lasting a few weeks so that peak numbers of pollinators are needed during a short time. The floral diversity formerly provided by hedges, weed patches, field margins and uncultivated land that could sustain abundant and diverse pollinator assemblages to cover such periods have often been eliminated in intensive agricultural systems.

Several features associated with modern agriculture make farms poor habitats for wild bees and other pollinators, and many agricultural practices impact directly or indirectly on pollinator populations (Kremen *et al.*, 2002). Agricultural intensification has led to a more homogeneous landscape characterized by large weed-free fields and fewer uncultivated habitats. Habitat loss and degradation, for example, loss of complex landscape structures between farmland and adjacent ecosystems, as well as the increased use of agrochemicals, have been linked to the reduction in beneficial arthropod species richness in agricultural landscapes (Kevan, 1999).

3.3.1. Vegetational simplification of agroecosystems

Crop monocultures sacrifice floral diversity and consequently the diversity of pollinating insects over large areas. A large body of research shows that cultivated fields surrounded by simple habitats (i.e. other monocultures) have significantly fewer bees than crops surrounded by uncultivated land; moreover, the number of bumble bees on crops increases with proximity to natural habitats (Ockinger and Smith, 2007). The conversion of land to agriculture results in a net loss of wild vegetation to support pollinators, reducing nesting sites and less-varied microhabitats for egg-laying and larval development. In this regard the loss of hedgerow habitats, which provide floral resources and nesting sites for wild bees at the margins of cultivated fields, is an undesirable trend associated with industrial agriculture (New, 2005).

Several entomologists and ecologists have suggested that isolation from the critical floral and nesting resources present in wild lands is likely to be the key factor explaining the decline in abundance and diversity of native bees in crop fields, and attendant loss of pollination services. Research in California showed that both native bee diversity and abundance are significantly related to the proportional area of wild habitat surrounding the farm (Kremen *et al.*, 2004). These researchers documented the individual species and aggregate community contributions of native bees to crop pollination on farms that varied both in their proximity to natural habitat and management type (organic *versus* conventional). On organic farms near natural habitat, they found that native bee communities could provide full pollination services, even for a crop with heavy pollination requirements (e.g. watermelon, *Citrullus lanatus*), without the intervention of managed honey bees. Conventional farms isolated from wild vegetation experienced greatly reduced diversity and abundance of native bees, resulting in insufficient pollination services from native bees alone.

However, when agricultural environments are considered alongside natural areas, recent studies have shown that pollinator density and diversity can actually increase across a gradient from natural forests to cultivated areas. Low-intensity diverse farming systems may provide abundant floral resources for pollinator species, if the matrix in which they occur is only moderately disturbed (Gikungu, 2006; Winfree *et al.*, 2007a)

3.3.2 The influence of adjacent habitats

Semi-natural land is thought to be important for bumble bees in agricultural landscapes. Canadian canola fields with semi-natural pastureland within 800 m of field edges had more bumble bees than fields completely surrounded by tilled cropland (Morandin *et al.*, 2007). Similarly, bee abundance was greatest in canola fields that had more uncultivated land within 750 m of field edges, and seed set was greater in fields with higher bee abundance. A cost–benefit model that estimates profit in canola agroecosystems with different proportions of uncultivated land was developed, in which it was shown that yield and profit could be maximized with 30 percent of land uncultivated within 750 m of field edges (Morandin and Winston, 2006). The economic and yield implications of maintaining uncultivated land to enhance pollinator services is discussed in the costs–benefits section (Chapter 6).

A study of the pollinator entomofauna associated with orchards and surrounding areas in the Okanagan Valley of British Columbia revealed the key role of flowering weedy vegetation adjacent to crop fields in harboring pollinators. The highest capture rates of wild bees came from flowers in uncultivated areas near orchards (ranging from approximately 10.4 to 17.5 bees/hour). These rates were much higher than those recorded within orchards (2.5 to 5.8 bees/hour). The lowest values were obtained in orchards far from uncultivated areas (Scott-Dupree and Winston, 1987).

Similarly in the Lower Fraser Valley of British Columbia, researchers found that both abundance and diversity of pollinators were lower on the crop plants (blueberry, raspberry, etc.) than on the surrounding native vegetation, with Shannon–Wiener Indices[2] in the natural areas ranging from 1.18 to 0.61 *versus* 0.75 to 0.29 on the crops (Mackenzie and Winston, 1984).

In Finland, bumble bee species richness and total density were higher in patches of farmland where field margins (1.5–2.5 m in width) had more dicotyledonous flowers rather than being grassy. Abundance and flowering phenology of a limited number of flower species during the bumble bee breeding season were the most important factors explaining bumble bee visits in field margins. The most important flower species was zigzag clover (*Trifolium medium*). The width of field margins was significantly related to the total density of bumble bees and cuckoo bumble bees (Backman and Tiainen, 2002).

Results from a study with sunflowers in South Africa show that if farmers allow ruderal plants to coexist with pollinator-dependent crops, diverse flower visitors are able to persist in isolated areas of cultivation areas, benefiting production. Such benefits maximize the positive effects of the remaining patches of natural habitat. As ruderal plants did not compete with sunflower for soil resources or reduce plantation area, this practice brought no added costs to farmers, even reducing herbicide application costs (Lagerlof *et al.*, 1992). In a more recent study (Carvalheiro *et al.*, 2011) conducted in South Africa on sunflower plots, researchers combined pollinator exclusion experiments with analysis of honey bee behaviour and flower-visitation webs. They found that the presence of weeds allowed pollinators to persist within sunflower fields, maximizing the benefits of the remaining patches of natural habitat to productivity of this large-scale crop. Weed diversity increased flower visitor diversity, hence ameliorating the measured negative effects of isolation from natural habitat. Although honey bees were

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[2] The Shannon-Wiener Index is one of several diversity indices used to measure diversity in categorical data. This measurement takes into account subspecies richness and proportion of each subspecies within a zone.

the most abundant visitors, diversity of flower visitors enhanced honey bee movement – with this being the main factor influencing productivity. When analysing variation in productivity throughout the farms, the researchers found that seed mass declined significantly with distance to natural habitat and increased significantly with species richness of ruderal flowers. The positive effect of ruderal flower diversity was significant at any distance from natural habitat and was independent of ruderal cover.

3.3.3. Field size

Another negative trend affecting pollinators is the ongoing increase in farm size with farms specialized in either crop or animal production. In southeastern Sweden, researchers found more than twice as many butterflies and five times more bumble bees in small farms (< 52 ha) than in large farms (> 135 ha). Larger fields are usually characteristic of monocultures, which use practices affecting farm landscape diversity and reducing the non-cultivated habitats that provide floral resources and nesting sites for wild bees at the margins of cultivated fields. Farms with large field sizes necessarily have a low proportion of hedgerows or other field margins. Since these are the places that provide nest sites and floral resources for wild pollinators when crops are not flowering, farms with large fields will have relatively few pollinators, regardless of the pesticide regime adopted (Belfrage *et al.*, 2005).

If field sizes are very large then there may simply not be enough wild bees to go around. Yield of crops may be limited if there are insufficient bees to visit all of the flowers. For example, in fields exceeding 12 ha in size the yield of field beans was reduced through inadequate pollination by long-tongued bumble bees (Free and Williams, 1976). Similarly, if field sizes exceeded 5 ha then yield of red clover in New Zealand declined through a shortage of bumble bees. At present, the area of land in the European Union and the United States under entomophilous crops is increasing, and some researchers have predicted a serious shortage of both wild and managed bees in the near future (Richards, 2001; Aizen *et al.*, 2009).

Farm size is also associated with different types of farming practices that may or may not encourage wild pollinators. For example, organic farming is mainly adopted by small farmers and organic farms have been shown to increase biodiversity (Hole *et al.*, 2004). But organic farms differ from conventional farms in more ways than just use of agrochemicals. Usually organic farmers cultivate many different crops enhancing farm diversity, and at times many small fields are surrounded by edges or edges enhancing landscape diversity. All these features help to conserve pollinators (Feber *et al.*, 1997). For example, in Sweden it was found that small organic farms had greater populations of bumble bees than large organic and conventional farms (Belfrage *et al.*, 2005).

3.3.4. Farming practices

3.3.4.1 Tillage

The introduction of new tillage practices (reduced, minimum or non-tillage) commonly causes changes in the composition and abundance of weed species present in cropping systems. In arable crops, such as soybean and maize, weed population shifts were observed when conventional tillage systems were changed to non-tillage (Ball and Miller, 1990). Annual grass populations usually increase in non-tillage systems (Wrucke and Arnold, 1985), whereas decreased populations of annual dicotyledonous weeds have been associated with non-tillage, which in turn may reduce floral resources for pollinators. Conversely, tillage practices that create special soil cover conditions influence pollinator abundance, as shown in a survey of 25 squash and pumpkin farms in West Virginia and Maryland. Researchers found that squash bee density was three times higher in no-tillage farms than in tilled farms. Many small farmers that leave residues on soil or practice mulching may be inadvertently encouraging wild bees (Shuler *et al*., 2005). Extensive tillage practices that inhibit or destroy nests should be avoided. In many cases, diverse farms with a variety of landscape features, including patches of bare soil, piles or hedgerows of stone and clump-forming grasses, can provide ample nest habitat for wild bees (Steffan-Dewenter, 2002).

3.3.4.2 Rotations

Crop rotations affect weed seedbanks because weed-control measures change with successive crops, thus influencing weed species composition abundance. In the few studies where rotation effects on weeds have been examined without herbicides as a confounding factor, rotation by itself led to reduced weed populations, especially where a small grain was included in the rotation. However, where crops are rotated, weed communities are more diverse than where crops are grown in monoculture, which again creates more favourable habitat and food conditions for pollinators (Ball, 1992). The operational principle at work here is density versus diversity, as rotations tend to reduce weed density but enhance weed species diversity.

3.3.4.3 Insecticide-induced pollinator declines

The use of pesticides in agriculture is well documented as causing pollinator declines, especially where spraying time coincides with flowering time. Insecticides pose a major threat to pollinators and pesticide-induced declines in bee abundance are reported yearly in many countries of the world. Deliberate misuse of pesticides, despite label warnings and recommendations, has caused major pollinator kills (Johansen, 1977). The use of diazinon to control aphids in alfalfa fields resulted in massive declines of pollinating alkali bees, which took several years to show recovery (Johansen and Mayer, 1990). Poisoning of honey bees (on which most attention has been focused) can result in direct mortality and displacement of queens. Less understood is the problem of sublethal effects, which reduce longevity and adversely affect foraging, memory and navigational abilities of some bees. Pesticides have been detected in contaminated honey or pollen indicating that foraging honey bees can contaminate the hive with pesticides or other pollutants (Buchmann and Nabhan, 1996). Bees are particularly sensitive to many organophosphate insecticides such as fenitothrion and malathion (Johansen and Mayer, 1990).

Wild pollinators are often more susceptible to pesticides than are domestic honey bees, and wild pollinators may be eliminated completely from a crop environment and its surrounds or may take several years to recover to normal pre-treatment levels (Johansen, 1977). While farmers may be aware that pesticides should not be applied to pollinator-dependent crops at the time of flowering, pesticides applied at other periods on crops will occur on weed flowers, and pollinators that visit these may be heavily impacted. Pollinators living on field margins can be affected by either intentional or accidental pesticide use and effects may be lethal or sublethal. Micro-scale effects of pesticide application are very variable and are likely to vary according to type of pesticide use, vulnerability of pollinator species, vegetation type and time of application. A recent butterfly survey conducted in the Netherlands emphasized the importance of timing of pesticide use, because most butterflies are likely to be affected mainly during their caterpillar stage on plants. Unfortunately, in that country 65 percent of agricultural pesticides are used from May to August, when caterpillars of many butterfly species are most abundant (New, 2005).

Application of pesticides to control non-agricultural pests in non-agricultural ecosystems can also affect pollination abundance and activity in nearby crops. From 1969 until 1978, aerial spraying of fenitrothion, an organophosphate highly toxic to bees, was used to control spruce budworm in Eastern Canada. Commercial blueberry production in the region largely depended on pollination by as many as 70 species of native insects including bumble bees, andrenid and halictid bees, all of which declined in blueberry fields near sprayed forests. Blueberry crops failed in 1970 and subsequent years until the pesticide was replaced by other less toxic compounds. It took up to eight years to recover normal population levels after cessation of aerial sprays of fenitrothion against spruce budworm in nearby coniferous forests (Kevan and Plowright, 1989).

Mosquito control programmes have been associated with major losses of honey bees in Canada and the United States. In Manitoba, efforts to combat outbreaks of western equine encephalitis by controlling its mosquito vectors resulted in damage to colonies of honey bees totaling US$90 000 in 1981 and US$850 000 in 1983 (Dixon and Fingler, 1982; 1984).

3.3.4.4. Weed removal

Herbicide use affects pollinators by reducing the availability of nectar plants. It is well known that herbicide spraying and mechanical weed control in alfalfa fields reduce nectar sources for wild bees (Stephen, 1955). The magnitude of the effect for each species is related to the length of its seasonal flight period. Many bees have a flight period that extends beyond the availability of alfalfa flowers. Some of these bee populations show massive declines due to the lack of suitable nesting sites and alternative food plants (Benedek, 1996). This situation is also common in other agroecosystems where flowering weeds are eliminated, especially during periods when the main crops are not flowering.

By destroying larval food sources and safe sites, herbicides can also severely affect pollinator populations (Kevan *et al.*, 1997). Moreby and Southway (1999) and Dover *et al.* (1990) found that wheat field headlands untreated with herbicide contained much higher populations of several groups of insects, including Coleoptera and Lepidoptera, than did those which had been treated. A major use of herbicides by some farmers is to control perennial weeds around crop edges. This is often accompanied by increase of annual grass weed species, so that a species and flower-impoverished community is established replacing a more diverse assemblage of dicotyledonous weeds, thus substantially reducing flower resources for beneficial invertebrates.

In the case of biocontrol agents, the failure to attain high populations of predators and parasitoids in weed free crops is aggravated due to the lack of floral resources. The high incidence of natural biocontrol agents of pestiferous insects in low-input agricultural systems has been ascribed to the availability of floral resources (Altieri and Nicholls, 2004). Successful establishment of several parasitoids has depended on the presence of weeds that provide nectar for the adult female wasps.

In the last 50 years, research has shown that outbreaks of certain types of crop pests are less likely to occur in weed diversified crop systems than in weed-free fields, mainly due to increased mortality imposed by natural enemies (Pimentel, 1961; Adams and Drew, 1965; Dempster, 1969; Flaherty, 1969; Smith, 1969; Root, 1973; Altieri *et al.*, 1977). Crop fields with a dense weed cover and high diversity usually have more predaceous and parasitic arthropods than weed-free fields, although if weeds are left uncontrolled crop yields can be significantly reduced (Perrin, 1975; Speight and Lawton, 1976). Altieri and Letourneau (1982) report relevant examples of cropping systems, in which the presence of tolerable levels of specific weeds has enhanced the biological control of particular pests. A literature survey by Baliddawa (1985) showed that population densities of 27 insect species were reduced in weedy crops compared to weed-free crops, mainly due to enhanced natural enemy populations.

3.3.4.5 Effects of genetically modified crops on pollinator impoverishment

A study of the effects of genetically modified crops on biodiversity did not find direct impacts from modified genes; however, a major impact was mediated through the weed population. The farm-scale evaluation carried out during 2005 in the United Kingdom found that conventional crops of beet and spring rape harboured more pollinators, such as butterflies and bees, because there were more weeds to provide food and shelter, as compared to biotech crops that are genetically engineered to tolerate herbicide applications (Hawes *et al.*, 2003). Many crops have now been modified with resistance to herbicides such as glyphosate, imidazolinone, sulfonylurea and glufosinates. Modification with herbicide resistance is most likely to cause environmental damage to pollinator systems as a result of the ease by which entomophilous weeds non-resistant to the herbicides will be removed from the agricultural landscape (O'Callaghan *et al.*, 2005).

Insect resistance, based on *Bacillus thuringiensis* (Bt) endotoxins, is the second most widely used trait (after herbicide resistance) in commercial genetically modified (GM) crops. Other modifications for insect resistance, such as proteinase inhibitors and lectins, are also being used in many experimental crops. Neither Bt cotton nor Bt maize requires bees for pollination, but cotton nectar is attractive to them and produces a useful honey. Maize pollen may be collected when other pollen sources are scarce (Groot and Dicke, 2002). Pre-release honey bee biosafety tests have been conducted for each Bt crop registered in the United States, including Cry9C maize and Cry3A potatoes. Each test involved feeding bee larvae and sometimes adults with purified Cry proteins in sucrose solutions at concentrations that greatly exceeded those recorded from the pollen or nectar of the GM plants in question. In each case, no effects were observed. The rationale for requiring larval and not adult bee tests is questionable, because adult bees ingest considerable quantities of pollen in their first few days post emergence. Larvae, particularly later instars, also consume pollen along with jelly secreted by nurse adult bees, but only recently have there been attempts to quantify pollen ingestion by individual larvae. Other studies with bees fed purified Bt proteins, with pollen from Bt plants, or bees allowed to forage on Bt plants in the field have also found a lack of effects (O'Callaghan *et al.*, 2005).

The effects of other insect resistant proteins and GM plants on honey bees and bumble bees have been investigated in a series of laboratory, glasshouse and field-based studies. Of these, only serine protease inhibitors (SPIs) affect honey bees and bumble bees, causing changes in bee digestive proteases and some reduction in survival when ingested at high concentrations. Whether bees in the field would be exposed to such levels of SPIs depends on expression levels in the pollen of the GM SPI-plants and the amounts and types of pollen foraged (Groot and Dicke, 2002).

When transgenic maize (*Zea*) pollen was deposited on the leaves of nearby *Asclepias syriaca*, larvae of the Monarch butterfly (*Danaus plexippus*) showed high mortality (Sears *et al.*, 2001). However, Bt Cry1A(c) transgenic pollen and nectar were found not to affect a wide range of other flower-visiting insects tested, and appear to have no effect on hive bees. Oil seed rape has been modified with other toxins such as chitinase, beta-1,3 glucanase and cowpea trypsin inhibitor, which are expressed in pollen and nectar. These are non-lethal to *Apis*, but the latter two compounds were shown to have a detrimental effect on bee behaviour (Picard-Nizou *et al.*, 1997).

4

AGRONOMIC STRATEGIES TO ENCOURAGE WEEDS BENEFICIAL TO POLLINATORS

Clockwise from top left: *A conventional-well weeded plantation adjacent to a mango farm; A Ghanaian mango farmer in his weed-rich, pollinator friendly plantation; A six foot buffer zone of wild vegetation; Stachytarpheta weeds between the mangoes.*

In the majority of cases, wild pollinators cannot be introduced suddenly to agricultural systems in adequate numbers. Managing farm conditions may therefore prove a more successful approach than managing pollinators themselves. The most important farm practices are those directly related to the life cycle of bees:

- Tillage, mulching, cover crops that may affect nesting sites and the survival of immature bees;
- Diversity of farms and surroundings which determine continual food supply and habitat conditions;
- Pesticide use that may remove floral resources (herbicides) or directly poison adults (insecticides); and
- Farm size and the nature of surrounding habitats, although these are less prone to manipulation by farmers.

This section pays special attention to the encouragement of weeds within and in crop field borders. As discussed above, much evidence suggests that encouragement of specific weeds in crop fields may improve the abundance and diversity of beneficial insects, including pollinators (Altieri and Whitcomb, 1979a). Naturally, careful manipulation strategies need to be defined to avoid weed competition with crops and interference with certain cultural practices (Zimdahl, 1980). Economic thresholds of weed populations, as well as factors affecting crop-weed balance within a crop season, need to be defined for specific cropping systems (Bantilan *et al.*, 1974). Defining periods of weed-free maintenance in crops so that densities of desirable weed numbers do not surpass tolerable levels during the critical period of competition, might prove to be a significant compromise between weed science and entomology, a necessary step to further explore ways to enhance beneficial insects in agroecosystems. Shifting the crop/weed balance so that beneficial weed presence is achieved and crop yields are not economically reduced may be accomplished by carefully using herbicides or selecting cultural practices that favour the crop cover over weeds (Altieri and Nicholls, 2004).

4.1 ESTABLISHING OR RESTORING WEEDY HEDGEROWS

In intensive, large-scale agricultural areas, where weeds are not tolerated, the priority should be to conserve or reinforce hedgerows and their constituent weedy plants, such as nettles, wild umbelliferae, comfrey, wild clovers (these being typical species one might find in Europe), as well as herbaceous plants – especially the more specialist long-corolla perennials that tend to produce more nectar than annuals (Corbet, 1995). In addition to pollen and nectar for adults and food plants for larvae, hedgerows provide shelter and supply the substrates that provide nesting sites for various pollinator species. Such substrates include undisturbed areas and bare ground, dry branches or logs, or sandy or earth bank (Willmer, 2011).

There are now many “grass and wildflower” and “nectar and pollen” seed mixtures available in Europe and North America (which contain some plants considered weed species) that can be planted around agricultural plots and which can attract significant numbers of bees and hoverflies (Pontin *et al.*, 2006). Many of these mixtures contain specific host plants for the larval stages of butterflies, moths and some beetles.

4.2 MAINTAINING TOLERABLE LEVELS OF WEED DENSITIES IN THE FIELD

Agroecological management can be directed at maintaining tolerable levels of desirable weeds that support populations of beneficial insects. Farmers can also introduce certain flowering weeds in the plants by sowing mixtures within or around fields. The following section, in turn, examines three of the most amenable weed management approaches compatible with pollinator management.

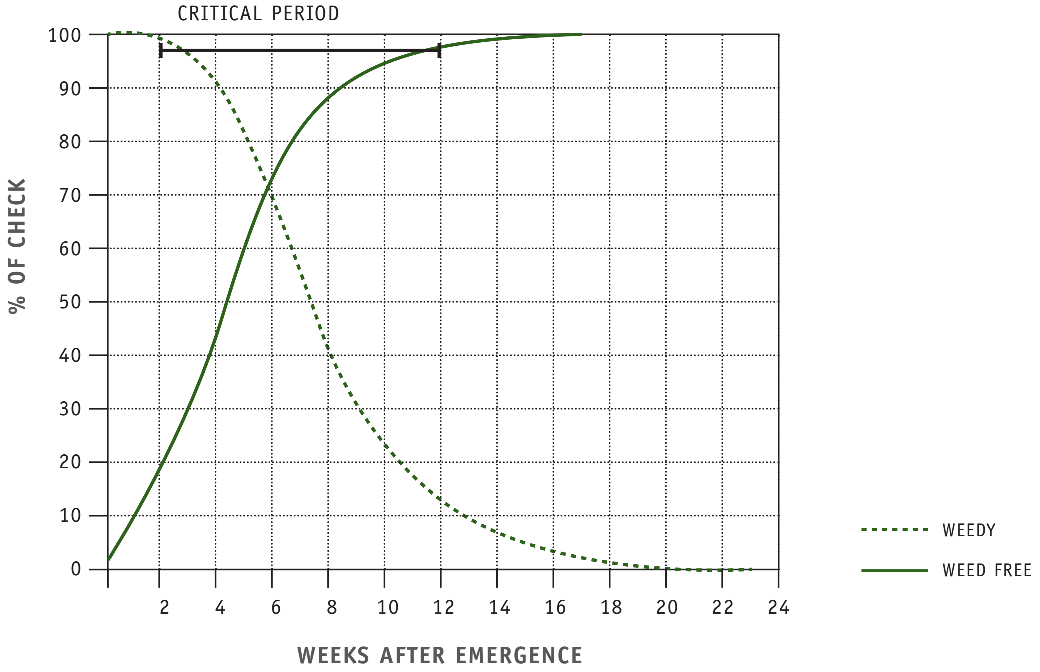
As an example of "beneficial weeds": there are cropping systems where no tillage is a long tradition in several countries. For example, in the inundation plain of the Oueme Valley in the Republic of Benin farmers do not till. They simply slash the persisting vegetation after flood recession and proceed to sowing in the dead mulch. In this context, vegetation of Acroceras zizanioides, a lowland grass weed, is much valued and the value of the land sharply increases if it is covered by this grass. Mulch of Acroceras zizanioides is valued because of its weeding properties. It is likely an allelopathic grass and its mulch keeps the plot weed free.

4.2.1 Defining weed thresholds and critical competition periods

Determining weed thresholds can help avoid excessive losses from weed interference. A competitive threshold can be defined as the weed density and duration of interference above which crop yield is reduced significantly, generally above 20 percent. The period threshold has been defined as the time period early in the crop season before any crop yield loss occurs due to weed interference. The importance of the period threshold lies in understanding the critical period during which remedial control action may be taken to avoid yield loss. This period varies from around two to up to eight weeks after crop emergence, depending on the crop species, weed species complex, and environmental and soil conditions. Period threshold may also be applied to define the time during which weed control must be maintained early in the crop cycle to avoid yield loss from weeds that may emerge later in the season (Oliver, 1988). It is difficult to work with weed thresholds because many weed species generally occur at the same time and mono- or oligo-specific weed stands are exceptions.

The critical period is a more practical approach to maintaining tolerable levels of desirable weed species. It can be determined for each farming system by removing weeds that emerge in the crop at various times during the growing season, or are allowed to compete throughout the season (Figure 2). The application of this method consists of keeping crops free of weeds during the critical period, and then permitting flowering weeds to grow, thus providing resources to pollinators, but without impacting crop production. For less competitive crops, a longer critical period (6 to 10 weeks) means that flowering weeds may not be well tolerated until after the period. In the case of crops such as onion, which do not tolerate weeds at all during the growing cycle, crop pollinator-friendly weeds must be kept on the field edges or at reserved spots in the field where they do not compete with the crop.

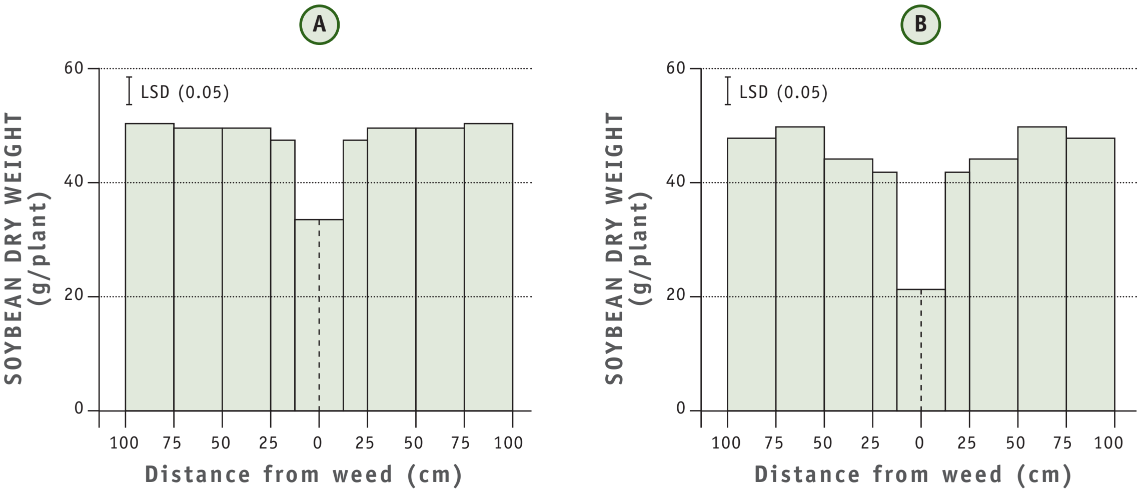
FIGURE 2. THE INFLUENCE OF TIME OF WEED EMERGENCE OR WEED REMOVAL ON PERCENT YIELD OF THE WEED-FREE CHECK AND MAGNITUDE OF THE CRITICAL PERIOD



Source: Nicholls, C. 2012

FIGURE 3. AREA OF INFLUENCE OF COMMON COCKLEBUR ON TOTAL PLANT DRY WEIGHT OF (A) "FORREST" AND (B) "CENTENNIAL" SOYBEANS AT 16 WEEKS AFTER EMERGENCE (AVERAGED OVER 1983 AND 1984).

Width of each block represents an average value for a soybean plant growing in that row segment. The 0 indicates where weed was growing.



Source: adapted from Monks (26).

All weed scientists agree that defining the maximum period that weeds can be tolerated without affecting final crop yields, or the point after which weed growth does not affect final yield, is of key importance. In general, weeds that emerge earlier in the growing season are more damaging to crop yields than populations that emerge later. On the other hand, crops differ in their sensitivity to different durations of weed competition, but the majority are most susceptible during the first third of their life cycle. The guiding principle here is to delay weed emergence relative to crop emergence (Liebman and Gallandt, 1997). Zimdahl (1980) has compiled data on duration of weed competition for particular crops and critical weed-free maintenance periods have been identified for various crop-weed associations. The important question then becomes how long exclusion efforts must be maintained before they can be relaxed to permit those weeds to emerge and provide the desired entomological benefits. As might be expected, the critical weed-free period for a given crop varies considerably among sites and years, due to climate and edaphic conditions affecting crop and weed emergence and growth rates, weeds species composition and weed density.

Thresholds based on weed density – maintaining a certain number of weed plants per defined area (no. plants/metre$^{2)}$ – are more difficult to attain. As a weed becomes established in the crop row it occupies a given space within the crop canopy. The area occupied by the weed is called the area of influence, and as this area increases the weed species becomes potentially more competitive. Figure 3 depicts the area of influence of common cocklebur on soybean biomass (total dry weight), showing that yield losses occur when cocklebur is at distances of less than 25–50 cm from soybean, depending on the variety. Using this information the tolerable densities of a particular weed can be determined (Coble and Mortensen, 1992).

4.2.2 Including forage crops in rotations

By rotating crops with different planting dates and growth periods, and contrasting competitive characteristics and dissimilar management practices, field weed composition and abundance can be altered. Densities of many weed species remain stable or decline when crops are rotated (i.e. wheat oil seed rape, maize-soybean, winter wheat), whereas the densities of weeds increase rapidly when a crop (wheat, maize, etc.) is grown continuously. The inclusion of perennial forage crops in rotations may offer opportunities to further weed suppression. Because little soil disturbance occurs in forage crops, the germination of many weed species is suppressed relative to tilled conditions, and consequently few new weed seeds may be added to the soil seed bank (Liebman and Dyck, 1993). Many forage crops themselves generally provide abundant resources for pollinators.

4.2.3 Designing competitive crop mixtures

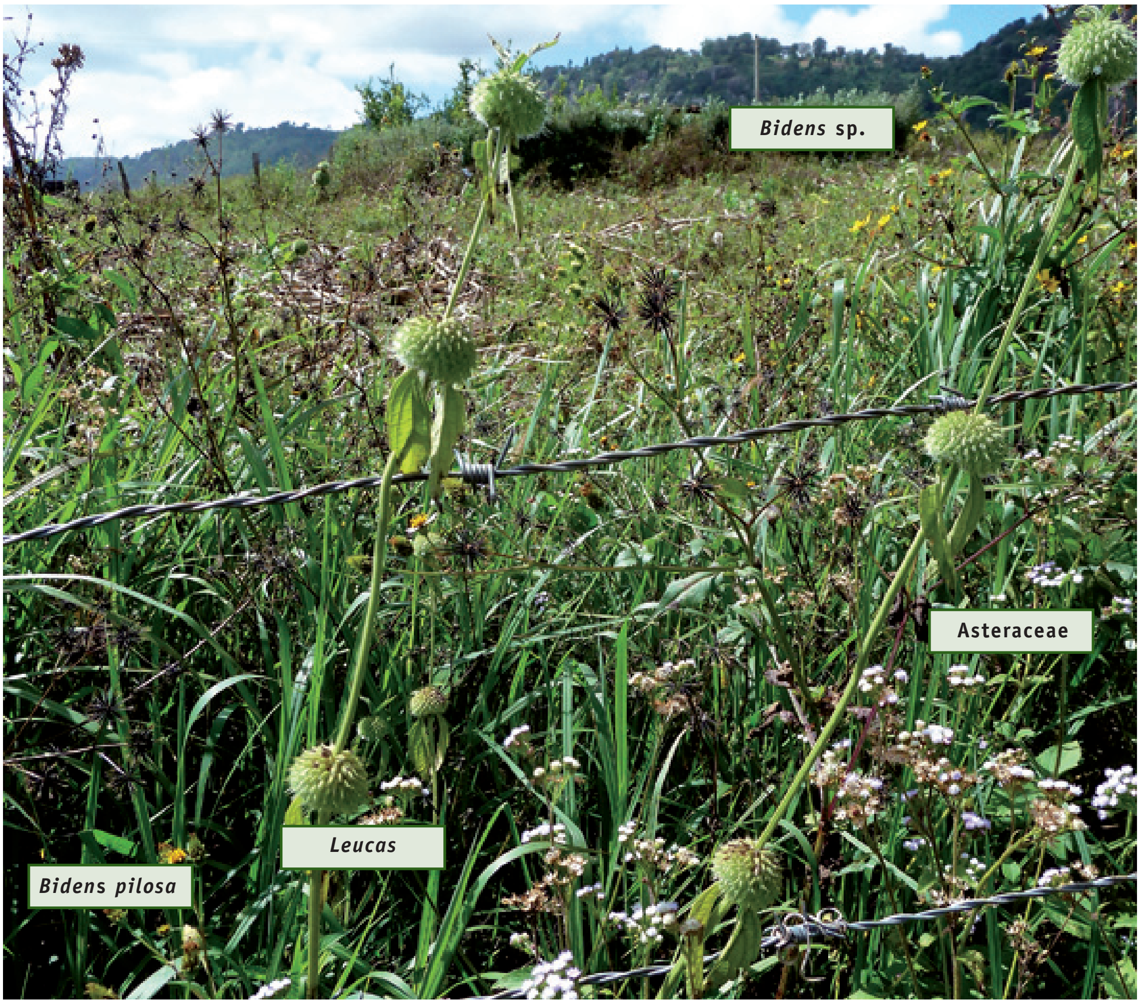
Effective weed suppressive intercropping systems capture a greater share of the available resources (nutrients, water, sunlight, etc.) that weeds would otherwise utilize. Many studies have shown that a variety of intercrops intercept more light, capture greater quantities of macronutrients and water, and produce higher yields, while containing lower weed densities than corresponding monocultures. Although these systems are well suited to small-scale labour-intensive farming systems, certain crop mixtures (i.e. maize-soybean strip cropping or mixtures of small grains with red clover) are compatible with farm machinery and thus can be adapted to large-scale systems (Liebman and Davis, 2000).

Many farmers use cover crops (usually legumes as green manures) as a rotational component, which suppress weeds by competing for resources, changing environmental factors that affect weed germination, and releasing phytotoxins (i.e. rye, fodder radish) that inhibit weed germination and growth. Through this mechanism, some species, such as hairy vetch, can suppress weed density by 70 to 80 percent (Liebman and Gallandt, 1997).

It is important to consider that the effects of cultural practices on weeds manifest differently depending on the type of farming system considered. For example, the effects of cultural practices in organic agriculture (e.g. fertilization and direct weed control) on crop-weed interactions usually manifest themselves more slowly compared with conventional agriculture. In such systems, weed management should be tackled over an extended time period and requires deep integration with other related cultural practices, with the aim of optimizing the whole cropping system rather than just weed control. Small and/or organic farmers using direct (physical) weed control can only be successful if preventive and cultural weed management is applied to reduce weed emergence (e.g. through appropriate choice of crop sequence, tillage, smother/cover crops) and improve crop competitive ability (e.g. through appropriate choice of crop genotype, sowing/planting pattern and crop diversity) (Barberi, 2002).

4.3 ATTAINING DESIRABLE WEED SPECIES COMPOSITION IN THE FIELD

In addition to reducing weed densities to levels that minimize the competitive interference of weeds, changes in the species composition of weed communities are desirable to ensure the presence of plants that attract beneficial insects. Manipulation of weed species composition can be achieved by several means (Altieri and Whitcomb, 1979b; Altieri and Letoumeau, 1982).



Edge of fallow area on the Korir farm used for the zero-grazed livestock to rest in and walk about during the day: note the high diversity of wildflowers.

4.3.1 Changes in the levels of key chemical constituents in the soil

The local weed complex can be affected indirectly by the manipulation of soil fertility. Fields in Alabama in the United States with low soil potassium were dominated by buckhorn plantain (*Plantago lanceolata*) and curly dock (*Rumex crispus*), whereas fields with low soil phosphorus were dominated by showy crotalaria (*Crotalaria spectabilis*), morning glory (*Ipomoea purpurea*), sicklepod (*Cassia obtusifolia*), *Geranium carolinianum* and coffee senna (*Cassia occidentalis*) (Hoveland *et al.*, 1976). Soil pH can influence the growth of certain weeds. For example, weeds of the genus *Pteridium* occur on acid soils, while *Cressa* sp. inhabits only alkaline soils. Other species (many Compositae and Polygonaceae) can grow in saline soils (National Academy of Sciences, 1969).

Studies conducted with synthetic fertilizers indicate that they can increase both the rate and total amount of weed germination and may promote more weed growth than crop growth. Nitrogen (N) fertilizer application increased *Avena fatua* panicle production by 140 percent and decreased wheat yield by 49 percent compared to unfertilized treatments. Timing of N fertilizer application can affect crop-weed competition, and most studies show that delayed fertilizer applications tend to increase crop biomass while reducing weed biomass (Liebman and Davis, 2000).

Organic materials (compost, crop residues, etc.) function as slow-release nutrient sources. If patterns of nutrient release can be predicted and regulated effectively, it may be possible to satisfy the nutrient requirements of large-seeded crops, while stressing small-seeded weeds early in the growing season (Liebman and Dyck, 1993; Davis and Liebman, 2001).

4.3.2 Use of herbicides

Repeated herbicide treatments can cause a shift in weed populations, or select for the development of resistant weed biotypes at the expense of susceptible community members (Horowitz *et al.*, 1962).

Buchanan (1977) has published a list of herbicides that suppress certain weeds while encouraging others. When a maximum rate of 06 kg/ha of trifluralin (a,a atrifluoro2, 6dinitroN, Ndipropylptoluidine) is applied before sowing, populations of velvetleaf (*Abutilon theophrasti*), jimson weed (*Datura stramonium*), venice mallow (*Hibiscus trionum*) and prickly sida (*Sida spinosa*) can be grown among cotton and soybeans without the presence of other unwanted weed species. This strategy is agronomically acceptable as long as the weeds that survive the herbicides appear after the critical period. Although most examples cited by Buchanan (1977) relate to weed control studies, similar methods may be developed to favour particular beneficial weeds in order to achieve early increases of beneficial insect populations.

As weed species differ in their sensitivity towards various active ingredients, they are differentially controlled by the same herbicide treatment. Herbicides are normally selective for certain crop species, but are also less active on some weed species. Against this background, researchers in the United Kingdom (Ulbert *et al.*, 2010) tested three selective herbicides with different active ingredients (amidosulfuron + iodosulfuron, fluroxypyr, mecoprop-P) at two application rates. They analysed cover of selected focal species (*Centaurea cyanus* and *Papaver rhoeas*) as well as weed species richness, winter wheat yield and weed community composition as influenced by herbicide treatments. Herbicide treatments involving fluroxypyr generally allowed for the selective retention of the regionally threatened weed species *C. cyanus*. Equally, the treatment allowed for the retention of *P. rhoeas*, a beneficial species of high value for associated trophic levels. At the same time, it provided considerable control of the competitive species *G. aparine*. Researchers concluded that herbicides with a high specificity provided a valuable contribution to the development of environmentally targeted weed management systems, while enhancing the ecological benefits derived from more desirable weeds. There is no doubt that herbicide treatments significantly affect weed species composition by controlling pernicious weeds potentially retaining beneficial or rare species occurring at moderate densities (Clements *et al.*, 1994). Of course, such an approach is inapplicable in organic farming systems or by resource-poor farmers that cannot afford the chemical inputs.

4.3.3. **Direct sowing**

Perhaps the best possibility to ameliorate the situation for pollinating insects in the modern agricultural landscape is to enrich remaining field margins by sowing plants, creating new zones with permanent vegetation or sowing weed species mixtures as strips every few rows within crop fields. In Sweden, the communities of pollinating insects in reclaimed field margins sown with specific weed flowers were compared with those of a margin with a naturally diverse flora and an adjacent pasture. The sown leguminous plants were very attractive to most insect groups, especially bees and bumble bees, and their pollen constituted an important part of the bees' total catch (Hausammann, 1996). The vegetation established by spontaneous succession especially attracted Syrphidae and other groups of Diptera. Butterflies were found in all vegetation types.

In Switzerland researchers have long investigated the use of weed strips sown within crop fields and composed of more than 25 herbaceous plants, including annual, biennial and perennial plants (e.g. *Sinapis alba, Centaurea cyanus, Oenothera biennis, Leucanthemum vulgare*, etc.). The main goal is to provide beneficial insects with a continuous offer of flowering herbs over the whole growing season (Nentwig *et al.*, 1998).

In the United Kingdom, plots sown with mixtures of six annual flowering plant species – borage (*Borago officinalis*), buckwheat (*Fagopyrum esculentum*), cornflower (*Centaurea cyanus*), mallow (*Malva sylvestris*), marigold (*Calendula officinalis*) and phacelia (*Phacelia tanacetifolia*) – in different proportions attracted a diversity of flower-visiting insects. Among the observed insects were the honey bee and eight species of bumble bees among 16 species of aculeate Hymenoptera, 17 species of Diptera, mostly syrphids, and 6 species of Lepidoptera. Sequential sowings provided nectar and pollen from early summer to late autumn during the period after arable crops had finished flowering and food for pollinators was scarce. Different sowing dates and plant species favoured different insect species (Carreck and Williams, 2002).

The application of this method, however, demands the careful investigation of certain weed seed germination requirements. Some seeds remain in enforced dormancy and germinate only under specific environmental conditions. Most weed seeds have specialized requirements for germination, making it difficult to sow weeds for experimental purposes (Anderson, 1968). Nevertheless, today it is possible to find in the market many weed seed mixtures (mostly flowering plants) recommended for planting in and around crop fields to create habitats for beneficial insects, in Europe and North America.

4.3.4 Soil disturbance

The weed species composition of recently plowed cropped fields can be manipulated by changing the season of disturbance. In northern Florida, field plots plowed at different times of year exhibited different weed species composition. Within these plots, populations of herbivorous insects fluctuated according to composition and abundance of weed hosts. Large numbers of chrysomelids and leafhoppers were collected in treatment plots where preferred weed hosts reached high cover values. As these herbivores served as alternative prey, the number of predaceous arthropods feeding on them varied in direct proportion to the size of populations of their preferred herbivorous prey as determined by the presence of weed hosts and the season of plowing (Altieri and Whitcomb, 1979b). The authors proposed plowing strips of land within a crop in different seasons to encourage specific weeds that, in turn, provide an alternative food and habitat to specific predators. If this is undertaken early in the season, a balance of natural enemies can be maintained in the field before outbreaks of pest species occur. Similar manipulations may favour resources for pollinators.

4.3.5 Modifying weed spatial patterns

It may be possible to influence weed spatial distribution and promote weed occurrence in clumps within fields as opposed to uniform distribution. For a given average density over a broad area, clumped weeds are expected to be less damaging to crop yield than randomly or evenly distributed weeds (Aldrich, 1984). Clumped weeds in a field spot may reduce yields in the local area, but provide a source of beneficials that colonize the rest of the field from the clump.

BOX **1. PRACTICAL TIPS FOR ENCOURAGING POLLINATOR FRIENDLY WEEDS**

One of the challenges that bees face in agricultural landscapes is lack of season-long food sources (Bohart, 1972). Large monocultures of bee-pollinated crops, like almond, canola or watermelon may provide a few weeks of abundant food, but a lack of within-field or adjacent wild plants blooming before and after the main crop blooms can result in a decline of healthy pollinator numbers. Encouraging blooming weeds or establishing diverse plantings can provide sufficient floral diversity to support resident pollinators. Bee diversity is often maximized in landscapes where 15 or more flowering plant species are present. As different bees have different flower preferences, this season-long food supply is especially critical early and late in the year (Willmer, 2011). Native bees remain dormant throughout the winter and often need immediate food sources upon emergence in the spring. Bees that over-winter as adults, like bumble bees, often need late season nectar sources to build up their energy reserves for the long winter. Similarly, honey bees spend winter inside the hive living off honey from nectar they collected over the summer months. Without enough honey, honey bees can starve over the winter resulting in the entire hive dying off.

Since the most obvious need for pollinating species is diversity of nectar and pollen sources, it is important to consider the following when choosing plants (including selected weedy species) for the farm (Bohart, 1972; Shepherd *et al.*, 2003):

- Choose plants that flower at different times of the year to provide nectar and pollen sources throughout the growing season.
- As a general rule, allow a minimum of three plant species that bloom at any given time during the growing season: spring, summer and autumn.
- Encourage combinations of annuals and perennials.
- Provide a variety of flower colours and shapes to attract different pollinators.
- Encourage plants in clumps, rather than single plants, to better attract pollinators.
- Provide weed and floral diversity as strips every few crop rows or as mixtures in fields margins.
- Whenever possible, choose native plants. Native plants will attract more native pollinators and can serve as larval host plants for some species of pollinators.
- In addition to needing season-long food, nesting locations are important. Since the majority of native bees nest in the ground, farming practices that inhibit or destroy nests, like the widespread use of plastic mulch or extensive tilling, should be avoided. In many cases, diverse farms with a variety of landscape features including patches of bare soil, piles or hedges of stone and clump-forming grasses can provide ample nest habitat.

In addition, cropping systems can be managed to enhance environmental opportunities for insect pollinators. For example, the inclusion of forage plants as part of a normal crop rotation can be very desirable. Clovers benefit soil quality but also support bees and some longer-tongued flies. Some suitable intercropping systems that include a flowering crop are good for encouraging hoverflies and other species. Some intercropping systems that include a tall and a shorter crop (i.e. maize and bean polycultures) can help provide an ideal microclimate within the system, so that pollinating insects can maintain their thermal and water balance more easily as well as moving between plants more effectively (Willmer, 2011).

5

WHOLE CROP MANAGEMENT SYSTEMS AND THEIR IMPACTS ON WEEDS AND POLLINATORS

Diverse ground cover between apricot orchard trees, Italy

The previous section reviewed the impacts of different land management practices on pollinators. This section considers management systems in the same way, where systems may be defined as a commonly grouped set of practices, as opposed to individual practices themselves. For example, intensive arable management systems may include certain groups of pesticides sprayed at certain times, large monocultural fields, regularly tilling at certain times and limited crop rotation. A counterpart organic system may practice alternative weed and pest control in smaller, diversified fields that are rotated regularly. The following sections consider the effects of broadly different systems.

5.1 THE EFFECTS OF INTENSIVE AGRICULTURAL SYSTEMS ON WEEDS AND POLLINATORS

There has been wide discussion of the impacts of intensive agricultural systems on species diversity and, more recently, on diverse landscapes providing ecosystem services (Kremen, 2005; Dobson *et al.*, 2006, Hajjar *et al.*, 2008), where ecosystem services are ecosystem functions to which people ascribe value, usually monetary. Such systems may include a range of practices that appear detrimental to the persistence of many insect species, such as the use of herbicides and pesticides, the cultivation of some genetically modified (GM) crops, expansive non-zoophilous crop landscapes, and ecologically damaging types and timings of spraying and tillage. It is particularly important to acknowledge that these factors are rarely mutually exclusive with ecological communities subjected regularly to a cocktail of pressures (Potts *et al.*, 2010). However, to maintain yields of highly productive zoophilous crops, populations of pollinator species must be sufficiently high to operate at appropriate levels of pollination efficiency. Maintenance of the arable weed community and adjacent field-margin plant species is inherently linked to crop yield, as these provide habitat connectivity and may support a more diverse invertebrate pollinator community (Carvell *et al.*, 2004; Ricketts, 2004; Chacoff and Aizen, 2006) crucial to both productivity and the persistence of rare plants. Intensive land management systems are less likely to support such diverse communities due to the additive effects of the above pressures.

Many modern pesticides have been designed to rid crops of pest species while maintaining “useful” animal services, such as pollination. They have, however, been linked to a perceived decline in a key global pollinator species, the honey bee (*Apis mellifera*) (Brittain *et al.*, 2010b; Potts *et al.*, 2010), and can prove toxic to species of bumble bee (*Bombus* spp.) (Mommaerts *et al.*, 2006). This decline is not necessarily confined to pest/insecticides interactions, as the relationship between insecticides, pathogens and environmental stressors may be a contributing factor (Potts *et al.*, 2010). Studies of the effects of pesticides on key pollinators are numerous, and long-term changes have been observed in foraging behaviour, memory and pollen handling (Kevan, 1999; Suchail *et al.*, 2001). Some research suggests that the additive effects of multiple pesticide exposures may contribute to honey bee mortality (Johnson *et al.*, 2010) and colony collapse. Brittain *et al.* (2010b) observed a decline in wild *Bombus* spp. and Lepidoptera pollinator species at field, landscape and regional scale, attributed to the effects of such exposure and the use of herbicides. Some measures already in place, such as timing of application, aim to avoid unnecessary impacts of pesticides on pollinator species. Brittain *et al.* (2010a) suggest that application of toxic insecticides earlier in the flowering season can lead to a reduction in pollinator visitation rate, and that late season application has no significant effect. However, evidence suggests that continuous contact of pollinators with dusted or sprayed crops can contribute to pollinator mortality and reduced foraging efficiency (Johnson *et al.*, 2010).

Similarly, the use of herbicides has led to the decline of important arable weed species, both common and threatened (Fried *et al.*, 2009). Such species have been identified as important to higher trophic level invertebrates, in addition to avian insectivores and granivores, both as a direct food source and indirectly by attracting pollenivores and nectarivores as invertebrate prey. A differential susceptibility of weed species to herbicides exists: more resistant or nitrophilous species can become dominant in the presence of herbicide applications, and herbicide-susceptible species may show poor success (Hyvönen, 2007). Nevertheless, recovery of common and rare arable weed species is linked to elimination of herbicide use (Fried *et al.*, 2009). Spray drift or leaching of biocides to arable non-crop plant species from both zoophilous and non pollinator-dependent crops remains problematic. A large percentage of aircraft-distributed spray never meets the target (Pimentel, 1995) with a plethora of factors affecting the likelihood of drift to non-target areas. These include crop type, canopy height, proximity to non-target species, wind speed/direction and spray droplet size. Mitigation of these effects requires further research (Felsot *et al.*, 2011). Non-target sprays can result in reduction in floral diversity and density (Hald, 1999), creating potential for fewer floral resources for pollinators such as bees and butterflies (Longley and Sotherton, 1997).

The use of genetic modification has resulted in crop species resistant to pest and/or herbicides, increasing crop yield but creating concern over out-crossing of deleterious or beneficial genes to wild populations of related plants. The potential for out-crossing can reach up to 6 km for insect-pollinated plants. This was observed in pollination of cowpea flowers by carpenter bees, *Xylocopa flavorufa*, although typically outcrosses would occur, if at all, at much smaller distances of less than 50 m (Pasquet *et al.*, 2008). Warwick *et al.* (2009) observed increases and decreases in the fitness of non-crop hybrids resulting from crosses with genetically modified species. For example, increased disease resistance could come at a cost of reduced fertility and an up to 35 percent reduction in seed set. Conversely, other species stand to increase fitness under high disease pressure. Moreover, pollinator activity can be adversely affected (Prendeville and Pilson, 2009) where different bee species show preferences for transgenic cultivars due to enhanced floral traits in nectar quantity and inflorescence size. Subsequently, pollination rates of non-transgenic individuals may be reduced in favour of genetically modified individuals. It is clear that generalizations cannot yet be made as to the effects of transgenic out-crossing, and each species may respond differently.

Applying chemicals to agricultural crops is not limited to herbicides or pesticides; for example, there have been a number of studies into the role of added fertilizer on plant communities (McLaughlin and Mineau, 1995). Leaching of both applied nutrients and livestock by-products to adjacent terrestrial ecosystems can lead to a shift in plant community composition, favouring smaller, weedy species (Tilman *et al.*, 2002). The consequences of community shifts have a range of implications for flowering times, obligate or specialist relationships, and pollination strategies of the new dominant species. If, for example, plants utilizing a wind-pollination strategy replace existing zoophilous species, there may be implications for pollination and gene flow to neighbouring communities, and reduced food abundance for ecosystem service providers.

A further factor in food resource reductions for pollinator species is the threat of habitat fragmentation, leaving areas of diverse or obligate food sources in low supply and/or poorly connected. The effects of habitat fragmentation (islandization) are well studied, and are considered to be a major driver for species loss in both plant and arthropod species (Rathcke and Jules, 1993; Aizen and Feinsinger, 1994a, 1994b; Ashworth *et al.*, 2004). Fragmentation in the pollination context is largely attributed to the physical destruction of native habitats to accommodate extensive landscapes of non-zoophilous monocultures that subsequently lack appropriate connectivity between natural or diverse habitats (Steffan-Dewenter and Westphal, 2008). Moreover, this can cause loss of physical space for pollinator nests or colony establishment, resulting in a reduction of both species number and individual abundance (Rathcke and Jules, 1993). Consequently, farmers have become reliant on the use of imported or apiary-managed honey bees to provide the pollination services required to maintain agricultural productivity (Dar *et al.*, 2010). Coupled with fragmentation is the mechanical disturbance of agricultural land, typically utilized by pollinators for nesting. The meta-analysis undertaken by Williams *et al.* (2010) suggests that below ground nesting pollinators were more negatively affected by tillage practice (timing, depth) than were above ground nesting species. This result seems intuitively obvious and is consistent with Shuler *et al.* (2005), who observed a reduction in bee presence in tilled squash fields compared to untilled fields. However, above ground nesting species may be more negatively affected by other agriculturally influenced factors, such as isolation from natural habitat. Indeed, at the landscape level, isolation from florally diverse natural and semi-natural areas can reduce pollinator richness by 34 percent and visitation rate by 27 percent when isolated by approximately 1 km. Honey bee abundance can remain unchanged at this distance, so this result suggests that wild pollinators are an important asset in productivity, and (semi-) natural habitat is critical for maintenance of such communities (Garibaldi *et al.*, 2011).

5.2 THE IMPORTANCE OF LESS INTENSIVE FARMING SYSTEMS

The importance of biodiversity for food production and its role in ensuring the sustainability of the ecosystem services it provides are increasingly understood as crucial to global food production and security (De Schutter, 2010). There appears to be little dispute that organic farming regimes benefit biodiversity, zoophilous wildflowers and pollinator abundance on a local scale (Gabriel and Tscharntke, 2007; Hodgson *et al.*, 2010). This has been largely attributed to the utilization of biological controls such as integrated pest management (IPM) – where enhanced natural enemy effectiveness aims to target one or more pest species – in place of chemical control methods. Fuller *et al.* (2005) observed consistently higher levels of plant diversity in a large-scale comparison of 89 conventional and organic farm pairs, with less consistency in other taxa. As non-crop species are usually not suppressed by herbicides in organic farming, plant diversity increases sooner and, through a "bottom-up" effect, increases invertebrate and bird numbers over time. An additional explanation for a slower response by animals is that organic farms often occur in landscapes dominated by conventional farming and lack appropriate connectivity, so colonization may take more time. At a landscape level, a meta-analysis by Bengtsson *et al.* (2005) suggested that, with correct management, conventional systems combined with organic systems would benefit diversity more than either alone as a result of landscape heterogeneity, but that this effect would be lost in diverse landscapes. It should be noted that the scale of the studies examined limited the meta-analysis, as many of these did not consider landscape surroundings. Such management could entail a combination of habitat manipulation and management of natural areas. Examples of these combined systems include: the creation of natural strips by allowing a succession of uncultivated areas, the creation of refugia for protected or favourable species, supplementary field margin planting, and pond and hedgerow management. The success of these recommendations may depend on the assumption that non-agricultural areas are also present in a predominantly agricultural landscape, and such areas would require management that may lie outside a farmer's ability or interest. Indeed, for a farmer to take on such a range of management responsibilities may require incentives or payments beyond that, for example, of an Environmental Stewardship Scheme (ESS) (Natural England, 2010a, 2010b, 2010c; Gutman, 2007). More recent ideas suggest that this would require implemention of a market model for ecosystem services, possibly similar to those already in place: paying a premium for organically farmed goods, ESS and "approved source" paper goods, to name but a few (Gutman, 2007; Farley and Constanza, 2010; FAO, 2011).

A number of studies have reported biological control success in reducing the impacts of destructive invertebrate species, such as the well-documented attempt to control cassava mealybug in Africa (Herren and Neuenschwander, 1991), providing an insight into the potential use of natural enemies. Despite this and other dramatic successes in biocontrol of insects (Gurr and Wratten, 2000), there remains debate about the universal application of these methods, and whether or not it may be best to simply enhance inherent natural controls. There is some evidence to suggest that pest species are less prevalent in organic farms, particularly those that are well managed (Bengtsson *et al.*, 2005). Observations by Sandhu *et al.* (2010) provide experimental evidence of the greater efficiency of natural enemies in organic farms with up to 50 percent predation in 24 hours of areas baited by aphid and blowfly eggs, compared to up to 6 percent predation in 24 hours on conventional farms. Moreover, productivity comparisons conclude that successfully weed/pest-managed organic farms can yield up to 64 to 114 percent of that of conventional farms (Posner *et al.*, 2008), although there is significant variability in the extent of pest and weed control depending on crop type, farm, time of year, weather and weed control method. The use of pesticides can reduce the populations of natural enemies, while the provision of supplementary planting can increase the fitness and efficiency of natural enemies by providing shelter, nectar, alternative prey and pollen for protein, known collectively by the acronym SNAP (Jonsson *et al.*, 2008; Barnes *et al.*, 2009). For example, beetle banks can harbour over 1 000 predatory invertebrate individuals per square metre (Zehnder *et al.*, 2007). Alternatively, choosing specific host plants such as *Phacelia tanacetifolia*, *Fagopyrum esculentum*, *Lobularia maritima* or *Coriandrum sativum* to provide resource subsidies in New Zealand, for example, can increase parasitism rates of pest species (Fiedler *et al.*, 2008; Gurr *et al.*, 2012). The study by Fiedler *et al.* (2008) highlighted the "stacked" ecosystem services that can arise as a byproduct of habitat management such as IPM. Interestingly, that review omitted the potential crop pollination benefits of adding floral resources. As Hanley *et al.* (2011) observed, potentially beneficial pollinator "spill-over" to field margin plants can occur in the presence of a mass flowering crop (MFC) of field bean (*Vicia faba*). This raises the prospect of "reverse spill-over" pollination enhancement from IPM plants such as *Phacelia* to zoophilous crops. This concept has been explored in fields adjacent to diverse forest fragments (Ricketts, 2004; Chacoff and Aizen, 2006), but not to enhance crop pollination rate by adding zoophilous flowering plants near or within such crops.

The timing and location of crops and enhancement plantings can, however, have adverse effects on the availability of resources for, and presence of, pollinators. Hanley *et al.* (2011) observed significantly smaller populations of pollinators on mass-flowering crop field margins after the crop had completed its flowering stage. This is consistent with studies of the effects of crop type on bumble bee species (Westphal *et al.*, 2009), where MFCs promote colony growth due to a large, uniform food resource. Loss of the mass resource after flowering is a limiting factor in reproduction, so the actual benefits to the colony are short-term, and may not serve to increase long-term abundance or fulfill conservation aims. The implications of such findings are that floral resources should be in plentiful supply throughout key pollinator life cycles (Westphal *et al.*, 2003). This concept may deliver three beneficial effects: (i) increase abundance of rare or threatened pollinator species; (ii) deliver the potential for reverse spill-over pollination services to zoophilous crops and, with appropriate plant selection; and (iii) provide the basis for an IPM protocol to include enhancement of pollinator fitness as one of its goals.

5.3 POLLINATOR MANAGEMENT AND FARMING SYSTEMS

Much of the management and conservation efforts of policymakers and international communities in pollinator initiatives have been based around measures to encourage bees on-farm, specifically honey bees (Kremen *et al.*, 2004; Pettis and Delaplane, 2010) and bumble bees (*Bombus* spp.) within the European community (Goulson *et al.*, 2005; Fitzpatrick *et al.*, 2007), as these are key pollinator species for crop plants and fruits in Europe, and several species are rare or in local decline. In response to European Commission (EC) guidelines, agri-environment schemes (AES) have been implemented across Europe. In the United Kingdom, monetary incentive programmes operate at different levels under ESS (Natural England, 2010a, 2010b, 2010c). Within these schemes farmers can employ various methods to manage disused farmland or include areas of natural wildlife on their land adjacent to or within arable fields, for example, by extending and/or augmenting natural field margins with native or beneficial wildflower species. As such, ESS can be considered an integrative approach, where habitat manipulation is integrated throughout farms and field systems, as opposed to setting aside larger individual areas of land. Stewardship schemes have been recorded to benefit biodiversity at local and landscape levels. Marshall *et al*. (2006) also observed an increase in pollinator abundance on margins and in the centre of the crop as a result of prescribed AES field margin planting. As such, this management practice may have the potential to benefit crop pollination and increase pollinator abundance.

In studies outside habitat manipulation on-farm, Chacoff and Aizen (2006) and Ricketts (2004) observed the benefits for crop pollination of field proximity to diverse tropical forest fragments. Coffee plantations had elevated crop yield when situated closer to forest fragments, attributable to the increase in pollinator abundance – a consequence of habitat availability and diverse food availability.

The findings of these studies have implications for the productivity benefits of ecosystem services and habitat manipulation. For example, does increasing diversity and abundance of native wildflower increase yield in zoophilous crops? And does pollinator presence translate to increased pollination rate (Marshall *et al*., 2006)? Or can the deliberate use of non-native flowers such as *Phacelia* for biological control increase pollinator diversity and crop yield through more efficient pollination rate and pest control (Fiedler *et al*., 2008)?

In addition to ESS, the European Community introduced set-aside schemes, whereby land was left fallow or planted with wildflower mixes to compensate for loss of natural habitat and to protect soils from overuse (Levin and Jepsen, 2010). As a result of the elimination of set-aside incentives, much of the set-aside land was recultivated and natural habitat was lost (Tscharntke *et al*., 2011). Similar schemes were present in the United States to prevent over-production. Despite the lack of incentives, set aside is still adopted on a shorter-term basis in crop-rotation systems, where land is left fallow, and in environmentally sensitive areas (Kovács-Hostyánszki *et al*., 2011). This practice has been shown to be beneficial to pollinating insects, such as *Bombus* spp. and Lepidoptera (Alanen *et al*., 2011). Set-aside was also adopted in the United States, where fields were left for much longer periods and successional change progressed further, allowing time for establishment of populations and colonization by local fauna (Van Buskirk and Willi, 2004; Corbet, 1995). The meta-analysis by Van Buskirk and Willi (2004) suggests that there is an unequivocal benefit to biodiversity, including increased abundance of species previously in decline. The key difference between set-aside and integrated conservation is the connectivity between natural habitats (Donald and Evans, 2006). Punctuating landscapes with set-aside fields may not provide the connectivity between these habitats which could slow or prevent colonization by less mobile species. Furthermore, the loss of incentives for set-aside fields, and the recultivation of previously diverse plots, could lead to further fragmentation in landscapes dominated by conventional agriculture.

The effect of crop type on pollinator activity and abundance has also received some attention. Experimental evidence suggests that fields cultivated with mass-flowering crops (MFC) enhance the abundance of pollinators at a landscape scale (Westphal *et al.*, 2003), and promote colony size and landscape-level forager density (Herrmann *et al.*, 2007). As noted previously, Hanley *et al.* (2011) observed a significant increase in visitation rate of various *Bombus* species to plant species in the margins of mass-flowering crop fields compared to non-zoophilous wheat (*Triticum aestivum*) fields. Such results suggest that mass-flowering crops facilitate pollinator activity on native plants rather than acting as a sink for this activity, although it is important to note that visitation rate does not necessarily translate to pollination. Studies such as these may lay the foundations for research into the potential of mass-flowering crops as a conservation or management tool. This should, however, be approached with caution as a recent study (Holzschuh *et al.*, 2011) suggests that the presence of MFCs can cause pollinator dilution, which leads to a reduction in pollination of wild plant populations over a 1 km radius, potentially reducing pollination of plants reliant on a particular pollinator species. Furthermore, as noted in other sections, reliance on mass-flowering crops is not recommended as they usually flower for a fraction of the active season of many pollinator species.

5.4 AN ASSESSMENT OF THE EFFECTIVENESS OF POLLINATOR MANAGEMENT SYSTEMS

The most common form of pollinator management systems comes from the various agri-environment schemes (AES) around the world, developed to encourage farmers to prioritize land stewardship over production. For example, these schemes may broadly advocate and compensate for the planting of a nectar and pollen-rich flower mix or the maintenance of a species-rich grassland field. An assessment of all such measures worldwide is beyond the scope of the present publication. However, many of the benefits and drawbacks of AES are applicable at a number of scales and to a number of habitat manipulation measures. Since the highly cited review of agri-environment schemes (AES) by Kleijn and Sutherland (2003), a number of studies have been undertaken across Europe examining the efficacy of such schemes. Such schemes have been shown to benefit plant species diversity (Knop *et al.*, 2006), pollinator species diversity and population abundance at a landscape (Heard *et al.*, 2007) and local level (Carvell *et al.*, 2004), including honey bees and bumble bees (Pywell *et al.*, 2006), and farmland moths (Fuentes-Montemayor *et al.*, 2011).

Conclusions are often mixed, however. For example, Albrecht *et al.* (2007) report significantly higher pollinator species diversity, abundance and pollination services in intensively managed agricultural fields in close proximity to fields under agri-environment protocols. However, this effect was diluted with distance from the scheme, emphasizing the need for connectivity or close proximity between AES fields to provide consistent benefits to conventional fields. Similarly, results from studies have sometimes been contradictory. While Pywell *et al*. (2005) found that the increased abundance of field margin flowers had no effect on bumble bee abundance in field margins at a regional scale, Lye *et al.* (2009) suggest that bumble bee queens and colony foundation benefit through nest site availability as a result of the increased resources.

The development of AES in the future can learn from studies that have reported serious problems with the current systems. Kleijn *et al*. (2004) undertook an extensive survey specifically targeting AES efficacy in the Netherlands. The survey highlighted shortfalls in promoting targeted species, which were attributed to the intensity of agriculture in that region. They also found that AES were only important for the most common species. The results from landscape-scale studies point towards the need to adopt AES throughout the landscape, so as to obtain real benefits, as schemes applied in isolated farms are less likely to enhance insect and plant populations (Rundlöf *et al*., 2008; Merckx *et al*., 2009). Furthermore, Bengtsson *et al*. (2005) have advocated a heterogeneous landscape of differing management and agricultural regimes. This allows a number of differing species-rich habitats and areas for a wider range of species, as opposed to one large expanse of organic farms or a single species-rich grassland habitat in a sea of conventionally grown crops (Winqvist *et al*., 2011). Likewise, regional biodiversity may not be enhanced if the same AES plans for heterogeneity are implemented across landscapes (Fahrig *et al*., 2011).

At the farm scale, care is required in applying centrally administered schemes and advice if actual benefits are to be realized. For example, adding supposedly functional diversity to farmland can be at best ineffective if the plant traits are not well researched, with some commercially available "wildflower" seed mixes containing seeds of potential weeds such as Californian poppy (*Eschscholzia californica*), poorly-competitive biennials such as parsnip (*Pastinaca sativa*), or those that may benefit insect pest species more than pollinators. Instead, augmenting such seed mixes or combining wildflowers with grass species could further benefit biodiversity through AES, depending on the farmland setting (Haaland *et al*., 2011).

This is not to say that agri-environment schemes should be abandoned or that farmscale efforts are likely to fail. On the contrary, such schemes should be constantly developed using feedback from many of the above studies (Kleijn and Sutherland, 2003; Franzén and Nilsson, 2008). The additional and often unconsidered benefits of habitat management to the farm, landscape and society, targeted at a single service such as pollination, can often outweigh the associated costs (Fiedler *et al*., 2008; Wratten *et al*., 2013). It is, perhaps, the difficulty inherent in estimating the monetary value of such benefits that explains in part the reluctance of some landowners to adopt certain schemes or systems (Wratten *et al*., 2013).

Model scenarios of the trade-offs between ecosystem services, biodiversity and commodity production suggest that where management or farming focuses on market returns (i.e. maximizing productive output), the provision of biodiversity and multiple ecosystem services may be reduced if there is no payment policy for ecosystem services. For example, if a farmer dedicates a higher proportion of management effort and space to crop production so as to increase market returns, this may be to the detriment of ecosystem services and biodiversity conservation. However, when ecosystem services or biodiversity are prioritized, there is little tradeoff between the two (Nelson *et al*., 2009; Lavorel *et al*., 2011). In fact, Lavorel *et al*. (2011) suggest that ecosystem service "hot spots" coincide with areas of high species diversity and functional diversity, and that ecosystem services can act synergistically, which suggests that good management can result in important ecosystem service levels, while simultaneously conserving biodiversity. In one study, incorporating payment for ecosystem services provisions in market-driven approaches acted to balance the market return tradeoff, so that biodiversity and ecosystem services were less impacted (Nelson *et al*., 2009). In contrast, observations by Kleijn and Sutherland (2003) suggest that farmers with an ecological or conservation ethos are more successful at AES management. Subsequently, when incentives are introduced, agri-environmental schemes may be considered a "financially beneficial inconvenience" where the minimum management possible is undertaken to gain payment. Studies of multiple ecosystem services highlight the importance of teasing apart the mechanisms driving delivery of ecosystem services, such as land use, management, biotic and abiotic factors, and particularly functional traits (Kremen, 2005; Butler *et al*., 2011). They also emphasize that social and economic factors must be considered. Continued study in this area should further examine synergies and tradeoffs, providing guidance and information on the most appropriate way to simultaneously manage ecosystem services, commodity production and biodiversity conservation.

6

COST-BENEFITS TO CROP PRODUCTIVITY OF PROMOTING POLLINATOR FRIENDLY WEEDS

Orchard tree and rambutan climber, in a mixed planting

6.1 CONTRIBUTION OF WEEDS TO CROP PRODUCTIVITY (VIA POLLINATION)

Unquestionably, weeds stress crop plants through interference processes. However, substantial evidence suggests that weed presence in crop fields cannot automatically be judged to be damaging and in need of immediate control. In fact, crop/weed interactions are overwhelmingly site specific and vary according to the plant species involved, weed densities, time of competition in relation to crop cycle, environmental factors and management practices. Similarly, weed control methods cannot be solely rated on the basis of their effectiveness, because factors such as access (to mechanical implements, hoes and herbicides), cost, resulting net income, timeliness of operations and alternative uses of labour are also key to the selection of chemical, mechanical or manual control tactics. Another issue is the question of valuable ecosystem services, such as pollination, which may be lost when weeds are removed – even if the control method proves economically more profitable. Even if farmers realize that selected weeds may provide valuable forage resources to pollinators that will benefit their crops, the choice of hand-weeding to selectively remove weeds and leave beneficial ones may prove considerably more costly than using herbicides. Therefore, hand-weeding may not at first glance seem a viable option. However, herbicide applications generally remove all weeds, including pollinator-friendly weeds. Weed control and the removal of alternative foraging resources could easily offset the economic advantages of herbicides, especially in the case of a pollinator-dependent crop. Various authors have recorded 19 to 37 percent increases in the yield of several crops as a result of using honey bees as crop pollinators (Allen-Wardell *et al*., 1998; Klein *et al*., 2007). Thus, the economics of weed control methods have to be balanced against the needs of crops for pollinators. It is important to ensure that the provision of flowering weeds will not reduce crop yields; otherwise, the advantages of conserving pollinators will be offset. This is an area of research that needs further attention.

Data are available to calculate the benefits of greater pollination from leaving more uncultivated land (dominated by blooming weeds) around crop fields. The best available study exploring the potential economic benefit of uncultivated area for pollinators was conducted in a typical canola Canadian agroecosystem. Mean seed set in open-pollinated canola fields was 18.1 ± 0.2 seeds/pod. Mean amount of uncultivated land within 750 m of field edges was 91.1 ± 12.0 ha (n = 22 fields). The rest was composed primarily of tilled field crops. In 2002 and 2003, the transgenic (GMHT) and conventional varieties in the study area yielded an average of 1 120, 1 568, 1 344 and 1 568 kg/ha, respectively. Taking an average yield of 1 400 kg/ha, a typical quarter section (64 ha) of canola would yield 89 600 kg. Prices for canola seed have fluctuated between US$0.22 and US$0.39 kg^{-1} for the last five years. Using a typical but conservative price estimate for the 2002 and 2003 seasons of US$0.27 kg-1, gross revenue was US$24 192 per quarter section. Approximately US$17 000 of this consisted of input costs, resulting in a profit of US$7 192 per section.

From this study area, a typical agricultural landscape with canola on a scale of 4 km^2 could have five 800 m × 800 m canola fields. If all five fields had approximately 64 ha of uncultivated land within 750 m of field edges, profit per field, at 1 335 kg/ha yield and a market value of US$0.27 kg-1, would be US$6 069. The profit from the five canola fields in this landscape would be US$30 345. However, if a central section of 64 ha had not been cultivated or was allowed to revert to a semi-natural state, there would be 128 ha of uncultivated land within 750 m from the four remaining cultivated canola field edges, and the bee abundance index would increase from a mean 30.1 to 63.9 in each field, with a corresponding pollination deficit change of -6.7 to -4.9 – an increase of 1.8 seeds/pod. Yield would increase from 1 335 to 1 467 kg/ha and gross revenue per field would equal US$25 350. Because wild pollinators provide a "free" pollination service, input costs per field would remain the same (US$17 000 per quarter section) and profit would be US$8 350 quarter section, representing a 38 percent increase in profit per field. Net value of canola in this second landscape scenario (four fields) would be US$33 400 – a 10 percent increase in landscape profit over five fields without a central uncultivated area. Harvesting and transport costs may increase slightly with greater yields, but this is not included in the analysis (Morandin and Winston, 2005).

Landscape profit rose sharply with an increase from 0 to approximately 20 percent of uncultivated land. Rate of profit increase decreased from 20 percent to 30 percent of uncultivated land, indicating that the most benefit of uncultivated land was seen when increasing from low to moderate amounts. Above 32.7 percent, declining amounts of cultivated canola outweighed the benefits of greater pollination from more uncultivated land. Thus, maximum landscape profit was achieved with just over 30 percent of the landscape uncultivated (Morandin and Winston, 2006).

The value of wild and/or managed pollinators in commercial crop production has been estimated in many countries using different methods. Ascribed values have varied dramatically depending on the methodology used, with managed honey bee annual values in the United States estimated at between US$1.6 billion and US$14.6 billion. Recently, the annual value of maintaining feral honey bee pollination ecosystem services in Australia, by preventing the introduction of *varroa* mites, was calculated as between AUS$16.4 and AUS$38.8 million (US$12.6–30.7 million) (Losey and Vaughan, 2006; Gallai *et al.*, 2009).

Current methods either underestimate the service value (by equating the value of pollination services to the direct cost of the service) or overestimate it (by equating the value of pollination services to the proportion of total production value dependent on insect pollination). To distinguish between the managed and wild components, researchers in South Africa calculated the value of managed pollination as the proportion of pollination attributed to manage pollinators multiplied by the insect-dependent production value. In turn, the value of wild pollination was calculated as the difference between the (total) insect-dependent production and managed pollination values. Using this method, the contribution of managed honey bee pollination was found to be between US$28.0 million and US$122.8 million, for which only US$1.8 million is presently being paid. Similarly, the contribution of wild pollinators was found to be between US$49.1 million and US$310.9 million for which there is no direct payment from producers. These values illustrate the importance of maintaining natural and other forage areas for the conservation of insect pollinators (Allsopp *et al.*, 2008).

6.2 BROADER ECONOMIC CONSIDERATIONS

The costs and benefits of enhancing any ecosystem service are generally difficult to compartmentalize, simply because nature is often not conducive to this kind of categorization (Gomez-Baggethun *et al.*, 2010). Depending on the foraging range of the pollinating species, the service of pollination may not be restricted within the boundaries of one farm. If this is the case, a single farmer's assessment of the costs and benefits of reducing weed control are unlikely to consider impacts on the wider landscape, other farms nearby or on society (Zhang *et al.*, 2007). Such problems with true valuation are compounded by the results of studies that suggest that habitat improvements, such as pollinator forage provision, are more likely to succeed if applied to the surrounding landscape (Rundlöf *et al.*, 2008; Merckx *et al.*, 2009).

Cost-benefit analysis also does not often take into account the side effects of measures to improve habitats (Jackson *et al.*, 2007). For example, many commercially available wildflower seed mixes recommended to farmers as part of agri-environment schemes in Europe are designed to attract both pollinators and natural enemies (Haaland *et al.*, 2011). Depending on the crop around which these plants are sown, these non-crop flowers will therefore carry dual benefits, both of which may not be accounted for. These mixtures may also suppress weeds in field margins (Pywell *et al.*, 2005), facilitate the survival of rare plants and insects of conservation value (e.g. Marshall and Moonen 2002), provide food to farmland birds (Boatman, 1989), enhance agroecosystem resilience (Hooper *et al.*, 2005), and provide aesthetic benefits (Forbes *et al.*, 2009), all of which may be beneficial or present indirect savings to the farmer or society.

More research is required to ensure that the opposite does not occur. Some non-crop flowering plants are also attractive to species of insect pests, and research has shown that some species that are thought to enhance the fitness of natural enemies can also be rewarding to the pests they are supposed to be attacking (Baggen and Gurr, 1998; Lavandero *et al.*, 2005).

This need to consider the external benefits and the inadvertent costs of many natural habitat enhancements highlights the importance of understanding the ecology of the pollination system involved in crop production. The need to use the "right kind of biodiversity" (Landis *et al.*, 2000) is important in encouraging both the effective pollinators of the crops, and to encourage a community of pollinators that will provide alternatives in the event of environmental fluctuations. Reliance on a single species, such as the honey bee, or managed solitary bee species, such as *Osmia lignaria* or *Megachile rotundata*, is now considered a strategy that carries a high degree of risk. The rental of hives of pollinators is a large cost in itself, and bees may need food supplements or the regular moving of hives. The costs of these factors also need to be weighed against those of weed control and enhancing floral resources for wild bee communities.

Only been a small number of studies in relatively simple crop systems have demonstrated the economic benefit of pollination conservation, such as the Canadian canola production study described above (Morandin and Winston, 2006). Similar effects have been found in coffee production, though with differing profit levels due to different landscape composition. In Costa Rica, wild bees from tropical rainforest fragments within 1 km increased coffee yields by 20 percent, which translated into a profit of US$60 000 for one farm, or US$393 worth of pollination services per hectare of forest (Ricketts *et al*., 2004). However, in Indonesia the figure was only US$55/ha of forest (Priess *et al*., 2007).

Assessing the myriad potential costs and benefits of pollination has so far proven difficult for researchers, let alone farmers, so alternative ways of assessing the important factors may be required. For example, Raudsepp-Hearne *et al*. (2010) developed a valuation system based on "bundles" of ecosystem services that often occur together. In this way, the interactions between services are captured and the double-counting problem of summing inventories of services is avoided. Alternatively, Farber *et al*. (2006) detail a framework in which the changes in ecosystem services occurring under different management strategies are valued using techniques appropriate to each type of service, including non-monetary methods. The changes are then scored, weighted and summed to determine the most effective strategy overall. The presentation of services in such a way makes economic valuations more relevant to farmers.

Until further research of this type is conducted to demonstrate the economic incentives of providing alternative forage for pollinators, farmers are unlikely to take valuable land out of production (Kremen and Chaplin, 2007). Where pollination shortages are not yet being experienced, or where farms are located in favourable landscapes, the challenge involved in improving pollinator communities may be too great (Kremen and Chaplin, 2007). The above research is vital, however, to the development of "packaged" management actions, such as service-providing units (Luck *et al*., 2003; Luck *et al*., 2009), which make effective small-scale and low-cost recommendations that result in major improvements, and contribute to a farmer's agri-environment scheme assessment.

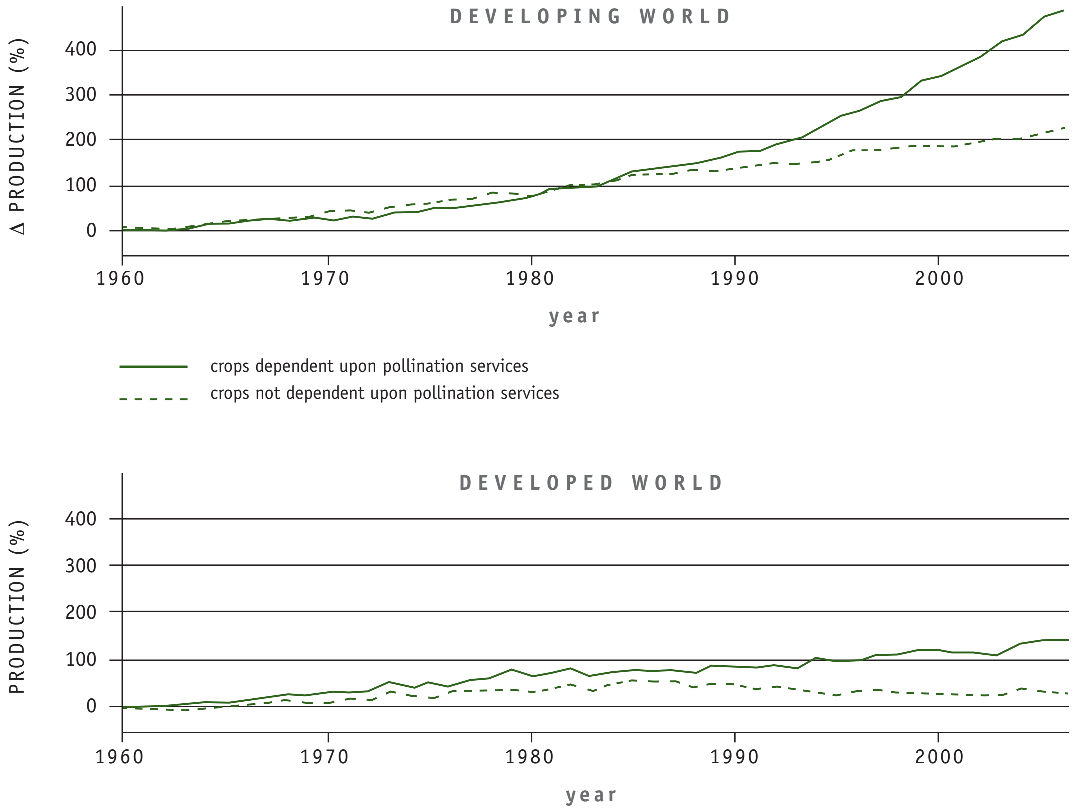
7

CONCLUSION

Sunflowers close to wild habitat, Yolo County, CA USA

Researchers have reported that the area devoted to pollinator-dependent crops has increased faster than that of nondependent crops in both the developed and developing worlds (Aizen *et al.*, 2009. Therefore, demand for animal pollination service is rising simultaneous with the decline in pollinator abundance and diversity. The global population of managed honey bee hives has increased by about 45 percent during the last half century (Figure 4). But with the much more rapid (> 300 percent) increase in the fraction of agriculture that depends on animal pollination, during the last half century, the global capacity to provide sufficient pollination services may be under stress (Aizen and Harder, 2009).

FIGURE 4. TEMPORAL TRENDS IN TOTAL CROP PRODUCTION FROM 1961 TO 2006



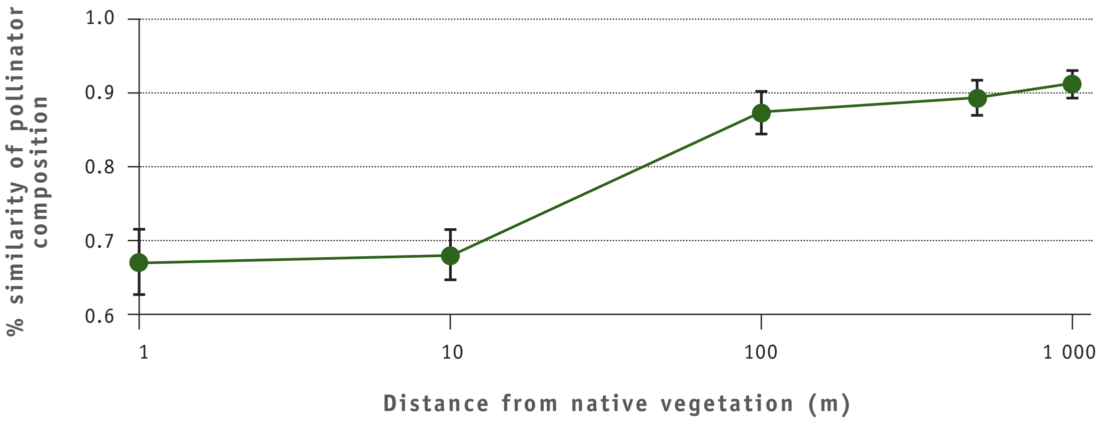
Source: Aizen *et al*, 2009

A pollinator crisis seems more acute in landscapes dominated by annual crops (e.g. grains and oil seeds), as these intensively managed monocultures do not provide environmental opportunities for beneficial insects. High levels of disturbance or vast areas of uniform crops hamper the establishment of pollinator populations and this could prove critical for some crops, such as canola, flax, safflower, sunflower, tomatoes, peppers, strawberries and cucurbits, and for cole crops that require insect pollination for seed production.

In such areas of intensive farming, field margins, field edges and paths, headlands, fence lines, rights of way, nearby uncultivated patches of land and so on, are important refuges for many pollinators, yet the value of these areas to agricultural productivity is unknown, and few farmers manage such areas to enhance beneficial entomofauna. Many crops grown near fragments of native forests get significant pollination benefits, as shown in grapefruit crops close to subtropical forests in Argentina, where Chacoff and Aizen (2006) found greater pollinator diversity close to the margins (Figure 5). Research on agricultural landscapes where pollen deposition and crop yield were positively related to the amount of uncultivated land in proximity to fields, indicates a challenging association between crop production and pollination services provided by wild bees from natural areas (Ricketts *et al.*, 2008).

In most agroecosystems, weeds are ever-present biological components within and around fields, adding to the complexity of interacting trophic levels mediating a number of cropinsect

FIGURE 5. EFFECTS OF DISTANCE FROM NATIVE VEGETATION ON SIMILARITY OF POLLINATOR SPECIES RICHNESS FOR GRAPEFRUIT CROPS IN ARGENTINA



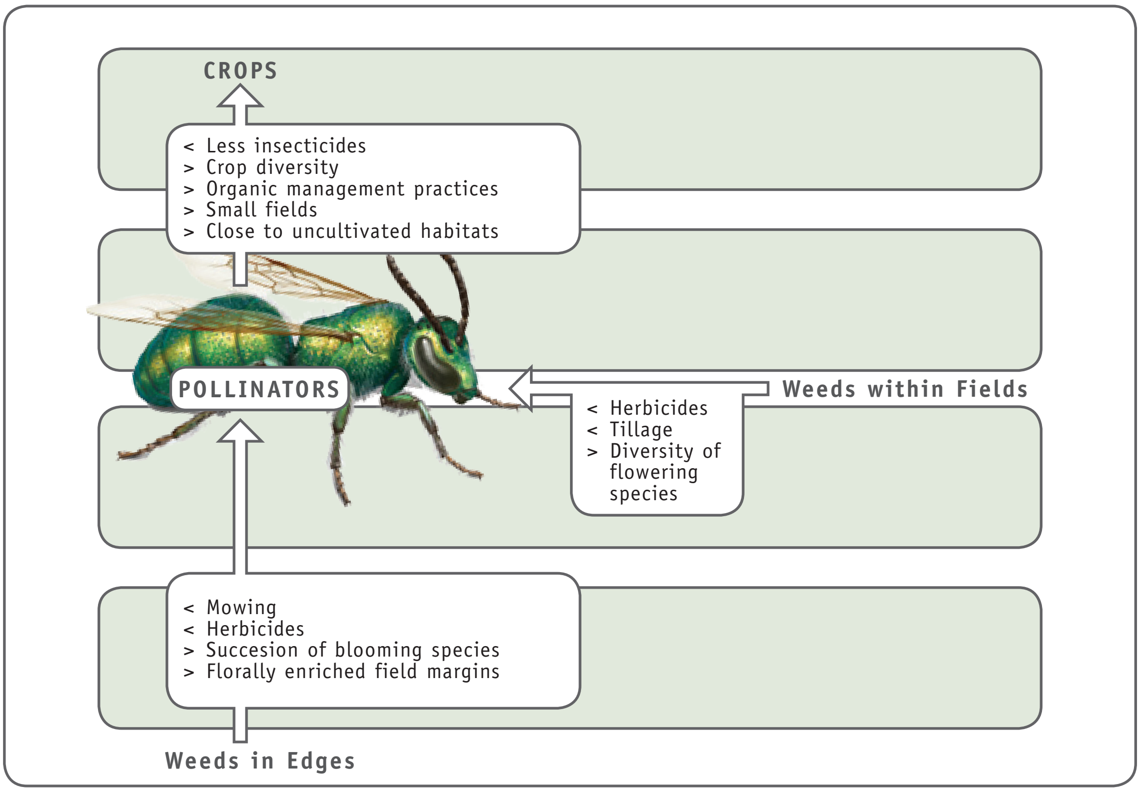
Remnants of semi-natural habitat along one edge of intensive grapefruit (Mach) plantation in the northwest of Argentina

Source: after Chacoff and Aizen (2006).

interactions with major effects on final yields. An increasing awareness of these ecological relationships elevates weed management as a key strategy to rectify habitat simplification by increasing vegetational diversity in agroecosystems, and thus food resources for beneficial insects. Figure 6 describes strategies for promoting desirable flowering weed diversity within and around fields to encourage pollinators as well as other practices that would complement such strategies.

Appropriate management of non-cropped areas to encourage wild pollinators may prove to be a cost-effective means of maximizing crop yield. Depending on the crops they grow, farmers may wish to encourage particular species. For example, field beans grown in the United Kingdom require healthy populations of the long-tongued bumble bees, *B. pascuorum* and *B. hortorum*. To encourage them, the farmer might sow wildflower strips containing deep flowers, such as white deadnettle (*Lamium album*) and red clover (*T. pratense*). Of course, the crops themselves provide vast areas of forage, but only for short periods. However, planting a succession of crops that flower at different times could greatly enhance pollinator abundance while simultaneously maximizing yields.

FIGURE 6. STRATEGIES TO ENCOURAGE WEED FLORAL DIVERSITY WITHIN AND AROUND CROP FIELDS TO CONSERVE AND ENHANCE INSECT POLLINATORS



Similarly, managing flowering weeds at desirable levels to provide alternative forage to pollinators within crop fields has been a totally neglected habitat management tactic for encouraging pollinators. Many advances, however, have been achieved in the area of biological control where entomologists and agroecologists continually manipulate weeds and other floral diversity to enhance predators and parasitoids of pests (Altieri and Nicholls, 2004). The same principles that apply in biological control can be applied to enhance pollinator services, thus simultaneously achieving plant protection and pollination.

In annual crops, allowing weed diversity after the critical period of weed competition or providing weeds as field borders or strips every few crop rows, has proven to be agronomically feasible. In orchards, cover crop management, although not solely directed at weed control, can enhance soil quality and habitat for beneficial insects, thus positively affecting pollination in many fruit crops. The challenge is to identify a mixture of weed groundcover species that encourages bee visitations without competing with the fruit crop. It is of particular importance to find species that produce an abundance of nectar and pollen, yet flower before and after pollinator-dependent crops, thus helping to sustain wild bee populations in the local area. For example, a perennial cover crop would permit ground-nesting bees to establish in orchards that otherwise provide resources only over the short blooming period of the trees.

Clearly, a more comprehensive strategy for managing pollinators in agroecosystems is needed. In addition to understanding the biology of flowers and the behaviour of pollinators, it is important to understand how to manage agroecosystems in order to provide nesting habitats, as well as continuing alternative sources of forage that can sustain populations of pollinators year around.

So far, weed management with the specific aim of enhancing wild pollinator populations is in its infancy, and at present is largely based on educated guesswork. More research is warranted to advance knowledge on identifying beneficial weed species and ways to sponsor them to attract pollinators, while not reducing yields through interference. However, the basic concepts of managing weeds and non-crop plants to cause the least damage, and provide additional benefits, are ones that farmers can and do put into practice every day.

REFERENCES

Abel, C.A. & Wilson, R.L. 1998. The use of diverse plant species for increasing *Osmia cornifrons* (Hymenoptera: Megachilidae) in field cages. *Journal of the Kansas Entomological Society*, 71: 23–28.

Abrol, D.P. 2006. Foraging behaviour of bees as influenced by quality and quantity of rewards from flowers. *Journal of Asia-Pacific Entomology*, 9: 145–148.

Adams, J.B. & Drew, M.E. 1965. Grain aphids in New Brunswick. Ill. Aphid populations in herbicide-treated oat fields. *Canadian Journal of Zoology*, 43: 789–794.

Aizen, M.A. & Feinsinger, P. 1994a. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, 75: 330–351.

Aizen, M.A. & Feinsinger, P. 1994b. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano". *Ecol. Appl.*, 4: 378–392.

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. 2009. Long term global trends in crop yields and production reveal no current pollinator shortage but increasing pollinator dependency. *Curr. Biol.*, 18: 1572–1575.

Aizen, M.A. & Harder, L.D. 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr. Biol.*, 19: 915–918.

Alanen, E-L., Hyvönen, T., Lindgren, S., Härmä, O. & Kuussaari, M. 2011. Differential responses of bumble bees and diurnal Lepidoptera to vegetation succession in long-term set-aside. *Journal of Applied Ecology*, 48: 1251–1259. DOI: 10.1111/j.1365-2664.2011.02012.x.

Alaux, C., Ducloz, F., Crauser, D. & Le Conte, Y. 2010. Diet effects on honey bee immunocompetence. *Biology Letters*, 6: 562–565. DOI: 10.1098/rsbl.2009.0986.

Albrecht, M., Duelli, P., Müller, C., Kleijn, D. & Schmid, B. 2007. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology*, 44: 813–822. DOI: 10.1111/j.1365-2664.2007.01306.x.

Aldrich, R.J. 1984. *Weed-crop ecology-principles in weed management.* North Scituate, MA, Breton Publishers.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P. & Walker, S. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, 12: 8–17.

Alm, J., Ohmeiss, T.E., Lanza, J. & Vriesenga, L. 1990. Preference of cabbage white butterflies and honey-bees for nectar that contains amino-acids. *Oecologia*, 84: 53–57. DOI: 10.1007/bf00665594.

Allsopp, M., de Lange, W.J. & Veldtman, R. 2008. Valuing insect pollination services with cost of replacement. *PLOS One*, 3(9): e3128. DOI: 10.1371/Journal.pone. 0003128.

Altieri, M.A., v. Schoonhoven, A. & Doll, J.D. 1977. The ecological role of weeds in insect pest management systems: a review illustrated with bean (*Phaseolus vulgaris L.*) cropping systems. *PANS*, 23(2): 195–205.

Altieri, M.A. & Whitcomb, W.H. 1979a. The potential use of weeds in the manipulation of beneficial insects. *HortScience*, 14(1): 12–18.

Altieri, M.A. & Whitcomb, W.H. 1979b. Manipulation of insect populations through seasonal disturbance of weed communities. *Protection Ecology*, 1: 185–202.

Altieri, M.A. & Letourneau, D.K. 1982. Vegetation management and biological control in agroecosystems. *Crop Protection*, 1: 405–430.

Altieri, M.A. & Nicholls, C.I. 2004. *Biodiversity and pest management in agroecosystems*. New York, Harworth Press.

Amiet, F., Herrmann, M., Müller, A. and Neumeyer, R. 2004. Apidae 4: *Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis*. Fauna Helvetica. Vol. 9. Centre Suisse de Cartographie de la Faune (CSCF)/Schweizerische Entomologische Gesellschaft (SEG), 274 pp.

Ambrosino, M.D., Luna, J.M., Jepson, P.C. & Wratten, S.D. 2006. Relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects, and herbivores. *Environmental Entomology*, 35: 394–400.

Anderson, R.N. 1968. *Germination and establishment of weeds for experimental purposes*. Washington, DC, Weed Science Society of America.

Arthur, A.D., Li, J., Henry, S. & Cunningham, S.A. 2010. Influence of woody vegetation on pollinator densities in oilseed Brassica fields in an Australian temperate landscape. *Basic and Applied Ecology*, 11: 406–414. DOI: 10.1016/j.baae.2010.05.001.

Ashworth, L., Aguilar, R., Galetto, L. & Aizen, M.A. 2004. Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *J. Ecol.*, 92: 717–719.

Backman, J-P.C. & Tiainen, J. 2002. Habitat quality of field margins in a Finnish farmland area for bumble bees (Hymenoptera: *Bombus* and *Psithyrus). Agriculture, Ecosystems and Environment*, 89: 53–68

Baggen, L.R. & Gurr, G.M. 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, Phthorimaea operculella (Lepidoptera: Gelechiidae). *Biological Control*, 11: 9–17.

Baker, H.G. & Baker, I. 1973. Amino-acids in nectar and their evolutionary significance. *Nature*, 241: 543–545. DOI: 10.1038/241543b0.

Baker, H.G. & Baker, I. 1983. A brief historical review of the chemistry of floral nectar. In: B. Bentley & T.S. Elias, eds. *The biology of nectaries*, pp. 126–152. New York, Columbia University Press.

Baker, H.G. & Baker, I. 1986. The occurrence and significance of amino-acids in floral nectar. *Plant Systematics and Evolution*, 151: 175–186. DOI: 10.1007/bf02430273.

Baliddawa, C.W. 1985. Plant species diversity and crop pest control: an analytical review. *Insect Sci. Appl.*, 6: 479–487.

Ball, D.A. & Miller, S.D. 1990. Weed seed population response to tillage and herbicide use in three irrigated cropping sequences. *Weed Science*, 38: 511–517.

Ball, D.A. 1992. Weed seed-bank response to tillage, herbicides, and crop rotation sequences. *Weed Science*, 40: 654–659.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J-S., Nakashizuka, T., Raffaelli, D. & Schmid, B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9: 1146–1156. DOI: 10.1111/j.1461-0248.2006.00963.x.

Bantilan, R.T, Palada, M. & Harwood, R.R. 1974. Integrated weed management. I. Key factors affecting weed-crop balance. *Philippine Weed Science Bulletin*, 1: 14–36.

Barberi, P. 2002. Weed management in organic agriculture: are we addressing the right issues? *Weed Research*, 42: 177–193.

Barnes, A.M., Wratten, S.D. & Sandhu, H.S. 2009. Harnessing biodiversity to improve vineyard sustainability. *Outlooks on Pest Management*, 20: 250–255. DOI: 10.1564/20dec04.

Barthell, J.F., Randall, J.M., Thorp. R.W. & Wenner, A.M. 2001. Promotion of seed set in yellow star-thistle by honey bees: evidence of an invasive mutualism. *Ecological Applications*, 11: 1870–1883.

Bascompte, J., Jordano, P., Melian, C.J. & Olesen, J.M. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100: 9383–9387. DOI: 10.1073/pnas.1633576100.

Batra, S.W.T. 1995. Bees and pollination in our changing environment. *Apidologie*, 26: 361–370. DOI: 10.1051/apido:19950501.

Belfrage, K, BJörklund, J. & Salomonsson, L. 2005. The effects of farm size and organic farming on diversity of birds, pollinators, and plants in a swedish landscape. *Ambio*, 8(34): 582–588.

Benedek, P. 1972. Possible indirect effect of weed control on population changes of wild bees pollinating lucerne. *Acta Pathol. Acad. Sci. Hung.*, 7: 267–278.

Benedek, P. 1996. Structure and density of lucerne pollinating wild bee populations as affected by changing agriculture. *Acta Horticulturae*, 437: 353–357.

Bengtsson, J., Ahnström, J. & Weibull, A-C. 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology*, 42: 261–269. DOI: 10.1111/j.1365-2664.2005.01005.x.

Bennett, E.M., Peterson, G.D. & Gordon, L.J. 2009. Understanding relationships among multiple ecosystem services. *Ecology Letters*, 12: 1394–1404. DOI: 10.1111/j.1461-0248.2009.01387.x.

Bianchi, F., Booij, C.J.H. & Tscharntke, T. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B-Biological Sciences*, 273: 1715–1727.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313: 351–354.

Bjerknes, A-L., Totland, O., Hegland, S.J. & Nielsen, A. 2007. Do alien plant invasions really affect pollination success in native plant species? *Biological Conservation*, 138: 1–12. DOI: 10.1016/j.biocon.2007.04.015.

Blanche, K.R., Ludwig, J.A. & Cunningham, S.A. 2006. Proximity to rainforest enhances pollination and fruit set in orchards. *Journal of Applied Ecology*, 43: 1182–1187.

Boatman, N.D. 1989. Selective weed control in field margins. *In BCPC Symposium Proceedings 1989*, pp. 85–794. Farnham, UK, British Crop Protection Council.

Bohart, G.E. 1972. Management of habitats for wild bees. Proceedings of the Tall Timbers Conference on Ecological Animal Control by Habitat Management, 3: 253–266.

Boonithee, A., Juntawong, N., Pechhacker, H. & Hüttinger, E. 1991. Floral visits to select crops by four apis species and trigona SP in Thailand. *Acta Horticulturae*, 288: 74–80.

Bosch, J. & Blas, M. 1994. Foraging behavior and pollinating efficiency of Osmia-Cornuta and Apis-Mellifera on almond (Hymenoptera, Megachilidae and Apidae). *Applied Entomology and Zoology*, 29: 306–306.

Bosch, J. & Kemp, W.P. 2002. Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bulletin of Entomological Research*, 92: 3–16. DOI: 10.1079/ber2001139.

Bosch, J., Kemp, W.P. & Trostle, G.E. 2006. Bee population returns and cherry yields in an orchard pollinated with Osmia lignaria (Hymenoptera: Megachilidae). *Journal of Economic Entomology*, 99: 408–413.

Bowers, M.A. 1986. Resource availability and timing of reproduction in bumble bee colonies (Hymenoptera, Apidae). *Environmental Entomology*, 15: 750–755.

Branquart, E. & Hemptinne, J.L. 2000. Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphinae). *Ecography*, 23: 732–742. DOI: 10.1034/j.1600-0587.2000.230610.x.

Brian, A.D. 1957. Differences in the flowers visited by four species of bumble-bee and their causes. *Journal of Animal Ecology*, 26: 71–98.

Brighenti, D.M., Brighenti, C.R.G., Cirillo, M.A. & Santos, C.M.B. 2010. Optimization of the components of an energetic diet for Africanized bees through the modelling of mixtures. *Journal of Apicultural Research*, 49: 326–333. DOI: 10.3896/ibra.1.49.4.05.

Brittain, C., Bommarco, R., Vighi, M., Barmaz, S., Settele, J. & Potts, S.G. 2010. The impact of an insecticide on insect flower visitation and pollination in an agricultural landscape. *Agricultural and Forest Entomology*: 12(3): 259–266. DOI: 10.1111/j.1461-9563.2010.00485.x.

Brittain, C., Bommarco, R., Vighi, M., Settele, J. & Potts, S.G. 2010a. Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biological Conservation*, 143: 1860–1867.

Brittain, C.A., Vighi, M., Bommarco, R., Settele, J. & Potts, S.G. 2010b. Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology*, 11: 106–115. DOI: 10.1016/j.baae.2009.11.007.

Bromenshenk, J.J., Henderson, C.B., Wick, C.H., Stanford, M.F., Zulich, A.W., Jabbour, R.E., Deshpande, S.V., McCubbin P.E., Seccomb, R.A., Welch, P.M., Williams, T., Firth, D.R., Skowronski, E., Lehmann, M.M., Bilimoria, S.L., Gress, J., Wanner, K.W. & Cramer, R.A. Jr. 2010. Iridovirus and microsporidian Linked to honey bee colony decline. *Plos One*, 5. DOI: e1318110.1371/journal.pone.0013181.

Brookes, B., Small, E., Lefkovitch, L.P., Damman, H. & Fairey, D.T. 1994. Attractiveness of alfalfa (Medicago-Sativa L) to wild pollinators in relation to wildflowers. *Canadian Journal of Plant Science*, 74: 779–783.

Brosi, B.J. 2009. The complex responses of social stingless bees (Apidae: Meliponini) to tropical deforestation. *Forest Ecology and Management,* 258: 1830–1837. DOI: 10.1016/j.foreco.2009.02.025.

Brosi, B.J., Daily, G. & Ehrlich, P. 2007. Bee community shifts with landscape context in a tropical countryside. *Ecological Applications*, 17: 418–430.

Brosi, B.J., Daily, G.C., Shih, T.M., Oviedo, F. & Duran. G. 2008. The effects of forest fragmentation on bee communities in tropical countryside. *Journal of Applied Ecology*, 45: 773–783. DOI: 10.1111/j.1365-2664.2007.01412.x.

Brown, J.C. & Albrecht, C. 2001. The effect of tropical deforestation on stingless bees of the genus Melipona (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. *Journal of Biogeography*, 28: 623–634. DOI: 10.1046/j.1365-2699.2001.00583.x.

Brown, J.H. & Kodric-Brown, A. 1979. Convergence, competition, and mimicry in a temperate community of hummingbird-pollinated flowers. *Ecology*, 60: 1022–1035. DOI: 10.2307/1936870.

Buchanan, G.A. 1977. Weed biology and competition. In: B. Truelove, ed. *Research methods in weed science*, 2nd edition, pp. 25–41. Auburn, AL, Southern Weed Science Society, Auburn University.

Buchmann, S.L. 1985. Bees use vibration to aid pollen collection from non-poricidal flowers. *Journal of the Kansas Entomological Society*, 58: 517–525.

Buchmann, S.L. 1987. The ecology of oil flowers and their bees. *Annual Review of Ecology and Systematics*, 18: 343–369. DOI: 10.1146/annurev.ecolsys.18.1.343.

Buchmann, S.L. & Nabhan, G.P. 1996. *The forgotten pollinators*. Washington, DC, Island Press.

Bugg, R.L. 1994. Habitat manipulation to enhance the effectiveness of aphidophagous hover flies (Diptera: Syrphidae). Sustainable Agriculture: News and Technical Reviews from the University of Calfornia Sustainable Agriculture Research and Education Program, 5: 12–15.

Burkle, L. & Irwin, R. 2009. Nectar sugar limits larval growth of solitary bees (Hymenoptera: Megachilidae). *Environmental Entomology*, 38: 1293–1300.

Butler, J.R., Wong, G.Y., Metcalfe, D.J., Honzák, M., Pert, P.L., Rao, N., van Grieken, M.E., Lawson, T., Bruce, C., Kroon, F.J. & Brodie, J.E. 2011. An analysis of trade-offs between multiple ecosystem services and stakeholders linked to land use and water quality management in the Great Barrier Reef, Australia. *Agriculture, Ecosystems & Environment*. DOI: 10.1016/j.agee.2011.08.017.

Callaway, R.M. 1995. Positive interactions among plants. *Botanical Review*, 61: 306–349. DOI: 10.1007/bf02912621.

Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F. & Griswold, T.L. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America*, 108: 662–667.

Cane, J.H. 1997. Congruent efficiencies of pollination and pollen harvest for bees at Vaccinium (Ericaceae). *Bulletin of the Ecological Society of America*, 78: 63.

Canto-Aguilar, M.A. & Parra-Tabla, V. 2000. Importance of conserving alternative pollinators: assessing the pollination efficiency of the squash bee, Peponapis limitaris in Cucurbita moschata (Cucurbitaceae). *Journal of Insect Conservation*, 4: 203–210.

Carreck, N.L., Osborne, J.L., Capaldi, E.A. & Riley, J.R. 1999. Tracking bees with radar. *Bee World*, 80: 124–131.

Carreck, N.L. & Williams, I.H. 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, 6: 13–23.

Carvalheiro, L.G., Seymour, C.L., Veldtman, R. & Nicolson, S.W. 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *Journal of Applied Ecology*, 47: 810–820. DOI: 10.1111/j.1365-2664.2010.01829.x.

Carvalheiro, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S. & Nicolson, S.W. 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*, 14: 251–259. DOI: 10.1111/j.1461-0248.2010.01579.x.

Carvell, C. 2002. Habitat use and conservation of bumble bees (Bombus spp.) under different grassland management regimes. *Biological Conservation*, 103: 33–49.

Carvell, C. 2004. The response of foraging bumble bees to successional change in newly created arable field margins. *Biological Conservation*, 118: 327–339. DOI: 10.1016/j.biocon.2003.09.012.

Carvell, C., Meek, W.R., Pywell, R.F, Goulson, D. & Nowakowski, M. 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, 44: 29–40. DOI: 10.1111/j.1365-2664.2006.01249.x.

Carvell, C., Meek, W.R., Pywell, R.F. & Nowakowski, M. 2004. The response of foraging bumble bees to successional change in newly created arable field margins. *Biological Conservation*, 118: 327–339.

Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F. & Nowakowski, M. 2006. Assessing the value of annual and perennial forage mixtures for bumble bees by direct observation and pollen analysis. *Apidologie*, 37: 326–340.

Chacoff, N.P. & Aizen, M.A. 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *Journal of Applied Ecology*, 43: 18–27.

Chambers, R.J., Sunderland, K.D., Stacey, D.L. & Wyatt, I.J. 1986. Control of cereal aphids in winter wheat by natural enemies: aphid-specific predators, parasitoids and pathogenic fungi. *Journal of Applied Biology*, 108: 219–231.

Clausen, H.D, Holbeck, H.B. & Reddersen, J. 2001. Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. *Biological Conservation*, 98: 167–178. DOI: 10.1016/s0006-3207(00)00151-8.

Clements, D.R., Weise, S.F. & Swanton, C.J. 1994. Integrated weed management and weed species diversity. *Phytoprotection*, 75(1): 1–18.

Coble, H.D. & Mortenses, D.A. 1992. The threshold concept and its application to weed science. *Weed Technology*, 6: 191–195.

Comba, L., Corbet, S.A., Hunt, L. & Warren, B. 1999. Flowers, nectar and insect visits: evaluating British plant species for pollinator-friendly gardens. *Annals of Botany*, 83: 369–383. DOI: 10.1006/anbo.1998.0835.

Corbet, S.A. 1995. Insects, plants and succession – advantages of long-term set-aside. *Agriculture Ecosystems & Environment*, 53: 201–217. DOI: 10.1016/0167-8809(94)00581-x.

Corbet, S.A., Bee, J., Dasmahapatra, K., Gale, S., Gorringe, E., Ferla, B.L., Moorhouse, T., Trevail, A., van Bergen, Y. & Vorontsova, M. 2001. Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. *Annals of Botany*, 87: 219–232.

Corlett, R.T. 2004. Flower visitors and pollination in the Oriental (Indomalayan) Region. *Biological Reviews*, 79: 497–532. DOI: 10.1017/s1464793103006341.

Cortopassi-Laurino, M. & Gelli, D.S. 1991. Pollen analysis, physicochemical properties and antibacterial action of Brazilian honeys from Africanized honey bees (Apis-Mellifera L) and stingless bees. *Apidologie*, 22: 61–73. DOI: 10.1051/apido:19910108.

Cortopassi-Laurino, M., Imperatriz-Fonseca, V.L., Roubik, D.W., Dollin, A., Heard, T., Aguilar, I., Venturieri, G.C., Eardley, C. & Nogueira-Neto, P. 2006. Global meliponiculture: challenges and opportunities. *Apidologie*, 37: 275–292. DOI: 10.1051/apido:2006027.

Cox-Foster, D.L., Conlan, S., Holmes, E.C., Palacios, G., Evans, J.D., Moran, N.A., Quan, P-L., Briese, T., Hornig, M., Geiser, D.M., Martinson, V., vanEngelsdorp, D., Kalkstein, A.L., Drysdale, A., Hui, J., Zhai, J., Cui, L., Hutchison, S.K., Simons, J.F., Egholm, M., Pettis, J.S. & Lipkin, W.I. 2007. A metagenomic survey of microbes in honey bee colony collapse disorder. *Science*, 318: 283–287. DOI: 10.1126/science.1146498.

Crane, E. 1990. Bees and beekeeping – science, practice and world resources. Ithaca, NY, Cornell University Press.

Cresswell, J.E., Osborne, J.L. & Goulson, D. 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumble bees. Ecological Entomology, 25: 249–255.

Dafni, A., Kevan, P., Gross, C.L. & Goka, K. 2010. Bombus terrestris, pollinator, invasive and pest: an assessment of problems associated with its widespread introductions for commercial purposes. *Applied Entomology and Zoology*, 45: 101–113. DOI: 10.1303/aez.2010.101.

Dar, S.A., Khan, Z.H. & Abass, A. 2010. Pollinator decline: a major issue in crop production. *Research Journal of Agricultural Sciences 2010*, 1(4): 491–493

Davis, A.S. & Liebman, M. 2001. Nitrogen source influences wild mustard growth and competitive effect on sweet corn. *Weed Science*, 49: 558–566.

De Schutter, O. 2010. General Assembly Special Rappoteur. Development.

Decourtye, A., Mader, E. & Desneux, N. 2010. Landscape enhancement of floral resources for honey bees in agro-ecosystems. *Apidologie*, 41: 264–277. DOI: 10.1051/apido/2010024.

Delaplane, K.S. & Mayer, D.F. 2000. *Crop pollination by bees*. Wallingford, UK, CABI Publishing.

Dempster, J.P. 1969. Some effects of weed control on the numbers of the small cabbage white (Pieris rapae L.) on brussel sprouts. *Journal of Applied Ecology*, 6: 339–405.

Diaz, S., Lavorel, S., de Bello, F., Quetier, F., Grigulis, K. & Robson, M. 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, 104: 20684–20689. DOI: 10.1073/pnas.0704716104.

Dixon, D.P. & Fingler, B.G. 1982. The effects of the 1981 Manitoba emergency mosquito control program on honey bees. In: *Western Equine Encephilitis in Manitoba*, pp. 243–247. Winnipeg, Government of Manitoba.

Dixon, D.P. & Fingler, B.G. 1984. The effects of the mosquito control program on bees. In: Final Technical Report on Environmental Monitoring Program for the 1983 Spraying of Malathion to Combat Western Equine Encephalitis, pp. 101–121. Winnipeg, Government of Manitoba.

Dobson, A., Lodge, D., Alder, J., Cumming, G.S., Keymer, J., McGlade, J., Mooney, H., Rusak, J., Sala, O., Wolters, V., Wall, D. & Xenopoulos M. 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, 87: 1915–1924.

Donald, PF. & Evans, A.D. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, 43: 209–218. DOI: 10.1111/j.1365-2664.2006.01146.x.

Dover, J.W., Sotherton, N. & Gobbett, K. 1990. Reduced pesticide inputs on cereal field margins: the effects on butterfly abundance. *Ecol. Entomol.*, 15: 17–24.

Dramstad, W. & Fry, G. 1995. Foraging activity of bumble bees (Bombus) in relation to flower resources on Arable Land. *Agriculture Ecosystems & Environment*, 53: 123–135. DOI: 10.1016/0167-8809(94)00561-r.

Duchateau, M.J. 1989. Ovarian development and egg laying in workers of Bombus terrestris. *Entomologia Experimentalis et Applicata*, 51: 199–213

Duffield, G.E., Gibson, R.C., Gilhooly, M., Hesse, A.J., Inkley, C.R., Gilbert, F.S. & Barnard, C.J. 1993. Choice of flowers by foraging honey-Bees (Apis-Mellifera) – possible morphological cues. *Ecological Entomology*, 18: 191–197. DOI: 10.1111/j.1365-2311.1993.tb01089.x.

Ebeling, A., Klein, A.M., Schumacher, J., Weisser, W.W. & Tscharntke, T. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, 117: 1808–1815.

Ellis, W.N. 1995. Flower visitation, plant's life forms, plant's life forms and ecological characteristics (Syrphidae, Parasitica). *Proc. Sec. Appl. Entomol. Netherlands Entomol. Soc.* (NEV), 6: 53–58.

Eltz, T., Bruhl, C.A., van der Kaars, S., Chey, V.K. & Linsenmair, K.E. 2001. Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest. *Insectes Sociaux*, 48: 273–279. DOI: 10.1007/pl00001777.

Eltz, T., Bruhl, C.A., van der Kaars, S. & Linsenmair, K.E. 2002. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. *Oecologia*, 131: 27–34. DOI: 10.1007/s00442-001-0848-6.

Engels, W., Schultz, U. & Radler, M. 1994. Use of the tübingen mix for bee pasture in Germany. In: A. Matheson, ed. *Forage for bees in an agricultural landscape*. Cardiff, International Bee Research Association, pp. 57–65.

Evans, J.D., Spiewok, S., Teixeira, E.W. & Neumann, P. 2008. Microsatellite loci for the small hive beetle, Aethina tumida, a nest parasite of honey bees. *Molecular Ecology Resources*, 8: 698–700. DOI: 10.1111/j.1471-8286.2007.02052.x.

Faegri, K. & van der Pijl, L. 1979. *The principles of pollination ecology*, 3rd rev. edition. Oxford, Pergamon Press.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J-L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14: 101–112. DOI: 10.1111/j.1461-0248.2010.01559.x.

Farber, S., Costanza, R., Childers, D.L., Erickson, J., Gross, K., Grove, M., Hopkinson, C.S., Kahn, J., Pincetl, S., Troy, A., Warren, P. & Wilson, M. 2006. Linking ecology and economics for ecosystem management. *Bioscience*, 56: 121–133.

Farley, J. & Costanza, R. 2010. Payments for ecosystem services: from local to global. *Ecological Economics*, 69: 2060–2068. DOI: 10.1016/j.ecolecon.2010.06.010.

FAO (Food and Agriculture Organization of the United Nations).2011. Save and Grow: A Policymaker's Guide to the Sustainable Intensification of Smallholder Crop Production. FAO, Rome, Italy.

Feber, R.E., Firbank, L.G., Johnson, P.J. & Macdonald, D.W. 1997. The effects of organic farming on pest and non-pest butterfly abundance. *Agriculture, Ecosystems and Environment*, 64: 133–139.

Felsot, A.S., Unsworth, J.B., Linders, J.B.H.J., Roberts, G., Rautman, D., Harris, C. & Carazo, E. 2011. Agrochemical spray drift; assessment and mitigation--a review. *Journal of environmental science and health*. Part. B, Pesticides, food contaminants, and agricultural wastes, 46: 1–23. DOI: 10.1080/03601234.2010.515161.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology Evolution and Systematics*, 35: 375–403. DOI: 10.1146/annurev.ecolsys.34.011802.132347.

Fiedler, A.K., Landis, D.A. & Wratten, S.D. 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. *Biological Control*, 45: 254–271. DOI: 10.1016/j.biocontrol.2007.12.009.

Fitzpatrick, Ú., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V. & Brown, M.J.F. 2007. Rarity and decline in bumble bees – a test of causes and correlates in the Irish fauna. *Biological Conservation*, 136: 185–194. DOI: 10.1016/j.biocon.2006.11.012.

Flaherty, D. 1969. Ecosystem trophic complexity and the Willamette mite, *Eotetranychus willamettei* (Acarine: Tetranychidae) densities. *Ecology*, 50: 911–916.

Forbes, S.L., Cohen, D.A., Cullen, R., Wratten, S.D. & Fountain, J. 2009. Consumer attitudes regarding environmentally sustainable wine: an exploratory study of the New Zealand marketplace. *Journal of Cleaner Production*, 17: 1195–1199.

Frank, T. 1999. Density of adult hoverflies (Dipt., Syrphidae) in sown weed strips acid adjacent fields. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, 123: 351–355. DOI: 10.1046/j.1439-0418.1999.00383.x.

Franzén, M. & Nilsson, S.G. 2004. Land use and occurrence of Andrena hattorfiana and other threatened wild bees (Hymenoptera, Apoidea) at Stenbrohult, Linnaeus' birth place. *Entomologisk Tidskrift*, 125: 1–10.

Franzén, M. & Nilsson, S.G. 2008. How can we preserve and restore species richness of pollinating insects on agricultural land? *Ecography*, 31: 698–708.

Free, J.B. 1993. *Insect pollination of crops.* London, Academic Press.

Free, J.B. & Williams, I.H. 1976. Pollination as a factor limiting the yield of field beans (*Vicia faba* L.). *Journal of Agricultural Science*, 87: 395–399.

Freitas, B.M. & Pereira, J.O.P. 2004. *Solitary bees: conservation, rearing and management for pollination.* Imprensa Universitária UFC, Fortaleza.

Freitas, B.M., Imperatriz-Fonseca, V.L., Medina, L.M., Kleinert, A.D.P., Galetto, L., Nates-Parra, G. & Quezada-Euan, J.J.G. 2009. Diversity, threats and conservation of native bees in the Neotropics. *Apidologie*, 40: 332–346. DOI: 10.1051/apido/2009012.

Fried, G., Petit, S., Dessaint, F. & Reboud, X. 2009. Arable weed decline in Northern France: crop edges as refugia for weed conservation? *Biological Conservation*, 142: 238–243. DOI: 10.1016/j.biocon.2008.09.029.

Frund, J., Linsenmair, K.E. & Bluthgen, N. 2010. Pollinator diversity and specialization in relation to flower diversity. *Oikos*, 119: 1581–1590. DOI: 10.1111/j.1600-0706.2010.18450.x.

Fuentes-Montemayor, E., Goulson, D. & Park, K.J. 2011. The effectiveness of agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. *Journal of Applied Ecology*, 48: 532–542. DOI: 10.1111/j.1365-2664.2010.01927.x.

Fuller, R.J., Norton, L.R., Feber, R.E., Johnson, P.J., Chamberlain, D.E., Joys, A.C., Mathews, F., Stuart, R.C., Townsend, M.C., Manley, W.J., Wolfe, M.S., Macdonald, D.W. & Firbank, L.G. 2005. Benefits of organic farming to biodiversity vary among taxa. *Biology Letters*, 1: 431–434. DOI: 10.1098/rsbl.2005.0357.

Fussell, M. & Corbet, S.A. 1991. Forage for bumble bees and honey-bees in farmland – a case-study. *Journal of Apicultural Research*, 30: 87–97.

Fussell, M. & Corbet, S.A. 1992. Flower usage by bumble bees – a basis for forage plant management. *Journal of Applied Ecology*, 29: 451–465.

Gabriel, D. & Tscharntke, T. 2007. Insect pollinated plants benefit from organic farming. *Agriculture Ecosystems & Environment*, 118: 43–48. DOI: 10.1016/j.agee.2006.04.005.

Galil, J. & Neeman, G. 1977. Pollen transfer and pollination in the common fig (*Ficus carica L.)*. *New Phytologist*, 79: 163–171.

Gallai, N., Sallesc, J-M., Setteled, J. & Vaissiere, B.E. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollination decline. *Ecological Economics*, 68: 810–821.

Garibaldi, L.A, Aizen, M.A., Cunningham, S.A & Klein, A.M. 2009. Pollinator shortage and global crop yield. *Communicative & Integrative Biology*, 2(1): 37–39.

Garibaldi, L., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R. & Klein, A.M. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14: 1062–1072. DOI: 10.1111/j.1461-0248.2011.01669.x.

Gathmann, A. & Tscharntke, T. 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71: 757–764. DOI: 10.1046/j.1365-2656.2002.00641.x.

Gemmill-Herren, B. & Ochieng, A.O. 2008. Role of native bees and natural habitats in eggplant (Solanum melongena) pollination in Kenya. *Agriculture Ecosystems & Environment*, 127: 31–36. DOI: 10.1016/j.agee.2008.02.002.

Genersch, E., Yue, C., Fries, I. & de Miranda, J.R. 2006. Detection of Deformed wing virus, a honey bee viral pathogen, in bumble bees (Bombus terrestris and Bombus pascuorum) with wing deformities. *Journal of Invertebrate Pathology*, 91: 61–63. DOI: 10.1016/j.jip.2005.10.002.

Genissel, A., Aupinel, P., Bressac, C., Tasei, J.N. & Chevrier, C. 2002. Influence of pollen origin on performance of Bombus terrestris micro-colonies. *Entomologia Experimentalis Et Applicata*, 104: 329–336. DOI: 10.1046/j.1570-7458.2002.01019.x.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. *Journal of Ecology*, 94: 295–304. DOI: 10.1111/j.1365-2745.2006.01098.x.

Gikungu, M.W. 2006. Bee diversity and some aspects of their ecological interactions with plants in a successional tropical community. PhD dissertation, Rheinishchen Friedrich-Wilhels-Universitat Bonn, Germany.

Gilbert, F.S. 1981. Foraging ecology of hover-flies – morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecological Entomology*, 6: 245–262. DOI: 10.1111/j.1365-2311.1981.tb00612.x.

Gillespie, M. & Wratten, S.D. 2012. The importance of viticultural landscape features and ecosystem service enhancement for native butterflies in New Zealand vineyards. *Journal of Insect Conservation*, 16: 13–23.

Gilliam, M., Buchmann, S.L., Lorenz, B.J. & Roubik, D.W. 1985. Microbiology of the larval provisions of the stingless bee, Trigona-Hypogea, an obligate necrophage. *Biotropica*, 17: 28–31. DOI: 10.2307/2388374.

Gomez-Baggethun, E., de Groot, R., Lomas, P.L. & Montes, C. 2010. The history of ecosystem services in economic theory and practice: from early notions to markets and payment schemes. *Ecological Economics*, 69: 1209–1218. DOI: 10.1016/j.ecolecon.2009.11.007.

Goodell, K. 2003. Food availability affects Osmia pumila (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia*, 134: 518–527. DOI: 10.1007/s00442-002-1159-2.

Goulson, D. 2003. Conserving wild bees for crop pollination. *Food, Agriculture & Environment*, 1(1): 142–144.

Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annual Review of Ecology Evolution and Systematics*, 34: 1–26. DOI: 10.1146/annurev.ecolsys.34.011802.132355.

Goulson, D. & Darvill, B. 2004. Niche overlap and diet breadth in bumble bees; are rare species more specialized in their choice of flowers? *Apidologie*, 35: 55–63. DOI: 10.1051/apido:2003062.

Goulson, D. & Hanley, M.E. 2004. Distribution and forage use of exotic bumble bees in South Island, New Zealand. *New Zealand Journal of Ecology*, 28: 225–232.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. 2005. Causes of rarity in bumble bees. *Biological Conservation*, 122: 1–8. DOI: 10.1016/j.biocon.2004.06.017.

Goulson, D., Lye, G.C. & Darvill, B. 2008. Decline and conservation of bumble bees. *Annual Review of Entomology*, 53: 191–208.

Goulson, D., Lye, G.C. & Darvill, B. 2008. Diet breadth, coexistence and rarity in bumble bees. *Biodiversity and Conservation*, 17: 3269–3288. DOI: 10.1007/s10531-008-9428-y.

Greco, C.F., Holland, D. & Kevan, P.G. 1996. Foraging behaviour of honey bees (Apis mellifera L) on staghorn sumac [Rhus hirta Sudworth (ex-typhina L)]: differences and dioecy. *Canadian Entomologist*, 128: 355–366.

Greenleaf, S.S. & Kremen, C. 2006a. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation*, 133: 81–87. DOI: 10.1016/j.biocon.2006.05.025.

Greenleaf, S.S. & Kremen, C. 2006b. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences of the United States of America*, 103: 13890–13895.

Grixti, J.C., Wong, L.T., Cameron, S.A. & Favret, C. 2009. Decline of bumble bees (Bombus) in the North American Midwest. *Biological Conservation*, 142: 75–84. DOI: 10.1016/j.biocon.2008.09.027.

Groot, A.T and Dicke, M. 2002. Insect resistant transgenic plants in a multiple-trophic level. *Plant Journal*, 31: 387–406.

Gruber, B., Eckel, K., Everaars, J. & Dormann, C.F. 2011. On managing the red mason bee (Osmia bicornis) in apple orchards. *Apidologie*, 42: 564–576. DOI: 10.1007/s13592-011-0059-z.

Guldberg, I.D. and Atsatt, P.R. 1975. Frequency of reflection and absorption of ultraviolet light in flowering plants. *American Midland Naturalist*, 93: 35–43.

Gupta, J.K. 2013. Wild pollinators and pesticides on apples in Himachal Pradesh, India: community learning and innovation. In: D.W. Roubik, ed., *Pollinator Safety in Agriculture*, Chapter 2. Rome, FAO.

Gurr, G.M. & Wratten, S. 2000. *Biological control: measures of success*. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Gurr, G.M., Wratten, S. & Snyder, W.E. 2012. Biodiversity and insect pests – key issues for sustainable management. Oxford, Wiley Blackwell.

Gutman, P. 2007. Ecosystem services: foundations for a new rural–urban compact. *Sustainable Development*, 2: 383–387. DOI: 10.1016/j.ecolecon.2007.02.027.

Haaland, C., Naisbit, R.E. & Bersier, L-F. 2011. Sown wildflower strips for insect conservation: a review. *Insect Conservation and Diversity*, 4: 60–80. DOI: 10.1111/j.1752-4598.2010.00098.x.

Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T. & Thies, C. 2009. Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. *Journal of Applied Ecology*, 46: 1106–1114. DOI: 10.1111/j.1365-2664.2009.01685.x.

Hagen, M. & Kraemer, M. 2010. Agricultural surroundings support flower-visitor networks in an Afrotropical rain forest. *Biological Conservation*, 143: 1654–1663.

Hajjar, R., Jarvis, D.I. & Gemmill-Herren, B. 2008. The utility of crop genetic diversity in maintaining ecosystem services. *Agriculture, Ecosystems & Environment*, 123: 261–270. DOI: 10.1016/j.agee.2007.08.003.

Hald, A.B. 1999. Weed vegetation (wild flora) of long established organic versus conventional cereal fields in Denmark. *Annals of Applied Biology*, 134: 307–314. DOI: 10.1111/j.1744-7348.1999.tb05269.x.

Hanley, M.E., Franco, M., Pichon, S., Darvill, B. & Goulson, D. 2008. Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Functional Ecology*, 22: 592–598. DOI: 10.1111/j.1365-2435.2008.01415.x.

Hanley, M.E., Franco, M., Dean, C.E., Franklin, E.L., Harris, H.R., Haynes, A.G., Rapson, S.R., Rowse, G., Thomas, K.C., Waterhouse, B.R. & Knight, M.E. 2011. Increased bumble bee abundance along the margins of a mass flowering crop: evidence for pollinator spill-over. *Oikos*, 120: 1618–1624.

Hanley, M.E. & Goulson, D. 2003. Introduced weeds pollinated by introduced bees: cause or effect? *Weed Biology and Management*, 3: 204–212.

Haydak, M.H. 1970. Honey bee nutrition. *Annual Review of Entomology*, 15: 143–156.

Hausammann, A. 1996. Strip-management in rape crop: is winter rape endangered by negative impacts of sown weed strips? *J. Appl. Ent.*, 120: 505–512.

Hawes, C., Haughton, A.J., Osborne, J.L., Roy, D.B., Clark, S. J., Perry, J.N., Rothery, P., Bohan, D.A., Brooks, D.R., Champion, G.T., Dewar, A.M., Heard, M.S., Woiwod, I.P., Daniels, R.E., Young, M.W., Parish, A.M., Scott, R.J., Firbank, L.G & Squire, G.R. 2003. Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Phil. Trans. R. Soc. Lond. B*, 358: 1899–1913

Heard, M.S., Carvell, C., Carreck, N.L., Rothery., Osborne, J.L. & Bourke, A.F.G. 2007. Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters*, 3: 638–641. DOI: 10.1098/rsbl.2007.0425.

Heard, T.A. 1993. Pollinator requirements and flowering patterns of Macadamia-Integrifolia. *Australian Journal of Botany*, 41: 491–497. DOI: 10.1071/bt9930491.

Heard, T.A. 1999. The role of stingless bees in crop pollination. *Annual Review of Entomology*, 44: 183–206. DOI: 10.1146/annurev.ento.44.1.183.

Heard, T.A. & Exley, E.M. 1994. Diversity, abundance, and distribution of insect visitors to Macadamia Flowers. *Environmental Entomology*, 23: 91–100.

Hegland, S.J. & Boeke, L. 2006. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology*, 31: 532–538. DOI: 10.1111/j.1365-2311.2006.00812.x.

Hepburn, H.R., Radloff, S.E., Verma, S. & Verma, L.R. 2001. Morphometric analysis of Apis cerana populations in the southern Himalayan region. *Apidologie*, 32: 435–447.

Herbert, E.W. & Shimanuki, H. 1978. Chemical composition and nutritive-value of bee-collected and bee-stored pollen. *Apidologie*, 9: 33–40. DOI: 10.1051/apido:19780103.

Herren, H.R. & Neuenschwander, P. 1991. Biological control of cassava pests in Africa. *Annual Review of Entomology*, 36: 257–283.

Herrmann, F., Westphal, C., Moritz, R.F. & Steffan-Dewenter, I. 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. *Molecular Ecology*, 16: 1167–1178. DOI: 10.1111/j.1365-294X.2007.03226.x.

Hickman, J.M. & Wratten, S.D. 1996. Use of Phacelia tanacetifolia strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *Journal of Economic Entomology*, 89: 832–840.

Higes, M., Martín-Hernández, R., Garrido-Bailón, E., González-Porto, A.V, García-Palencia, P., Meana, A., del Nozal, M.J., Mayo, R. & Bernal, J.L. 2009. Honey bee colony collapse due to Nosema ceranae in professional apiaries. *Environmental Microbiology Reports*, 1: 110–113. DOI: 10.1111/j.1758-2229.2009.00014.x.

Higginson, A.D, Gilbert, F.S. & Barnard, C.J. 2006. Morphological correlates of nectar production used by honey bees. *Ecological Entomology*, 31: 269–276. DOI: 10.1111/j.1365-2311.2006.00789.x.

Higo, H.A., Rice, N.D., Winston, M.L. & Lewis, B. 2004. Honey bee (Hymenoptera: Apidae) distribution and potential for supplementary pollination in commercial tomato greenhouses during winter honey bee (Hymenoptera: Apidae). *J Econ Entomol.*, 97(2): 163–170.

Hobbs, G.A., Nummi, W.O. & Virostek, J.F. 1961. Food-gathering behaviour of honey, bumble, and leaf-cutter bees (Hymenoptera: Apoidea) in Alberta. *Canadian Entomologist*, 93: 409–419

Hobbs, G.A., Nummi, W.O. & Virostek, J.F. 1962. Managing colonies of bumble bees (Hymenoptera: Apidae) for pollination purposes. *Canadian Entomologist*, 94: 1121–1132

Hodgson, J., Kunin, W.E, Thomas, C.D., Benton, T.G. & Gabriel, D. 2010. Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecology Letters*, 13: 1358–1367. DOI: 10.1111/j.1461-0248.2010.01528.x.

Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V. & Evans, A.D. 2004. Does organic farming benefit biodiversity? *Biological Conservation*, 122: 113–130. ø

Holm, S.H., Rahman, M.H., Stølen, O. & Sørensen, H. 1985. Studies on pollination requirements in rapeseed (*Brassica campestris)*. In: Sørensen, H. (ed.) *Advances in the Production and Utiization of Cruciferous Crops*. W. Junk Publishers, Dordrecht, The Netherlands.

Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos*, 117: 354–361. DOI: 10.1111/j.2007.0030-1299.16303.x.

Holzschuh, A., Dorman, C.F., Tscharntke, T. & Steffan-Dewenter, I. 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination.Proc. R. Soc. B rspb20110268

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75: 3–35. DOI: 10.1890/04-0922.

Horne, M. 1995. Pollen preference and its relationship to nesting success of Megachile-rotundata (Hymenoptera, Megachilidae). *Annals of the Entomological Society of America*, 88: 862–867.

Horowitz, M.T., Blumdel, T., Hertz-linger, G. & Hulin, N. 1962. Effects of repeated applications of ten soil-active herbicides on weed populations, *Weed Res.*, 14: 97–109.

Hoveland, C.S., Buchanan, G.A. & Harris, M.C. 1976. Response of weeds to soil phosphorous and potassium. *Weed Science*, 24: 194–201.

Hubbell, S.P. & Johnson, L.K. 1978. Comparative foraging behaviour of six stingless bee species exploiting a standardised resource. *Ecology*, 59: 1123–1136.

Hyvönen, T. 2007. Can conversion to organic farming restore the species composition of arable weed communities? *Biological Conservation*, 137: 382–390. DOI: 10.1016/j.biocon.2007.02.021.

Idris, A.B. & Grafius, E. 1995. Wildflowers as nectar sources for Diadegma insulare (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). *Environ. Entomol.*, 24: 1726–1735.

Inoue, M.N. & Yokoyama, J. 2010. Competition for flower resources and nest sites between Bombus terrestris (L.) and Japanese native bumble bees. *Applied Entomology and Zoology*, 45: 29–35. DOI: 10.1303/aez.2010.29.

Irvin, N.A., Wratten, S.D, Frampton, C.M., Bowie, M.H., Evans, A.M. & Moar, N.T. 1999. The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand. *New Zealand Journal of Zoology*, 26: 105–115.

Jackson, L.E., Pascual, U. & Hodgkin, T. 2007. Utilizing and conserving agrobiodiversity in agricultural landscapes. *Agriculture Ecosystems & Environment*, 121: 196–210.

Jacometti, M.A., Wratten, S.D. & Walter, M. 2008. Enhancing ecosystem services in vineyards: using cover crops to decrease botrytis bunch rot severity. *International Journal of Agricultural Sustainability*, 5: 305–314.

Jaffe, R., Dietemann, V., Allsopp, M.H., Costa, C., Crewe, R.M., Dall'olio, R., de la Rua, P., El-Niweiri, M.A.A., Fries, I., Kezic, N., Meusel, M.S., Paxton, R.J., Shaibi, T., Stolle, E. & Moritz, R.F.A. 2010. Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses. *Conservation Biology*, 24: 583–593. DOI: 10.1111/j.1523-1739.2009.01331.x.

Jarlan, A., De Oliveira, D. & Gingras, J. 1997. Effects of Eristalis tenax (Diptera: syrphidae) pollination on characteristics of greenhouse sweet pepper fruits. *Journal of Economic Entomology*, 90: 1650–1654.

Jarlan, A., De Oliveira, D. & Gingras, J. 1997. Pollination by Eristalis tenax (Diptera: syrphidae) and seed set of greenhouse sweet pepper. *Journal of Economic Entomology*, 90: 1646–1649.

Jauker, F., Diekoetter, T., Schwarzbach, F. & Wolters, V. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, 24: 547–555. DOI: 10.1007/s10980-009-9331-2.

Jauker, F. & Wolters, V. 2008. Hover flies are efficient pollinators of oilseed rape. *Oecologia*, 156: 819–823.

Jay, S.C. 1986. Spatial management of honey-bees on crops. *Annual Review of Entomology*, 31: 49–65. DOI: 10.1146/annurev.en.31.010186.000405.

Jervis, M.A. & Heimpel, G.E. 1996. Phytophagy. In: M.A. Jervis, & N.A.C. Kidd, eds. *Insect natural enemies: practical approaches to their study and evaluation*, pp. 375–394. Dordrecht, The Netherlands, Springer.

Johansen, C.A. 1977. Pesticides and pollinators. *Ann. Rev. Entomol.*, 22: 177–192

Johansen, C.A & Mayer, D.F. 1990 *Pollinator protection: a bee and pesticide handbook*. Cheshire, CT. Wicwas Press.

Johnson, L.K. & Hubbell, S.P. 1975. Contrasting foraging strategies and coexistence of two bee species on a single resource. *Ecology*, 56: 1398–1406

Johnson, R.M., Ellis, M.D., Mullin, C. & Frazier, M. 2010. Pesticides and honey bee toxicity – USA. *Apidologie*, 41: 312–331. DOI: 10.1051/apido/2010018.

Jonsson, M., Wratten, S.D., Landis, D. & Gurr, G.M. 2008. Recent advances in conservation biological control of arthropods by arthropods. *Biological Control*, 45: 172–175. DOI: 10.1016/j.biocontrol.2008.01.006.

Julier, H.E. & Roulston, T.H. 2009. Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behavior and landscape effects. *Journal of Economic Entomology*, 102: 563–573.

Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Mueller, C.B. & Caflisch, A. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters*, 13: 442–452. DOI: 10.1111/j.1461-0248.2009.01437.x.

Kapatia, R. 1987. To assess the number of honey bee colonies required to pollinate cauliflower seed crop. M. Sc. Thesis, Department of Entomology and Apiculture. University of Horticulture & Forestry. Himachal Pradesh, India.

Kay, Q.O.N., Lack, A.J., Bamber, F.C. & Davies, C.R. 1984. Differences between sexes in floral morphology, nectar production and insect visits in a dioecious species, Silene-Dioica. *New Phytologist*, 98: 515–529. DOI: 10.1111/j.1469-8137.1984.tb04145.x.

Kearns, C.A. 2001. North American, dipteran pollinators: assessing their value and conservation status. *Conservation Ecology*, 5(1): 5.

Kearns, C.A. and Inouye, D.W. 1997. Pollinators, flowering plants, and conservation biology. *BioScience*, 47(5): 297–307.

Kearns, C.A., Inouye, D.W. & Waser, N.M. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, 29: 83–112. DOI: 10.1146/annurev.ecolsys.29.1.83.

Keil, P., Biesmeijer, J.C., Barendregt, A., Reemer, M. & Kunin, W.E. 2011. Biodiversity change is scale-dependent: an example from Dutch and UK hoverflies (Diptera, Syrphidae). *Ecography*, 34: 392–401. DOI: 10.1111/j.1600-0587.2010.06554.x.

Kells, A., Holland, J. & Goulson, D. 2001. The value of uncropped field margins For foraging numblebees. *Journal of Insect Conservation*, 5: 283–291.

Kells, A.R. & Goulson, D. 2003. Preferred nesting sites of bumble bee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation*, 109: 165–174. DOI: Pii s0006-3207(02)00131-310.1016/s0006-3207(02)00131-3.

Kevan, P.G. 1983. Insects as flower visitors and pollinators. *Ann. Rev. Entomol.*, 28: 407–53.

Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems & Environment*, 74: 373–393. DOI: 10.1016/S0167-8809(99)00044-4.

Kevan, P.G. & Plowright, R.C. 1989. Fenitrothion and insect pollination. In: W.R. Ernst, P.A. Pearce & T.L. Pollock, eds. *Environmental effects of fenitrothion use in forestry: impacts on insect pollinators, songbirds, and aquatic organisms*. Dartmouth, NS, Environment Canada, pp. 13–42.

Kevan, P.G, Clark, E.A. & Thomas, V.G. 1990. Insect pollinators and sustainable agriculture. *American Journal of Alternative Agriculture*, 5: 13–22.

Kevan, P.G., Greco, C.F. & Belaoussoff, S. 1997. Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths. *Journal of Applied Ecology*, 34: 1122–1136.

Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems and Environment*, 74(1–3): 373–393.

Kim, J.Y. 1999. Influence of resource level on maternal investment in a leaf-cutter bee (Hymenoptera: Megachilidae). *Behavioral Ecology*, 10: 552–556. DOI: 10.1093/beheco/10.5.552.

Kings Seeds n.d. [Website] (Available at www.kingsseeds.co.nz/shop/Field+Selection/Wildflowers/Low+Grow+Blend-5620.html) Accessed 10 January 2012.

Kjøhl, M., Nielsen, A. & Stenseth, N.C. 2011. *Potential effects of climate change on crop pollination*. FAO, Rome.

Kleijn, D., Berendse, F., Smit, R., Gilissen, N., Smit, J., Brak, B. & Groeneveld, R. 2004. Ecological effectiveness of agri-environment schemes in different agricultural landscapes in the Netherlands. *Conservation Biology*, 18: 775–786.

Kleijn, D. & Raemakers, I. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology*, 89: 1811–1823. DOI: 10.1890/07-1275.1.

Kleijn, D. & Sutherland, W.J. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, 40: 947–969. DOI: 10.1111/j.1365-2664.2003.00868.x.

Kleijn, D. & van Langevelde, F. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, 7: 201–214. DOI: 10.1016/j.baae.2005.07.011.

Klein, A.M. 2009. Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness. *Forest Ecology and Management*, 258: 1838–1845. DOI: 10.1016/j.foreco.2009.05.005.

Klein, A.M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology*, 16: 1003–1014. DOI: 10.1046/j.1523-1739.2002.00499.x.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270: 955–961. DOI: 10.1098/rspb.2002.2306.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. 2003. Pollination of Coffea canephora in relation to local and regional agroforestry management. *Journal of Applied Ecology*, 40: 837–845. DOI: 10.1046/j.1365-2664.2003.00847.x.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences*, 274: 303–313. DOI: 10.1098/rspb.2006.3721.

Kleinert-Giovannini, A. & Imperatriz-Fonseca, V.L. 1987. Aspects of the Trophic Niche of Melipona-Marginata-Marginata Lepeletier (Apidae, Meliponinae). *Apidologie*, 18: 69–100. DOI: 10.1051/apido:19870107.

Knight, M.E., Osborne, J.L., Sanderson, R.A., Hale, R.J., Martin, A.P. & Goulson, D. 2009. Bumble bee nest density and the scale of available forage in arable landscapes. *Insect Conservation and Diversity*, 2: 116–124. DOI: 10.1111/j.1752-4598.2009.00049.x.

Knop, E., Kleijn, D., Herzog, F. & Schmid, B. 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology*, 43: 120–127. DOI: 10.1111/j.1365-2664.2005.01113.x.

Knox, D.A., Shimanuk, H. & Herbert, E.W. 1971. Diet and longevity of adult honey bees Hymenoptera-Apidae. *Journal of Economic Entomology*, 64(6): 1415–1416.

Koeniger, N. & Koeniger, G. 1980. Observations and experiments on migration and dance communication of *Apis dorsata* in Sri Lanka, *J. Apic. Res.*, 19: 21–34.

Kovács-Hostyánszki, A., Kőrösi, Á., Orci, K.M., Batáry, P. & Báldi, A. 2011. Set-aside promotes insect and plant diversity in a Central European country. *Agriculture, Ecosystems. & Environment*, 141: 296–301. DOI: 10.1016/j.agee.2011.03.004.

Kraemer, M.E. and Favi, F.D. 2005. Flower phenology and pollen choice of Osmia lignaria (Hymenoptera: Megachilidae) in Central Virginia. *Environmental Entomology*, 34(6): 1593–1605.

Kremen, C. & R. Chaplin. 2007. Insects as providers of ecosystem services: crop pollination and pest control. In: *Insect Conservation Biology: proceedings of the Royal Entomological Society's 23rd Symposium*. (Stewart, A.J.A., New, T.R. & Lewis, O.T. (eds)) CABI Publishing, Wallingford, pp. 349-382

Kremen, C., Williams, N.M. & Thorp, R.W. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl Acad. Sci. USA*, 99: 16812–16816.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, 7: 1109–1119.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B. & LeBuhn, G. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol Lett.*, 10: 299–314

Kremen, C. 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters*, 8: 468–479. DOI: 10.1111/j.1461-0248.2005.00751.x.

Kremen, C. & Ostfeld, R.S. 2005. A call to ecologists: measuring, analyzing, and managing ecosystem services. *Frontiers in Ecology and the Environment*, 3: 540. DOI: 10.2307/3868610.

Kremen, C., Williams, N.M., Aizen, M., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A-M., Regetz, J. & Ricketts, T.H. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, 10: 299–314. DOI: 10.1111/j.1461-0248.2007.01018.x.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, 7: 1109–1119.

Kremen, C., Williams, N.M. & Thorp, R.W. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 99: 16812–16816. DOI: 10.1073/pnas.262413599.

Kuussaari, M., Hyvönen, T. & Härmä, O. 2011. Pollinator insects benefit from rotational fallows. *Agriculture, Ecosystems & Environment*, 143: 28–36. DOI: 10.1016/j.agee.2011.03.006.

Lagerlof, J., Stark, J. & Svensson, B. 1992. Margins of agricultural fields as habitats for pollinating insects. *Agriculture Ecosystems & Environment*, 40: 117–124.

Landis, D.A., Wratten, S.D. & Gurr, G.M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45: 175–201. DOI: 10.1146/annurev.ento.45.1.175.

Landis, D., Menalled, F.D., Costamagna, A.C. & Wilkinson, T.K. 2005. Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science*, 53(6): 902–908.

Larsen, T.H., Williams, N.M. & Kremen, C. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8: 538–547.

Larson, B.M.H., Kevan, P.G. & Inouye, D.W. 2001. Flies and flowers: taxonomic diversity of anthophiles and pollinators. *Canadian Entomologist*, 133: 439–465.

Lavandero, B., Wratten, S., Shishehbor, P. & Worner, S. 2005. Enhancing the effectiveness of the parasitoid Diadegma semiclausum (Helen): movement after use of nectar in the field. *Biological Control*, 34: 152–158.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M-P., Garden, D., Girel, J., Pellet, G. & Douzet, R. 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*, 99: 135–147. DOI: 10.1111/j.1365-2745.2010.01753.x.

Leius, K. 1967. Influence of wild flowers on parasitism of tent caterpillar and codling moth. *Canadian Entomologist*, 99: 444–446.

Leonhardt, S.D., Dworschak, K., Eltz, T. & Bluthgen, N. 2007. Foraging loads of stingless bees and utilisation of stored nectar for pollen harvesting. *Apidologie*, 38: 125–135. DOI: 10.1051/apido:2006059.

Levin, G. & Jepsen, M.R. 2010. Abolition of set-aside schemes, associated impacts on habitat structure and modelling of potential effects of cross-farm regulation. *Ecological Modelling*, 221: 2728–2737. DOI: 10.1016/j.ecolmodel.2010.08.015.

Liebman, M. & Dyck, E. 1993. Crop rotation and intercropping strategies for weed management. *Ecol. Appl.*, 3: 92–122.

Liebman, M. & Gallandt, E.R. 1997. Many little hammers: ecological management of crop-weed interactions. In: L.E. Jackson, ed. *Ecology in Agriculture*, pp. 291–342. San Diego, CA, Academic Press.

Liebman, M. & Davis, A.S. 2000. Integration of soil, crop and weed management in low – external input farming systems. *Weed Research*, 40: 27–47.

Longley, M. & Sotherton, N.W. 1997. Factors determining the effects of pesticides upon butterflies inhabiting arable farmland. *Agriculture, Ecosystems & Environment*, 61: 1–12. DOI: 10.1016/S0167-8809(96)01094-8.

Losey, J.E, and Vaughan, M. 2006. The economic value of ecological services provided by insects. *BioScience*, 56: 311–323.

Lovei, G.L., Hickman, J.M., McDougall, D. & Wratten, S.D. 1993. Field penetration of beneficial Insects from habitat islands – hoverfly dispersal from flowering crop strips. *Proceedings of the Forty-Sixth New Zealand Plant Protection Conference*, pp. 325–328.

Luck, G.W., Daily, G.C. & Ehrlich, P.R. 2003. Population diversity and ecosystem services. *Trends in Ecology & Evolution*, 18: 331–336. DOI: 10.1016/s0169-5347(03)00100-9.

Luck, G.W., Kremen, C., Harrington, R. & Harrison, P. 2009. The economic value of ecosystem services response. *Bioscience*, 59: 461–462. DOI: 10.1525/bio.2009.59.6.19.

Lye, G.C, Park, K., Osborne, J., Holland, J. & Goulson, D. 2009. Assessing the value of rural stewardship schemes for providing foraging resources and nesting habitat for bumble bee queens (Hymenoptera: Apidae). *Biological Conservation*, 142: 2023–2032. DOI: 10.1016/j.biocon.2009.03.032.

Macfarlane, R.P., Grundell, J.M. & Dugdale, J.S. 1992. Gorse on the Chatham Islands: seed formation, arthropod associates and control. *Proceedings of the 45th New Zealand Plant Protection Conference*, pp. 251–255.

MacKenzie, K., Javorek, S. & Rogers, D. 1997. The alfalfa leafcutting bee, Megachile rotundata Fabr: an alternative managed pollinator of lowbush blueberry. *Sixth International Symposium on Vaccinium Culture*, pp. 87–90.

MacKenzie, K.E. & Winston, M.L. 1984. Diversity and abundance of native bee pollinators of berry crops and natural vegetation in the lower Fraser Valley, British Columbia. *Can. Entomol.*, 116: 965–974.

Mallick, S.A. & Driessen, M.M. 2009. Impacts of hive honey bees on Tasmanian leatherwood Eucryphia lucida Labill. (Eucryphiaceae). *Austral Ecology*, 34: 185–195. DOI: 10.1111/j.1442-9993.2008.01920.x.

Markham, K.R., Mitchell, K.A., Wilkins, A.L., Daldy, J.A. & Lu, Y.R.. 1996. HPLC and GC-MS identification of the major organic constituents in New Zealand propolis. *Phytochemistry*, 42: 205–211. DOI: 10.1016/0031-9422(96)83286-9.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R. & Ward, L.K. 2003. The role of weeds in supporting biological diversity within crop fields. *Weed Res*., 43: 77–89.

Marshall, E.J.P, West, T.M. & Kleijn, D. 2006. Impacts of an agri-environment field margin prescription on the flora and fauna of arable farmland in different landscapes. *Agriculture, Ecosystems & Environment*, 113: 36–44. DOI: 10.1016/j.agee.2005.08.036.

Marshall, E.J.R. & Moonen, A.C. 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agriculture Ecosystems & Environment*, 89: 5–21.

Martin, N.H. 2004. Flower size preferences of the honey bee (Apis mellifera) foraging on Mimulus guttatus (Scrophulariaceae). *Evolutionary Ecology Research*, 6: 777–782.

Mayack, C. & Naug, D. 2009. Energetic stress in the honey bee Apis mellifera from Nosema ceranae infection. *Journal of Invertebrate Pathology*, 100: 185–188. DOI: 10.1016/j.jip.2008.12.001.

Mayer, D.F, Lunden, J.D. & Williams, R.E. 1991. Tralomethrin insecticide and domesticated pollinators. *American Bee Journal*, 131: 461–463.

Mclaughlin, A. & Mineau, P. 1995. The impact of agricultural practices on biodiversity. *Science*, 55: 201–212.

ME Assessment (MEA). 2005. *Ecosystems and human well being: Synthesis*. Washington, DC, Island Press.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M. 2002. The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, 106: 259–271. DOI: 10.1016/s0006-3207(01)00252-x.

Melendez-Ramirez, V., Parra-Tabla, V., Kevan, P.G., Ramirez-Morillo, I., Harries, H., Fernandez-Barrera, M. & Zizumbo-Villareal, D. 2004. Mixed mating strategies and pollination by insects and wind in coconut palm (Cocos nucifera L. (Arecaceae)): importance in production and selection. *Agricultural and Forest Entomology*, 6: 155–163. DOI: 10.1111/j.1461-9563.2004.00216.x.

Memmott, J. 1999. The structure of a plant-pollinator food web. *Ecology Letters*, 2: 276–280.

Memmott, J., Waser, N.M. & Price, M.V. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B-Biological Sciences*, 271: 2605–2611. DOI: 10.1098/rspb.2004.2909.

Merckx, T., Feber, R.E., Riordan, P., Townsend, M.C., Bourn, N.A.D., Parsons, M.S. & Macdonald, D.W. 2009. Optimizing the biodiversity gain from agri-environment schemes. *Agriculture Ecosystems & Environment*, 130: 177–182.

Meyer, B., Jauker, F. & Steffan-Dewenter, I. 2009. Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic and Applied Ecology* 10: 178–186. DOI: 10.1016/j.baae.2008.01.001.

Michener, C.D. 1964. Evolution of the nests of bees. *American Zoologist*, 4: 227–239.

Michener, C.D. 2007. *The bees of the world*, 2nd edition. Baltimore, MD, Johns Hopkins Univ. Press.

Mittelbach, G.G, Steiner, C.F., Scheiner, S.M., Gross, K.L, Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. 2001. What is the observed relationship between species richness and productivity? *Ecology*, 82: 2381–2396. DOI: 10.1890/0012-9658(2001)082[2381:witorb]2.0.co;2.

Moeller, D.A. 2004. Facilitative interactions among plants via shared pollinators. *Ecology*, 85: 3289–3301. DOI: 10.1890/03-0810.

Mommaerts, V., Sterk, G. & Smagghe, G. 2006. Hazards and uptake of chitin synthesis inhibitors in bumble bees Bombus terrestris. *Pest Management Science*, 62: 752–758. DOI: 10.1002/ps.

Moonen, A.C. & Marshall, E.J.P. 2001. The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. *Agriculture Ecosystems & Environment*, 86: 187–202.

Morales, C.L. & Traveset, A. 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, 12: 716–728. DOI: 10.1111/j.1461-0248.2009.01319.x.

Morandin, L.A. & Winston, M.L. 2005. Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecological Applications*, 15: 871–881. DOI: 10.1890/03-5271.

Morandin, L.A. & Winston, M.L. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agriculture Ecosystems & Environment*, 116: 289–292. DOI: 10.1016/j.agee.2006.02.012.

Morandin, L.A., Winston, M.L., Abbott, V.A. & Franklin, M.T. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic Applied Ecology*, 8: 117–124.

Moreby, S.J. & Southway, S.E. 1999. Influence of autumn applied herbicides on summer and autumn food available to birds in winter wheat fields in southern England. *Agriculture, Ecosystems and Environment*, 72: 285–297.

Mossagegh, M.S. 1993. New geographical distribution line of *Apis florea* in Iran. In: L.J. Conner, T. Rinderer, H.A. Sylvester & S. Wongsiri, eds. *Asian Apiculture*. Cheshire, Wicwas Press, pp. 64–66.

Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C. & Dorn, S. 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships. *Biological Conservation*, 130: 604–615.

Murray, T.E., Kuhlmann, M. & Potts, S.G. 2009. Conservation ecology of bees: populations, species and communities. *Apidologie*, 40: 211–236. DOI: 10.1051/apido/2009015.

Nadel, H. & Pena, J.E. 1994. Identity, behavior, and efficacy of Nitidulid beetles (Coleoptera, Nitidulidae) pollinating commercial Annona species in Florida. *Environmental Entomology*, 23: 878–886.

National Academy of Sciences. 1969. *Insect-pest management and control.* Principles of plant and animal pest control series, 3: 100–164

Natural England. 2010a. Entry Level Stewardship.

Natural England. 2010b. Higher Level Stewardship.

Natural England. 2010c. Organic Entry Level Stewardship.

Naug, D. 2009. Nutritional stress due to habitat loss may explain recent honey bee colony collapses. *Biological Conservation*, 142: 2369–2372. DOI: 10.1016/j.biocon.2009.04.007.

Naumkin, V.P. 1992. Species composition of insects-pollinators of buckwheat. In: *Proceedings, Fifth International Symposium on Buckwheat Research, Taiyuan. China*, pp. 443–446. Beijing, Agricultural Publishing House.

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., Chan, K.M., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H. & Shaw, M. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, 7: 4–11. DOI: 10.1890/080023.

Nentwig, W. 1998. Weedy plant species and their beneficial arthropods: potential for manipulation in field crops. In: C.H. Pickett and R.L. Bugg, eds. *Enhancing biological control: habitat management to promote natural enemies of agricultural pests*, pp. 49–72. Berkeley, CA, UC Press.

Nentwig, W., Frank, T. & Lethmayer, C. 1998. Sown weed strips: artificial ecological compensation areas an important tool in conservation biological control. In: P. Barbosa, ed. *Conservation Biological Control*, pp. 133–151. New York, Academic Press.

New, T.R. 2005. *Invertebrate conservation and agricultural ecosystems*. Cambridge, UK, Cambridge University Press.

Njoroge, G.N, Gemmill, B. & Bussmann, R. 2004. Pollination ecology of Citrullus lanatus at Yatta, Kenya. *International Journal of Tropical Insect Science*, 24(1): 73–77.

Norris, R.R. 1982. Interactions between weeds and other pests in the agroecosystem. In: J.L. Hatfield and I.J. Thomason, eds. *Biometeorology in integrated pest management*. New York, Academic Press, pp. 343–406

O'Callaghan, M., Glare, T.R., Burgess, E.P.J. & Malone, L.A. 2005. Effects of plants genetically modified for insect resistance on non- target organism. *Annual Review of Entomology*, 50: 271–292.

Ockinger, E. & Smith, H.G. 2007 Seminatural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, 44: 50–59.

Oldroyd, B.P. 2007. What's killing American honey Bees? *PLOS Biology*, 5: 1195–1199. DOI: e16810.1371/journal.pbio.0050168.

Oldroyd, B.P. & Nanork, P. 2009. Conservation of Asian honey bees. *Apidologie*, 40: 296–312. DOI: 10.1051/apido/2009021.

Olesen, J.M. & Jordano, P. 2002. Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, 83: 2416–2424. DOI: 10.2307/3071803.

Oliver, L.R. 1988. Principles of weed threshold research. *Weed Technology*, 2(4): 398–403.

Ollerton, J., Winfree, R. & Tarrant, S. 2011. How many flowering plants are pollinated by animals? *Oikos*, 120: 321–326. DOI: 10.1111/j.1600-0706.2010.18644.x.

O'Neill, K.M., O'Neill, R.P., Blodgett, S. & Fultz, J. 2004. Composition of pollen loads of Megachile rotundata in relation to flower diversity (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society*, 77: 619–625. DOI: 10.2317/e-24.1.

O'Neill, R.P. & O'Neill, K.M. 2011. Pollen load composition and size in the leafcutting bee Megachile rotundata (Hymenoptera: Megachilidae). *Apidologie*, 42: 223–233. DOI: 10.1051/apido/2010057.

Ostler, W.K. & Harper, K.T. 1978. Floral ecology in relation to plant species-diversity in Wasath Mountains of Utah and Idaho. *Ecology*, 59: 848–861.

Paini, D. & Roberts, J. 2005. Commercial honey bees (Apis mellifera) reduce the fecundity of an Australian native bee (Hylaeus alcyoneus). *Biological Conservation*, 123: 103–112. DOI: 10.1016/j.biocon.2004.11.001.

Paini, D.R. 2004. Impact of the introduced honey bee (Apis mellifera) (Hymenoptera: Apidae) on native bees: a review. *Austral Ecology*, 29: 399–407. DOI: 10.1111/j.1442-9993.2004.01376.x.

Parker, F.D., Batra, S.W.T. & Tepedino, V.J. 1987. New pollinators for our crops. *Agricultural Zoology Review*, 2: 279–304.

Pasquet, R.S., Peltier, A., Hufford, M.B., Oudin, E., Saulnier, J., Paul, L., Knudsen, J.T., Herren, H.R. & Gepts, P. 2008. Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. *Proceedings of the National Academy of Sciences of the United States of America*, 105: 13456–13461. DOI: 10.1073/pnas.0806040105.

Patiny, S., Rasmont, P. & Michez, D. 2009. A survey and review of the status of wild bees in the West-Palaearctic region. *Apidologie*, 40: 313–331. DOI: 10.1051/apido/2009028.

Patten, K.D., Shanks, C.H. & Mayer, D.F. 1993. Evaluation of herbaceous plants for attractiveness to bumble bees for use near cranberry farms. *Journal of Apicultural Research*, 32: 73–79.

Pauw, A. 2007. Collapse of a pollination web in small conservation areas. *Ecology*, 88: 1759–1769. DOI: 10.1890/06-1383.1.

Pereboom, J.J.M. 2000. The composition of larval food and the significance of exocrine secretions in the bumble bee Bombus terrestris. *Insectes Sociaux*, 47: 11–20. DOI: 10.1007/s000400050003.

Pereira, A.D, Bicalho, B., Radler, F. & Neto, D. 2003. Comparison of propolis from Apis mellifera and Tetragonisca angustula. *Apidologie*, 34: 291–298. DOI: 10.1051/apido:2003023.

Perrin, R.M. 1975. The role of the perennial stinging nettle Urtica dioica as a reservoir of beneficial natural enemies. *Annals of Applied Biology*, 81: 289–297.

Pettis, J.S. & Delaplane, K.S. 2010. Coordinated responses to honey bee decline in the USA. *Apidologie*, 41: 256–263. DOI: 10.1051/apido/2010013.

Picard-Nizou, A.L., Grison, R., Olsen, L., Pioche, C., Arnold, G. & Pham-Delegue, M.H. 1997. Impact of proteins used in plant genetic engineering toxicity and behavioral studies in the honey bee. *J. Econ. Entomol.*, 90: 1710–1716.

Pimentel, D. 1995. Amounts of pesticides reaching target pests: environmental impacts and ethics. *Journal of Agricultural and Environmental Ethics*, 8(1): 17–29.

Pimentel, D. 1961. Species diversity and insect population outbreaks. *Annals of Entomological Society of America* 54: 76–86.

Pimentel, D. 2005. Environmental and economic costs of the application of pesticides primarily in the United States. *Environment, Development and Sustainability*, 7: 229–252. DOI: 10.1007/s10668-005-7314-2.

Pitts-Singer, T.L. & James, R.R. 2008. Do weather conditions correlate with findings in failed, provision-filled nest cells of Megachile rotundata (Hymenoptera: megachilidae) in western North America? *Journal of Economic* Entomology, 101: 674–685. DOI: 10.1603/0022-0493(2008)101[674:dwccwf]2.0.co;2.

Podoler, H., Galon, I. & Gazit, S. 1985. The effect of Atemoya flowers on their pollinators – Nitidulid beetles. *Acta Oecologica-Oecologia Applicata*, 6: 251–258.

Pontin, D.R., Wade, M.R., Kehrli, P. & Wratten, S.D. 2006. Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. *Ann Appl Biol*, 148: 39–47.

Posner, J.L., Baldock, J.O. & Hedtcke, J.L. 2008. Organic and conventional production systems in the Wisconsin integrated cropping systems trials: I. Productivity 1990-2002. *Agronomy Journal*, 100: 253–260. DOI: 10.2134/agronj2007.0058.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25: 345–353.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, 84: 2628–2642. DOI: 10.1890/02-0136.

Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'Eman, G. & Willmer, P. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, 30: 78–85. DOI: 10.1111/j.0307-6946.2005.00662.x.

Praz, C.J., Müller, A. & Dorn, S. 2008. Specialized bees fail to develop on no-host pollen: do plants chemically protect their pollen? *Ecology*, 89: 795–804.

Prendeville, H.R. & Pilson, D. 2009. Transgenic virus resistance in cultivated squash affects pollinator behaviour. *Journal of Applied Ecology*, 46: 1088–1096. DOI: 10.1111/j.1365-2664.2009.01698.x.

Priess, J.A., Mimler, M., Klein, A.M., Schwarze, S., Tscharntke, T. & Steffan-Dewenter, I. 2007. Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. *Ecological Applications*, 17: 407–417. DOI: 10.1890/05-1795.

Proctor, M., Yeo, P. & Lack, A. 1996. *The natural history of pollination*. London, Harper Collins New Naturalist.

Pywell, R. 2005. Providing foraging resources for bumble bees in intensively farmed landscapes. *Biological Conservation*, 121: 479–494. DOI: 10.1016/j.biocon.2004.05.020.

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R. & Sherwood, A. 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumble bees in intensively farmed landscapes. *Biological Conservation*, 129: 192–206. DOI: 10.1016/j.biocon.2005.10.034.

Pywell, R.F., Warman, E.A., Sparks, T.H., Greatorex-Davies, J.N., Walker, K.J., Meek, W.R., Carvell, C., Petit, S. & Firbank, L.G. 2004. Assessing habitat quality for butterflies on intensively managed arable farmland. *Biological Conservation*, 118: 313–325.

Rader, R., Howlett, B.G., Cunningham, S.A., Westcott, D.A., Newstrom-Lloyd, L.E., Walker, M.K., Teulon, D.A.J. & Edwards, W. 2009. Alternative pollinator taxa are equally efficient but not as effective as the honey bee in a mass flowering crop. *Journal of Applied Ecology*, 46: 1080–1087. DOI: 10.1111/j.1365-2664.2009.01700.x.

Ramalho, M., Kleinert-Giovannini, A. & Imperatriz-Fonseca, V.L. 1990. Important bee plants for stingless bees (Melipona and Trigonini) and Africanized honey bees (Apis Mellifera) in neotropical habitats – a review. *Apidologie*, 21: 469–488. DOI: 10.1051/apido:19900508.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. L. Real, ed. *Pollination biology*. New York, Academic Press, pp. 305–330.

Rathcke, B.J. & Jules, E.S. 1993. Habitat fragmentation and plant–pollinator interactions. *Curr. Sci.*, 65: 273–277.

Ratti, C.M., Higo, H.A., Griswold, T.L. & Winston, M.L. 2008. Bumble bees influence berry size in commercial *Vaccinium* spp. cultivation in British Columbia. *Canadian Entomologist*, 140: 348–363.

Raudsepp-Hearne, C., Peterson, G.D. & Bennett, E.M. 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, 107: 5242–5247.

Rehman, K., Hussain, T., Soomro, A.H. & Khuhro, R.D. 1990. Pollinators activities on mango inflorescence. *Proceedings of Pakistan Congress of Zoology*, 10: 143–146.

Richards, A.J. 2001. Does low biodiversity resulting from modern agriculture practice affect crop pollination and yield? *Annals of Botany*, 88: 165–172.

Ricketts, T.H. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology*, 18: 1262–1271. DOI: 10.1111/j.1523-1739.2004.00227.x.

Ricketts, T.H, Daily, G.C, Ehrlich, P.R. & Michener, C.D. 2004. Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences of the United States of America*, 101: 12579–12582.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A. & Viana, B.F. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, 11: 499–515.

Robinson, R.A. & Sutherland, W.J. 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, 39: 157–176. DOI: 10.1046/j.1365-2664.2002.00695.x.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). *Ecological Monographs*, 43: 95–124.

Rortais, A., Arnold, G., Halm, M.P. & Touffet-Briens, F. 2005. Modes of honey bees exposure to systemic insecticides: estimated amounts of contaminated pollen and nectar consumed by different categories of bees. *Apidologie*, 36: 71–83. DOI: 10.1051/apido:2004071.

Roschewitz, I., Gabriel, D., Tscharntke, T. & Thies, C. 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology*, 42: 873–882. DOI: 10.1111/j.1365-2664.2005.01072.x.

Roubik, D.W. 1989. *Ecology and natural history of tropical bees.* New York, Cambridge University Press.

Roubik, D.W. 2006. Stingless bee nesting biology. *Apidologie*, 37: 124–143. DOI: 10.1051/apido:2006026.

Roubik, D.W. & Moreno, J.E. 1990. Social bees and palm trees: what do pollen diets tell us? In: G.K. Veeresh, B. Mallik & C.A. Viraktamath, eds. *Social Insects and the Environment*, pp. 427–428. New Delhi, Oxford and IBH Publishing Co.

Roulston, T.H. & Cane, J.H. 2000. Pollen nutritional content and digestibility for animals. *Plant Systematics and Evolution*, 222: 187–209. DOI: 10.1007/bf00984102.

Roulston, T.H., Cane, J.H. & Buchmann, S.L. 2000. What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs*, 70: 617–643. DOI: 10.1890/0012-9615(2000)070[0617:wgpcop]2.0.co;2.

Roulston, T.H. & Goodell, K. 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, 56: 293–312.

Ruiz-Gonzalez, M.X. & Brown, M.J.F. 2006. Honey bee and bumble bee trypanosomatids: specificity and potential for transmission. *Ecological Entomology*, 31: 616–622. DOI: 10.1111/j.1365-2311.2006.00823.x.

Rundlöf, M, Nilsson, H. & Smith, H.G. 2008. Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation*, 141: 417–426.

Sabara, H.A. & Winston, M.L. 2003. Managing honey bees (Hymenoptera: Apidae) for greenhouse tomato pollination. *Journal of Economic Entomology*, 96: 547–554.

Salatino, A., Teixeira, E.W., Negri, G. & Message, D. 2005. Origin and chemical variation of Brazilian propolis. *Evidence-Based Complementary and Alternative Medicine*, 2: 33–38. DOI: 10.1093/ecam/neh060.

Salveter, R. 1998. The influence of sown herb strips and spontaneous weeds on the larval stages of aphidophagous hoverflies (Dipt., Syrphidae). *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, 122: 103–114.

Sandhu, H., Porter, J. & Wratten, S. 2013. Experimental Assessment of Ecosystem Services in Agriculture, in Ecosystem Services in Agricultural and Urban Landscapes. In: S. Wratten, H. Sandhu, R. Cullen & R. Costanza, eds. John Wiley and Sons, Oxford. DOI: 10.1002/9781118506271.ch8

Sandhu, H.S., Wratten, S.D. & Cullen, R. 2010. The role of supporting ecosystem services in conventional and organic arable farmland. *Ecological Complexity*, 7: 302–310. DOI: 10.1016/j.ecocom.2010.04.006.

Sandhu, H.S., Wratten, S.D., Cullen, R. & Case, B. 2008. The future of farming: the value of ecosystem services in conventional and organic arable land: an experimental approach. *Ecological Economics*, 64: 835–848. DOI: 10.1016/j.ecolecon.2007.05.007.

Schlindwein, C., Wittmann, D., Martins, C.F., Hamm, A., Siqueira, J.A., Schiffler, D. & Machado, I.C. 2005. Pollination of Campanula rapunculus L. (Campanulaceae): how much pollen flows into pollination and into reproduction of oligolectic pollinators? *Plant Systematics and Evolution*, 250: 147–156. DOI: 10.1007/s00606-004-0246-8.

Schmidt, J.O. 1984. Feeding preferences of Apis mellifera L. (Hymenoptera: Apidae): individual versus mixed pollen species. *Journal of the Kansas Entomological Society*, 57: 323–327.

Schmidt, J.O., Thoenes, S.C. & Levin, M.D. 1987. Survival of honey-bees, Apis mellifera (Hymenoptera: Apidae), fed various pollen sources. *Annals of the Entomological Society of America*, 80: 176–183.

Schmidt, L.S., Schmidt, J.O., Rao, H., Wang, W.Y. & Xu, L.G. 1995. Feeding preference and survival of young worker honey-bees (Hymenoptera: Apidae) fed rape, sesame, and sunflower pollen. *Journal of Economic Entomology*, 88: 1591–1595.

Schneider, F. 1948. Beitrag zur Kenntnis der Generationsverhaltnisse und Diapause rauberischer Schwebfliegen (Syrphidae: Diptera). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 21: 245–285.

Schwarz, M.P. & Hurst, PS. 1997. Effects of introduced honey bees on Australia's native bee fauna. *Victorian Naturalist* (Blackburn), 114: 7–12.

Schweiger, O., Biesmeijer, J.C., Bommarco, R., Hickler, T., Hulme, P.E., Klotz, S., Kuehn, I., Moora, M., Nielsen, A., Ohlemueller, R., Petanidou, T., Potts, S.G., Pysek, P., Stout, J.C., Sykes, M.T., Tscheulin, T., Vila, M., Walther, G-R., Westphal, C., Winter, M., Zobel, M. & Settele, J. 2010. Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. *Biological Reviews*, 85: 777–795. DOI: 10.1111/j.1469-185X.2010.00125.x.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekoetter, T., Hendrickx, F., Herzog, F., Liira, J., Maelfait, J-P., Speelmans, M. & Dziock, F. 2007. Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos*, 116: 461–472. DOI: 10.1111/j.2007.0030-1299.15372.x.

Scott-Dupree, C.D. & Winston, M.L. 1987. Wild bee pollinator diversity and abundance in orchard and uncultivated habitats in the Okanagan Valley, British Columbia. *Can. Entomol.*, 119: 735–745.

Sears, M.K., Hellmich, R.L., Stanley-Horn, D.E., Oberhauser, K.S., Pleasants, J.M., Mattila, H.R., Siegfried, B.D. & Dively, G.P. 2001. Impact of Bt corn pollen on monarch butterfly populations: a risk assessment. *PNAS*, 98: 11937–11942.

Sheffield, C.S., Westby, S.M., Smith, R.F. & Kevan, P.G. 2008. Potential of bigleaf lupine for building and sustaining Osmia lignaria populations for pollination of apple. *Canadian Entomologist*, 140: 589–599.

Shepherd, M.D., Buchmann, S.L., Vaughan, M. & Black, S.H. 2003. *Pollinator Conservation Handbook*. Portland, OR, Xerces Society.

Shuler, R.E., Roulston, T.H. & Farris, G.E. 2005. Farming practices influence wild pollinator populations on squash and pumpkin. *Journal of Economic Entomology*, 98: 790–795.

Sihag, R.C. 2000. Ecobiology of the little honey bee (Apis florea) in semi-arid subtropical climates of India. In: M. Matsuka, L.R. Verma, S. Wongsiri, K.K. Shrestha & U. Partap, eds. *Asian bees and beekeeping: progress of research and development*, pp. 46–49.

Silva, B.B., Rosalen, P.L., Cury, J.A., Ikegaki, M., Souza, V.C., Esteves, A. & Alencar, S.M. 2008. Chemical composition and botanical origin of red propolis, a new type of Brazilian propolis. *Evidence-Based Complementary and Alternative Medicine*, 5: 313–316. DOI: 10.1093/ecam/nem059.

Simone-Finstrom, M. & Spivak, M. 2010. Propolis and bee health: the natural history and significance of resin use by honey bees. *Apidologie*, 41: 295–311. DOI: 10.1051/apido/2010016.

Sharma, N. 2001. Studies on the predatory complex of peach leaf curling aphid, Brachycaudus helichrysi (Kalt.) with special reference to the bug, Anthocoris minki (Dhorn), M. Sc. Thesis, Department of Entomology and Apiculture, University of Horticulture & Forestry, Himachal Pradesh, India.

Slaa, E.J., Sanchez Chaves, L.A., Malagodi-Braga, K.S. & Hofstede, F.E. 2006. Stingless bees in applied pollination: practice and perspectives. *Apidologie*, 37: 293–315. DOI: 10.1051/apido:2006022.

Slaa, E.J., Wassenberg, J. & Biesmeijer, J.C. 2003. The use of field-based social information in eusocial foragers: local enhancement among nestmates and heterospecifics in stingless bees. *Ecological Entomology*, 28: 369–379. DOI: 10.1046/j.1365–2311.2003.00512.x.

Smeets, P. & Duchateau, M.J. 2003. Longevity of Bombus terrestris workers (Hymenoptera: Apidae) in relation to pollen availability, in the absence of foraging. *Apidologie*, 34: 333–337. DOI: 10.1051/apido:2003026.

Smith, J.G. 1969. Some effects of crop background on populations of aphids and their natural enemies on brussels sprouts. *Annals of Applied Biology*, 63: 326–330.

Speight, M.R. & Lawton, J.H. 1976. The influence of weed cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. *Oecologia*, 23: 211–223.

Steffan-Dewenter, I. 2002. Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecol. Entomol.*, 27: 631–637.

Steffan-Dewenter, I. & Tscharntke, T. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, 121: 432–440. DOI: 10.1007/s004420050949.

Steffan-Dewenter, I. & Tscharntke, T. 2001. Succession of bee communities on fallows. *Ecography*, 24: 83–93.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C. & Tscharntke, T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83: 1421–1432. DOI: 10.2307/3071954.

Steffan-Dewenter, I., Potts, S.G. and Packer, L. 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.*, 20: 651–652.

Steffan-Dewenter, I. & Westphal, C. 2008. The interplay of pollinator diversity, pollination services and landscape change. *Journal of Applied Ecology*, 45: 737–741. DOI: 10.1111/j.1365-2664.2008.01483.x.

Stephen, W.P. 1955. Alfalfa pollination in Manitoba. *J. Econ. Entomol.*, 48: 543–548.

Stubbs, C.S. & Drummond, F.A. 1997. Management of the alfalfa leafcutting bee, Megachile rotundata (Hymenoptera: Megachilidae), for pollination of wild lowbush blueberry. *Journal of the Kansas Entomological Society*, 70: 81–93.

Stubbs, C.S. & Drummond, F.A. 2001. Bombus impatiens (Hymenoptera: Apidae): an alternative to Apis mellifera (Hymenoptera: Apidae) for lowbush blueberry pollination. *Journal of Economic Entomology*, 94: 609–616. DOI: 10.1603/0022-0493-94.3.609.

Stubbs, C.S., Drummond, F.A. & Osgood, E.A. 1994. Osmia-Ribifloris-Biedermannii and Megachile-Rotundata (Hymenoptera, Megachilidae) introduced into the Lowbush Blueberry Agroecosystem in Maine. *Journal of the Kansas Entomological Society*, 67: 173–185.

Suchail, S., Guez, D. & Belzunces, L.P. 2001. Discrepancy between acute and chronic toxicity induced by imidacloprid and its metabolites in Apis mellifera. *Environmental toxicology and chemistry/SETAC*, 20: 2482–2486.

Syme, P.D. 1975. The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. *Environmental Entomology*, 4: 337–346.

Telenga, N.A. 1958. Biological method of pest control in crops and forest plants in the USSR. In: *Report of the Soviet Delegation*. Ninth International Conference on Quarantine and Plant Protection, Moscow, pp. 1–15.

Tepedino, V.J., Alston, D.G., Bradley, B.A., Toler, T.R. & Griswold, T.L. 2007. Orchard pollination in Capitol Reef National Park, Utah, USA. Honey bees or native bees? *Biodiversity and Conservation*, 16: 3083–3094. DOI: 10.1007/s10531-007-9164-8.

Tepedino, V.J. & Parker, F.D. 1988. Alternation of sex-ratio in a partially bivoltine bee, Megachile-Rotundata (Hymenoptera, Megachilidae). *Annals of the Entomological Society of America*, 81: 467–476.

Teras, I. 1985. Food plants and flower visits of bumble bees Bombus Hymenoptera Apidae in southern Finland. *Acta Zoologica Fennica*, 179: 1–120.

Thomson, D.M. 2006. Detecting the effects of introduced species: a case study of competition between Apis and Bombus. *Oikos*, 114: 407–418. DOI: 10.1111/j.2006.0030-1299.14604.x.

Thresh, J.M. 1981. Pests, pathogens and vegetation: the role of weeds and wild plants in the ecology of crop pests and diseases. Pitman, Boston, MA.

Tilman, D., Cassman, K.G., Matson, P., Naylor, R. & Polasky, S. 2002. Agricultural sustainability and intensive production practices. *Nature*, 418: 671–677. DOI: 10.1038/nature01014.

Torchio, P.F. 1985. Field Experiments with the pollinator species, Osmia-Lignaria-Propinqua Cresson, in apple orchards .5. (1979-1980), methods of introducing bees, nesting success, seed counts, fruit yields (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society*, 58: 448–464.

Torchio, P.F. 1990. Diversification of pollination strategies for United States crops. *Environmental Entomology*, 19: 1649–1656.

Torres, C. & Galetto, L. 1998. Patterns and implications of floral nectar secretion, chemical composition, removal effects and standing crop in Mandevilla pentlandiana (Apocynaceae). *Botanical Journal of the Linnean Society*, 127: 207–223. DOI: 10.1111/j.1095-8339.1998.tb02098.x.

Tscharntke, T., Batáry, P. & Dormann, C.F. 2011. Set-aside management: how do succession, sowing patterns and landscape context affect biodiversity? *Agriculture, Ecosystems & Environment*, 143: 37–44. DOI: 10.1016/j.agee.2010.11.025.

Tuell, J.K., Fiedler, A.K., Landis, D. & Isaacs, R. 2008. Visitation by wild and managed bees (Hymenoptera: Apoidea) to Eastern US native plants for use in conservation programs, *Environmental Entomology,* 37: 707–718.

Tuell, J.K., Ascher, J.S. & Isaacs, R. 2009. Wild bees (Hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. *Annals of the Entomological Society of America*, 102: 275–287.

Ulbert, L., Steinmann, H. & Klimek, S. 2010. Using selective herbicides to manage beneficial and rare weed species in winter wheat. *Journal of Plant Diseases and Protection*, 117(5): 233–239.

van Buskirk, J. & Willi, Y. 2004. Enhancement of farmland biodiversity within set-aside land. *Conservation Biology*, 18: 987–994. DOI: 10.1111/j.1523-1739.2004.00359.x.

van Emden, H.F. 1965. The role of uncultivated land in the biology of crop pests and beneficial insects. *Scientific Horticulture*, 17: 121–136.

van Emden, H.F. 1963. Observations of the effects of flowers on the activity of parasitic Hymenoptera. *Entomologist's Monthly Magazine*, 98: 265–270.

van Engelsdorp, D., Hayes, J, Jr., Underwood, R.M. & Pettis, J. 2008. A survey of honey bee colony losses in the US, Fall 2007 to Spring 2008. *PLOS One*, 3. DOI: e407110.1371/journal.pone.0004071.

van Mele, P. 2007. A historical review of research on the weaver ant Oecophylla in biological control. *Agricultural and Forest Entomology*, 10: 13–22. DOI: 10.1111/j.1461-9563.2007.00350.x.

Vattala, H., Wratten, S., Phillips, C. & Wackers, F. 2006. The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. *Biological Control*, 39: 179–185. DOI: 10.1016/j.biocontrol.2006.06.003.

Vicens, N. & Bosch, J. 2000. Pollinating efficacy of Osmia cornuta and Apis mellifera (Hymenoptera: Megachilidae, Apidae) on 'red Delicious' apple. *Environmental Entomology*, 29: 235–240. DOI: 10.1603/0046-225x(2000)029[0235:peooca]2.0.co;2.

Villanueva-Gutierrez, R., Roubik, D.W. & Colli-Ucan, W. 2005. Extinction of Melipona beecheii and traditional beekeeping in the Yucatan peninsula. *Bee World*, 86: 35–41.

Walker, K.J., Critchley, C.N.R., Sherwood, A.J., Large, R., Nuttall, P., Hulmes, S., Rose, R. & Mountford, J.O. 2007. The conservation of arable plants on cereal field margins: an assessment of new agri-environment scheme options in England, UK. *Biological Conservation*, 136: 260–270. DOI: 10.1016/j.biocon.2006.11.026.

Walther-Hellwig. K., Fokul, G., Frankl, R., Buechler, R., Ekschmitt, K. & Wolters, V. 2006. Increased density of honey bee colonies affects foraging bumble bees. *Apidologie*, 37: 517–532. DOI: 10.1051/apido:2006035.

Walther-Hellwig, K. & Frankl, R. 2000. Foraging habitats and foraging distances of bumble bees, Bombus spp. (Hym., apidae), in an agricultural landscape. *Journal of Applied Entomology-Zeitschrift Fur Angewandte Entomologie*, 124: 299–306. DOI: 10.1046/j.1439-0418.2000.00484.x.

Warwick, S.I., Beckie, H.J. & Hall, L.M. 2009. Gene flow, invasiveness, and ecological impact of genetically modified crops. *Annals of the New York Academy of Sciences*, 1168: 72–99. DOI: 10.1111/j.1749-6632.2009.04576.x.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. & Ollerton, J. 1996. Generalization in pollination systems, and why it matters. *Ecology*, 77: 1043–1060. DOI: 10.2307/2265575.

Watson, J.C., Wolf, A.T. & Ascher, J.S. 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environmental Entomology*, 40: 621–632. DOI: 10.1603/en10231.

Wcislo, W.T. & Cane, J.H. 1996. Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology*, 41: 257–286. DOI: 10.1146/annurev.ento.41.1.257.

Westerkamp, C. 1991. Honey bees are poor pollinators – why? *Plant Systematics and Evolution*, 177: 71–75.

Westerkamp, C. 1996. Pollen in bee-flower relations – some considerations on melittophily. *Botanica Acta*, 109: 325–332.

Westerkamp, C. & Gottsberger, G. 2000. Diversity pays in crop pollination. *Crop Science*, 40: 1209–1222.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. 2003. Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, 6: 961–965.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumble bees. *Journal of Applied Ecology*, 46: 187–193. DOI: 10.1111/j.1365-2664.2008.01580.x.

White, A.J., Wratten, S.D., Berry, N.A. & Weigmann, U. 1995. Habitat manipulation to enhance biological control of Brassica pests by hover flies (Diptera, Syrphidae). *Journal of Economic Entomology*, 88: 1171–1176.

Wille, A. 1983. Biology of the stingless bees. *Annual Review of Entomology*, 28: 41–64. DOI: 10.1146/annurev.en.28.010183.000353.

William, R.D. 1981. Complementary interactions between weeds, weed control practices, and pests in horticultural cropping systems. *HortScience*, 16: 508–513.

Williams, I.H. 1994. The dependence of crop production within the European Union on pollination by honey bees. *Agricultural Zoology Reviews*, 6: 229–257.

Williams, I.H. 2002. Insect pollination and crop production: a European perspective. In P. Kevan & V.L. Imperatriz-Fonseca, eds. *Pollinating bees: the conservation link between agriculture and nature*, pp. 59–65. Brasilia, Ministry of Environment.

Williams, I.H. & Christian, D.G. 1991. Observations on Phacelia-Tanacetifolia Bentham (Hydrophyllaceae) as a food plant for honey-bees and bumble bees. *Journal of Apicultural Research*, 30: 3–12.

Williams, N.M, Crone, E.E., Roulston, T.H., Minckley, R.L, Packer, L. & Potts, S.G. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143: 2280–2291. DOI: 10.1016/j.biocon.2010.03.024.

Williams, N.M. & Kremen, C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, 17: 910–921. DOI: 10.1890/06-0269.

Williams, N. & Winfree, R. 2009. *Native bee benefits.* Bryn Mawr College and Rutgers University. http://rci.rutgers.edu/insects/NativeBeeBenefits2009.pdf

Williams, P. 2005. Does specialization explain rarity and decline British bumble bees? A response to Goulson et al. *Biological Conservation*, 122: 33–43. DOI: 10.1016/j.biocon.2004.06.019.

Williams, P., Colla, S. & Xie, Z.H. 2009. Bumble bee vulnerability: common correlates of winners and losers across three continents. *Conservation Biology*, 23: 931–940.

Willmer, P. 2011. *Pollination and floral ecology*. Princeton, NJ, Princeton University Press.

Wilson, E.O. 1992. *The Diversity of Life*. Harvard University Press

Winfree, R. 2010. The conservation and restoration of wild bees, In: Year in Ecology and Conservation Biology 2010 (Annals of the New York Academy of Sciences, Vol. 1195), pp. 169–197.

Winfree, R., Aguilar, R., Vazquez, D.P., LeBuhn, G. & Aizen, M.A. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90: 2068–2076.

Winfree, R., Griswold, T. & Kremen, C. 2007a. Effects of human disturbance on bee communities in a forest ecosystem. *Cons. Biol.*, 213(1): 223–223.

Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. 2007b. Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, 10: 1105–1113.

Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S. & Kremen, C. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology*, 45: 793–802.

Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Pärt, T., Thies, C., Tscharntke, T., Weisser, W.W. & Bommarco, R. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology*, 48: 570–579. DOI: 10.1111/j.1365-2664.2010.01950.x.

Wratten, S.D. & van Emden, H.F. 1995. Habitat management for enhanced activity of natural enemies of insect pests. In: D.M. Glen, M.P. Greaves & H.M. Anderson, eds. *Ecology and Integrated Farming Systems*. pp. 117–145. Chichester, UK, John Wiley and Sons.

Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R. & Tylianakis, J.M. 2003. Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia*, 134: 605–611. DOI: 10.1007/s00442-002-1128-9.

Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E. & Desneux, N. 2012. Pollinator habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems and Environment*. 159: 112-122. DOI:10.1016/j.agee.2012.06.020

Wrucke, M.A. & Arnold, W.E. 1985. Weed species distribution as influenced by tillage and herbicides. *Weed Sci.*, 33: 853–856.

Zehnder, G., Gurr, G., Keuhne, S., Wade, M., Wratten, S. & Wyss, E. 2007. Arthropod pest management in organic crops. *Annual Review of Entomology*, 52: 57–80.

Zhang, W., Ricketts, T.H., Kremen, C., Carney, K. & Swinton, S.M. 2007. Ecosystem services and dis-services to agriculture. *Ecological Economics*, 64: 253–260.

Zimdahl, R.L. 1980. *Weed-Crop Competition: A Review*. Corvallis, OR, International Plant Protection Center, Oregon State University.

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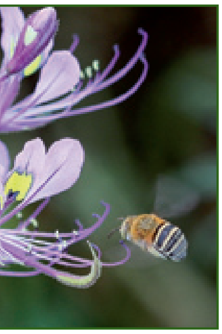
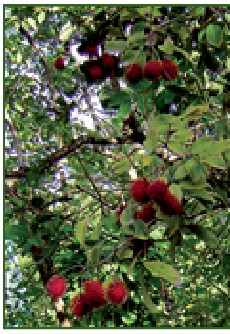
CROPS, WEEDS AND POLLINATORS
UNDERSTANDING ECOLOGICAL INTERACTION FOR BETTER MANAGEMENT

This publication looks at managing agricultural systems through an ecological approach, building upon beneficial biological interactions and finding positive synergies between pollination and weed management. These two aspects of agriculture consist of a multitude of interactions, both beneficial and harmful for the farmer and agriculture in general. If the practices applied to effectively control weeds can also benefit pollinators, there may be multiple benefits. As part of FAO's "Global Action on Pollination Services for Sustainable Agriculture", this publication was prepared in collaboration with experts to develop sound advice aimed for a wide range of countries and contexts to sustainably promote the twin goals of weed and pollinator management.







BIODIVERSITY & ECOSYSTEM SERVICES IN AGRICULTURAL PRODUCTION SYSTEMS

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