

Understanding the role of species richness for crop pollination services

**Alexandra-Maria Klein, Christine Müller, Patrick Hoehn,
and Claire Kremen**

14.1 Introduction

Flower visitation and pollination by animals are the first steps and therefore critical to the sexual reproduction of many plant species (Kearns *et al.* 1998), including up to 90 per cent of Angiosperms in tropical rainforests (Bawa 1990). Flower visitors are insects or vertebrates like hummingbirds or bats visiting flowers for receiving nectar and/or pollen, and the visitation can, but does not necessarily, result in pollination, the successful fertilization of the flower. Recent estimates showed that 35 per cent of global food production directly consumed by humans comes from crops that benefit from flower visitation, primarily by bees and other insects (Klein *et al.* 2007). Many of these crop plants increase fruit or seed quantity from 5–50 per cent when flower visitors are present under experimental conditions, and a small number of crops ($n = 13$) do not set fruit at all if pollinators are absent. Flower visitors can be also important for our dairy and meat industries, since many forage crops, like alfalfa, clover (Delaplane and Mayer 2000), and soybeans produced for cattle forage (Chiari *et al.* 2005) benefit from insect pollination for seed production. Flower visitors are also often important in modern agriculture to mediate gene flow between varieties in hybrid seed production (Greenleaf and Kremen 2006a, Van Deynze *et al.* 2005). Many wild plant populations have been shown to be limited by access to flower visitors (Ashman *et al.* 2004).

Intensification of land use by tilling, irrigation, and fertilizer and biocide use, along with declining habitat heterogeneity from increased field sizes,

monoculture plantings, and the modification of natural habitats by humans, significantly impacts pollinator communities across a variety of scales (Klein *et al.* 2007, Kremen *et al.* 2007, Ricketts *et al.* 2008). Local (field-level) alterations that impact pollinators and pollination include changes in: (1) the abundance and distribution of flower resources (Holzschuh *et al.* 2007, Klein *et al.* 2002, Williams and Kremen 2007, Tylianakis *et al.* 2008), (2) species richness of flowering plants (Ebeling *et al.* 2008, Ghazoul 2006, Potts *et al.* 2006), (3) availability of nesting sites and materials (Shuler *et al.* 2005, Kim *et al.* 2006), (4) light levels (Klein *et al.* 2003a, b), and (5) temporal continuity of floral resources (Greenleaf and Kremen 2006b). Examples of landscape-level factors affecting bee communities are the proportion and quality of natural or semi-natural habitats in the landscape (Greenleaf and Kremen 2006b, Kim *et al.* 2006, Kremen *et al.* 2002, 2004), the distance of natural or semi-natural habitats from crop systems (Klein *et al.* 2003a, b, Ricketts *et al.* 2004, Ricketts *et al.* 2008), and the presence of mass-flowering resources (Herrman *et al.* 2007, Westphal *et al.* 2003). Therefore, resource availability and the area and isolation of natural habitats are all important for the conservation of pollinator species richness, which provides a key service to crop production.

In this chapter, we discuss what is known about the relationship between flower-visiting species richness and pollination services. Following the introduction (Section 14.1), the relative importance of species richness, individual numbers, and combined effects in providing services to their mutualistic

plant partners are described (Section 14.2). Next, the mechanisms underlying the role of species richness in ensuring insect pollination (Section 14.3), and the evidence for and against *sampling effects* (Section 14.3.1), *niche complementarity* (Section 14.3.2), and *functional facilitation* are discussed (Section 14.3.3). Since the pollination of crop species is embedded within plant–flower visitor (PFv) webs including both other crop and wild plant species, the utility of analyzing quantitative plant–flower visitor interactions for managing and restoring crop pollination services is discussed (Section 14.4). This section starts with a paragraph about web structure and characteristics (Section 14.4.1), to explain how general PFv characteristics buffer species extinction and integration (Section 14.4.2). The role of higher trophic levels in PFv webs is discussed, and in Section 14.4.3 ideas are summarized of how PFv webs provide information for crop pollination services. Section 14.5 presents the current knowledge concerning the consequences of current and projected pollinator declines for global crop production and wild plant populations. The chapter ends with outstanding research gaps in the understanding of how flower-visiting species richness contributes to pollination services (Section 14.6).

14.2 The importance of flower-visitor species richness and individual numbers for pollination services

Pollination services strongly depend on the total of all individuals in a community, the so called aggregate abundance of flower visitors (Morris 2003, Vázquez *et al.* 2005). The European honey bee, *Apis mellifera* L., for example, is the world's most important crop-pollinating species because their high sociality and large colonies yield large populations that are readily managed and moved in and among agricultural fields (Free 1993, McGregor 1976), ensuring fruit set and increasing fruit production and yield (e.g. Chiari *et al.* 2005, Roubik 2002, Stern *et al.* 2001). Although honey bees can provide pollination services for the majority of crop species (Klein *et al.* 2007), in some areas crops can be solely pollinated by species-rich communities of wild non-honey bees (Kremen *et al.* 2002, Winfree *et al.* 2008).

Consequently, under honey bee-scarcity scenarios, species richness of wild species may ensure adequate crop pollination services (Klein *et al.* 2003a, Winfree *et al.* 2008). Given the economic importance of bee pollination (Gallai *et al.* 2008), wild bee species richness will be critical in ensuring pollination services in the face of declining honey bee numbers.

Species richness of flower-visiting communities may be important for several reasons, four of which have been recently studied. First, more species-rich communities frequently have higher aggregate abundance and therefore contribute more to pollination services (Kremen and Chaplin-Kramer 2007, Larsen *et al.* 2005). With agricultural intensification, both flower-visiting species richness and aggregate abundance decline, because compensation by pollinator species that tolerate agricultural intensification is lacking (Larsen *et al.* 2005, Winfree and Kremen 2008). With lower species richness and individual numbers, pollination services become inadequate, as was shown for watermelons that were only sufficiently pollinated on the low-intensity farms that supported the richest bee communities (Kremen *et al.* 2002, 2004). Similarly, intensively cultivated coffee was found to be pollinated inadequately, except for plants growing close to forest fragments that supported the richest bee community (Ricketts *et al.* 2004). The ubiquity of the positive relationship between flower-visitor species richness and individual numbers across agricultural systems (Kremen and Chaplin-Kramer 2007), and the possible lack of density compensation in these systems (Winfree and Kremen 2008) suggest that high species richness is often necessary to provide sufficient pollination services through aggregate abundance of flower-visiting species.

Second, temporal turnover between years is extremely high in bee communities and this turnover affects crop pollination services (Herrera 1988, Pías and Guitián 2006, Williams *et al.* 2001). Species richness on watermelon farms with high flower-visitor species richness remained high from year to year, but the identity of bee species changed (Kremen *et al.* 2002). Temporal stability of the pollination service between days within a season (measured as the inverse of the coefficient of variation), also increased on low-intensity farms (Kremen *et al.* 2004) that supported higher species

Table 14.1 Similarity in flower-visiting communities among four different crops blooming in Yolo County, California. Almond blooms in early spring (February), while the other three crops are summer-flowering (May–August). Jaccard index of similarity is presented. Data from Kremen *et al.* 2002, 2004, Greenleaf and Kremen, 2006a, b, and unpublished data.

| | Almond | Tomato | Watermelon | Sunflower | Pollinator species richness |
|------------|--------|--------|------------|-----------|-----------------------------|
| Almond | 1 | | | | 14 |
| Tomato | 0.313 | 1 | | | 7 |
| Watermelon | 0.179 | 0.219 | 1 | | 32 |
| Sunflower | 0.231 | 0.171 | 0.32 | 1 | 34 |

richness. Thus high species richness may ensure that flower visitors and pollination services are available to the plants over all days and years, but more studies are needed to test if temporal stability of pollination services is related to bee species richness or individual numbers.

Third, spatial preferences for different flower-visiting species using flowers located on different parts of the plant (Lortie and Aarsen 1999, Hambäck 2001) or in different locations in the field (Klein and Kremen unpublished data) can also lead to the necessity of high species richness for adequate pollination services. Spatial stability of pollination service between plants within sites along a land-use gradient (measured as the inverse of the coefficient of variation) can also be influenced by flower-visiting species richness (Klein *et al.* 2003a), but more experimental tests are needed before conclusions can be drawn about the generality of this relationship between spatial characteristics in pollination stability and flower-visiting species richness and individual numbers. More aspects of spatial stability and spatio-temporal species turnover will be discussed in Section 14.3.2.

Fourth, flower-visiting species richness is essential when different crops are grown within the same cultivation system. In California, four well-studied crops (watermelon, sunflower, tomato, and almond) share only 17–33 per cent of the species that visit and potentially pollinate them (Table 14.1). Almond blooms in February, March (winter to spring), while the other crops are all summer-flowering. Therefore, it is not surprising that the bee community was almost entirely dissimilar between almond and the other crops, while watermelon, sunflower, and tomato shared a substantial proportion of their visiting bee species. Flower visitors to tomato comprised a subset of the much richer visitor communities to watermelon or sunflower, which shared

about 30 per cent of their visitor community. Despite blooming at the same time, watermelon and sunflower clearly attracted different flower-visiting species, because they differ in flower morphology and pollen and nectar availability, and because of the dominance of specialists on sunflower, which is the only one of these four crops native to North America. Similarly, in New Jersey, wild bee communities visiting watermelon versus tomato crops were found to be distinct as identified by non-metric multidimensional scaling (an ordination method to analyze compositional differences among communities). The community differences were visible even when controlling for differences between farm sites and the differential attractiveness of the two crops (Winfree *et al.* 2008). Similarly, Meléndez-Ramírez *et al.* (2002) showed a low species overlap of bees (similarity and shared species) visiting different cucurbit crops (cucumber, melon, pumpkin, watermelon) in Yucatán, Mexico.

Fifth, different species respond differentially to disturbances such as land-use intensification (response diversity, Elmquist *et al.* 2003), potentially buffering the provision of pollination services across land-use gradients. On watermelon fields in New Jersey and Pennsylvania where bee communities provide a relatively consistent level of pollination services across a land-use intensity gradient (Winfree *et al.* 2008), differential responsiveness of bee species to land-use intensity may be a mechanism for achieving stability across the gradient (Winfree and Kremen 2008). In California, where pollination services decline dramatically across the landscape with increasing intensification (Kremen *et al.* 2002), differential responsiveness among bee species may dampen the effect of increasing land use, which would otherwise be even more dramatic (Winfree and Kremen 2008).

Table 14.2 Spatial variation (measured as CV, Coefficient of Variation) of insect-pollinated fruit set among highland (*C. arabica*) and lowland (*C. canephora*) coffee trees per site across a gradient of pollinator species richness in different coffee agroforestry systems (Klein *et al.* 2003a,b, Klein *et al.* 2008). (A) Results of simple regressions; (B) selected glm (generalized linear model) that explains the highest variance when including functional group richness, species richness, individual number and all interaction terms. Models were selected according to lowest AIC and highest P-values. AIC (Akaike Information Criterion) and significance level (^(*) $p < 0.1$, ^{*} $p < 0.05$; ^{**} $p < 0.01$; ^{***} $p < 0.001$ of different Models were fitted. Analyses were done in R, version 2.6.2.

| Response variable | Explanatory variable | AIC |
|--------------------------------|---|----------------------|
| <i>Coffea arabica</i> | | |
| A Simple regressions | | |
| CV bee pollinated fruit set | Functional group richness | 190.7*** |
| " | Species richness | 195.9*** |
| " | Individual number | 195.9** |
| B Selected glm model | | |
| CV bee pollinated fruit set | Functional group richness + species richness + individual number + (functional group richness × individual number) + (species richness × individual number) | 190.1** |
| <i>Coffea canephora</i> | | |
| A Simple regressions | | |
| CV bee pollinated fruit set | Functional group richness | 142.2* |
| " | Species richness | 143.4 ^(*) |
| " | Individual number | 144.2 |
| B Selected glm model | | |
| CV bee pollinated fruit set | Functional group richness + (species richness × individual number) | 141.5* |

Although species richness is often correlated with aggregate abundance in bee communities (Kremen and Chaplin-Kramer 2007), data on three crop species suggests that species richness may be even more important than aggregate abundance. The data were collected along land-use gradients in Indonesia differing in habitat and landscape management to 'experimentally' manipulate bee species richness and individual numbers in real world ecosystems. Flower-visiting observations and pollination experiments were conducted for three species representing three different breeding systems: (1) lowland coffee, *C. canephora*, a mainly self-incompatible species, (2) highland coffee, *Coffea arabica*, a mainly self-compatible species (Klein *et al.* 2003a, Klein *et al.* 2008); (3) and pumpkin, *Cucurbita moschata*, a monoecious species, meaning that female and male gametes are spatially and temporally separated (Delaplane and Mayer 2000). For all three crop species flower-visitor species richness was more important to explain pollination services when factoring out for the effect of flower-visiting individual numbers (Hoehn *et al.* 2008, Klein *et al.*

2008). Hence the studies demonstrate that bee species richness is essential for overall pollination services. Consequently, the following question arises: what are the mechanisms behind the relationship of species richness and pollination services?

14.3 Mechanisms for the effects of flower-visiting species richness on providing pollination services

Three mechanisms known to be important in BEF patterns may explain why diverse flower-visiting communities can function better than depauperate communities. First, under *sampling (selection) effects* (Loreau *et al.* 2001), high species richness increases the likelihood of random inclusion within the flower-visiting community on a given crop of an efficient and effective pollinating species. Second, under *niche complementarity* (Loreau *et al.* 2001), high species richness improves pollination services because species differ in their foraging behavior and may complement one another by visiting and pollinating different flower species, or in the spatial

or temporal distribution of visits within or among flowers of a species. Third, under *functional facilitation* (Cardinale *et al.* 2002) a given species has a positive effect on the functional capability of other species. For example, interspecific interactions during foraging can lead to higher frequencies of cross pollination (Klein *et al.* 2008).

All three mechanisms assume that different flower-visiting species differ in their morphology, physiology, behavior, or other traits, so that high species richness maximizes resource use and thus pollination success, as discussed in more detail below.

14.3.1 Sampling (selection) effect

The sampling effect asserts that in experimental designs with varying species richness, increasing richness results in a higher chance of including a species that makes a disproportionate contribution to ecosystem functioning (Loreau 2000). In this case, the species in the species pool that is the most efficient (e.g. produces the most seeds per visit or deposits the most high-quality pollen) in pollination would dominate the pollination service and mask minor benefits by other species in multi-species communities whenever it was present. Due to the difficulty of experimentally manipulating flower-visiting communities, little evidence for or against the role of random sampling effects in pollination function is available. In natural experiments along land-use intensity gradients, Larsen *et al.* (2005) found that the most species-rich communities visiting watermelon were the only ones contained the most effective flower-visiting species for pollination. However, they showed that this was not due to random sampling effects, but rather to non-random local extinction processes.

The three crop studies from Indonesia (Hoehn *et al.* 2008, Klein *et al.* 2008) indicate that not sampling effect but niche complementarity seems to be the predominant mechanism for high quality and quantity in pollination services. This prediction is based on the finding that functional group richness explained the pollination service better than species richness *per se*. In all three studies, functional group richness was classified using *a priori* groups of morphological and behavioural pollinator traits.

Generally, sampling effects might be more important in more specialized plant–flower visitor relationships, where a few visiting species, maybe due to proboscis length, are much better adapted to flower morphology than others and thus more effective as pollinators. In such cases a more species-rich community has a higher chance of including the most effective pollinator species by random chance.

14.3.2 Niche complementarity and spatial stability

The theory of complementarity between species assumes that high species richness increases functional effectiveness by increasing the efficiency of resource use over space and time. Therefore, contributions of many species will increase resource use with each additional, individual species through distinct resource partitioning, until a plateau is reached. For example, a diverse flower-visiting community whose members exhibit species-specific or functional group-specific use of spatio-temporal niches during flower visitation should lead to more efficient resource use. By exploiting different spatio-temporal niches (e.g. different parts of the flower, tree or field, different times of the day), different flower-visiting species might maximize their ability to obtain pollen and nectar resources (Herrera 1988). Resource use for flower visitors consists of gathering pollen and nectar and this action simultaneously pollinates the plant. More efficient resource use through complementarity could thus lead to better pollination services for the plants, for example, a greater number of flowers per plant are pollinated, or a better distribution of pollen on the stigma is obtained.

For pumpkin (Hoehn *et al.* 2008), characterizations of the species-specific differences in spatio-temporal pattern of flower visitation were also made in high and low-bee species richness systems. In the high bee species richness sites, pumpkins reached their maximum in seed numbers (hand-pollinated flowers served as reference) (319 ± 105 standard deviation), whereas in the low-bee species richness sites, the number of seeds per pumpkin was significantly lower (179 ± 44). Comparing the spatial (flower-visiting height of the plant) and the

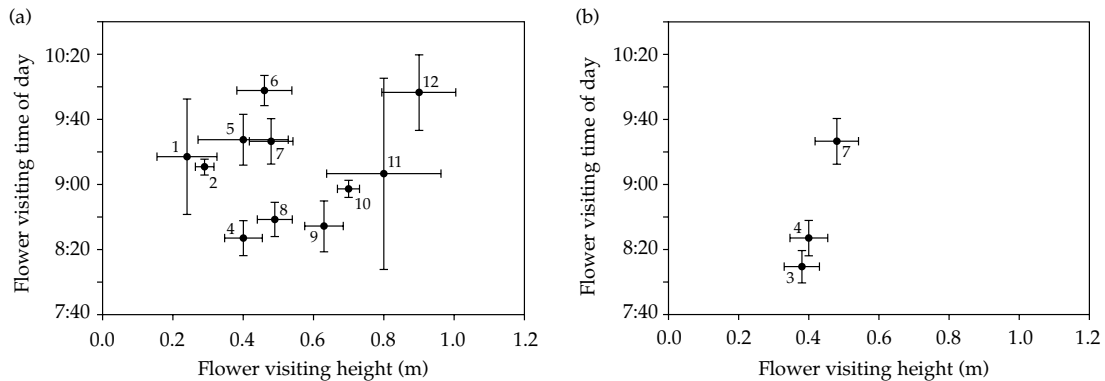


Figure 14.1 Flower height and forage time preferred by the most abundant flower-visiting bee species of planted pumpkin plants in two different habitat types: (a) grassland with high bee species richness and (b) forest with low bee species richness in Central, Sulawesi, Indonesia. Each habitat type was replicated with four plots in spatially separated sites. Experimental pumpkin patches of 2×5 m were planted in each plot and liquid fertilizer was applied every other week (for more information see Hoehn *et al.* 2008). Arithmetic means \pm standard errors are given. Numbers are presenting following bee species: 1 – *Nomia concinna*, 2 – *Lasioglossum* sp., 3 – *Apis cerana*, 4 – *Xylocopa dejeani*, 5 – *Nomia fulvata*, 6 – *Ceratina cognata*, 7 – *Trigona* sp., 8 – *Amegilla* sp., 9 – *Xylocopa confusa*, 10 – *Lasioglossum halictoides*, 11 – *Apis dorsata*, 12 – *Xylocopa nobilis*.

temporal (flower-visiting time of the day) activity of the flower-visiting species in both systems, it could be shown for the high species richness sites, comprising 10 species, that these species covered the entire spectrum of spatio-temporal niches. This increases the probability that flowers at any height were visited and flower visitors were active during the receptive period of the flowers (Fig. 14.1(a)). In contrast, the three bee species found visiting the low species richness sites did not cover all the spatio-temporal niches (Fig. 14.1(b)). In other words, in the low-bee species richness sites, spatial and temporal niches become unoccupied when bee species are lacking.

Another study on strawberries (Chagnon *et al.* 1993) demonstrates complementarity due to spatial factors. Here the crucial pollination trait was the species-specific behaviour of the bee interacting with the floral parts. Strawberries depend on pollen dispersion over the whole stigma to develop completely formed fruits. Small wild bees pollinated predominantly at the base of the stigma, while large honey bees were active on the centre of flowers, pollinating the apical part of the stigma. Absence of one of the two functional guilds causes deformed fruits, due to incomplete resource use by only one functional group. This example demonstrates that within-flower foraging behaviour can be strongly body size-

dependent. Also, in the pumpkin system, species-specific flower-visiting behaviour (time of visitation and height and duration of floral visit) was strongly related to the body size of the visiting species (Hoehn *et al.* 2008). Therefore, morphological traits can be responsible for differences in spatio-temporal floral resource use.

Additionally, Table 14.1 shows the spatial variation of insect-pollinated fruit set among coffee plants per site across different agroforestry systems comprising different bee communities. Simple relationships between insect-pollinated fruit set and functional group richness or species richness or individual numbers showed that for the spatial stability aspect, functional group richness seemed to play an important role. Nevertheless, models including interaction effects between functional group richness, species richness, and individual numbers explained fruit set similar to simple models using species richness alone (Table 14.1). Here, statistical limitations were reached, because of the collinear nature between functional group richness, species richness, and individual numbers in the real world (as opposed to experimental) study systems.

These case studies comprising species with different plant breeding systems show that high flower-visiting species richness including different

functional groups of flower visitors can lead to optimal (high levels with enhanced stability) pollination services for agricultural systems. Many studies show that flower-visiting communities are structured by behavioural niche differentiation, due to body size, circadian rhythm (as a result of differences in temperature tolerance), competition hierarchy, sociality, and other species-specific behavioural traits (Bishop and Armbruster 1999, Pinkus-Rendon *et al.* 2005, Stone 1994, Stone *et al.* 1999). Hence different functional traits of a species rich flower-visiting community can be important because niche complementarity between species maximize both resource use and pollination services provided.

14.3.3 Functional facilitation

A study by Greenleaf and Kremen (2006a) showed that wild bees contribute to sunflower pollination indirectly via facilitation. Hybrid sunflower seed production depends on animal-mediated pollen transfer from male (pollen- and nectar-producing) to female (only nectar-producing) parents. Although honey bees have low sunflower pollination efficiency per-visit, they are the only commercially available pollinators. Much higher pollination per visit efficiency of honey bees was achieved in areas with higher wild bee individual and species numbers. Encounters between honey bees and wild bees increased the likelihood that honey bees switched between female and male plants, thus increasing per-visit pollination efficiency. Otherwise, individual honey bee foragers tended to forage either on male plants for pollen or on female plants for nectar, and rarely transferred pollen between plants. Another potential facilitative mechanism could be dispersal of clumped pollen by honey bees of pollen deposited on female sunflowers by the wild bees. In the sunflower case, both individual and species number of the wild bee community significantly contributed to increasing the per visit pollination effectiveness of honey bees (Greenleaf and Kremen 2006a). However, in examples where only a few species are involved in interspecific interactions, species identity and individual numbers might be more important than species richness *per se* (Jonsson and Malmqvist 2003).

14.4 Plant–flower visitor interaction webs in crop pollination systems

Crop pollination studies are based on a given crop and its pollinating species, although crop plants may be influenced by interactions of their flower visitors with nearby wild plants, forming networks of dozens to hundreds of species. To date, mutualistic network approaches have only been applied in non-crop systems in order to understand ecological and evolutionary processes, but their application to crop systems may provide underlying information for managing and restoring flower-visiting species richness and crop pollination services. In Section 14.4.1 plant–flower visitor interaction webs (PFv webs) are shown and specific characteristics of the general structure highlighted, followed in Section 14.4.2 by a discussion of the importance of PFv web characteristics for species extinction and integration. Afterwards the role of higher trophic levels for PFv webs is described (Section 14.4.3). Section 14.4.4 summarizes some ideas of how quantitative PFv webs provide information to manage and restore flower-visiting species richness for crop pollination services.

14.4.1 PFv web structure and characteristics

Fully quantified plant–flower visitor webs provide the clearest description of the flower-visiting community structure, since they express the species individual numbers and the frequency of interactions among species (e.g. Forup *et al.* 2008, Memmott 1999, Fig. 2). Within such webs, the integration into the community of certain plants, like very rare species or an abundant flowering crop, or a managed pollinator, such as honey bees, can be studied (Gibson *et al.* 2006, Memmott and Waser 2002). Here, four PFv webs collected in an agricultural landscape in Dorset, UK, are shown to demonstrate the interactions between bees, crop, and wild plant species of surrounding flowering strips for bean (Fig. 14.2(a)), oilseed rape (Fig. 14.2(b)), and lupine (Fig. 14.2(c)). An additional PFv web in calcareous grassland is shown to visualize the differences between crop PFv webs and a PFv web of a semi-natural habitat without crop species (Fig. 14.2(d)). The webs of the crop fields are ordered from relatively poor

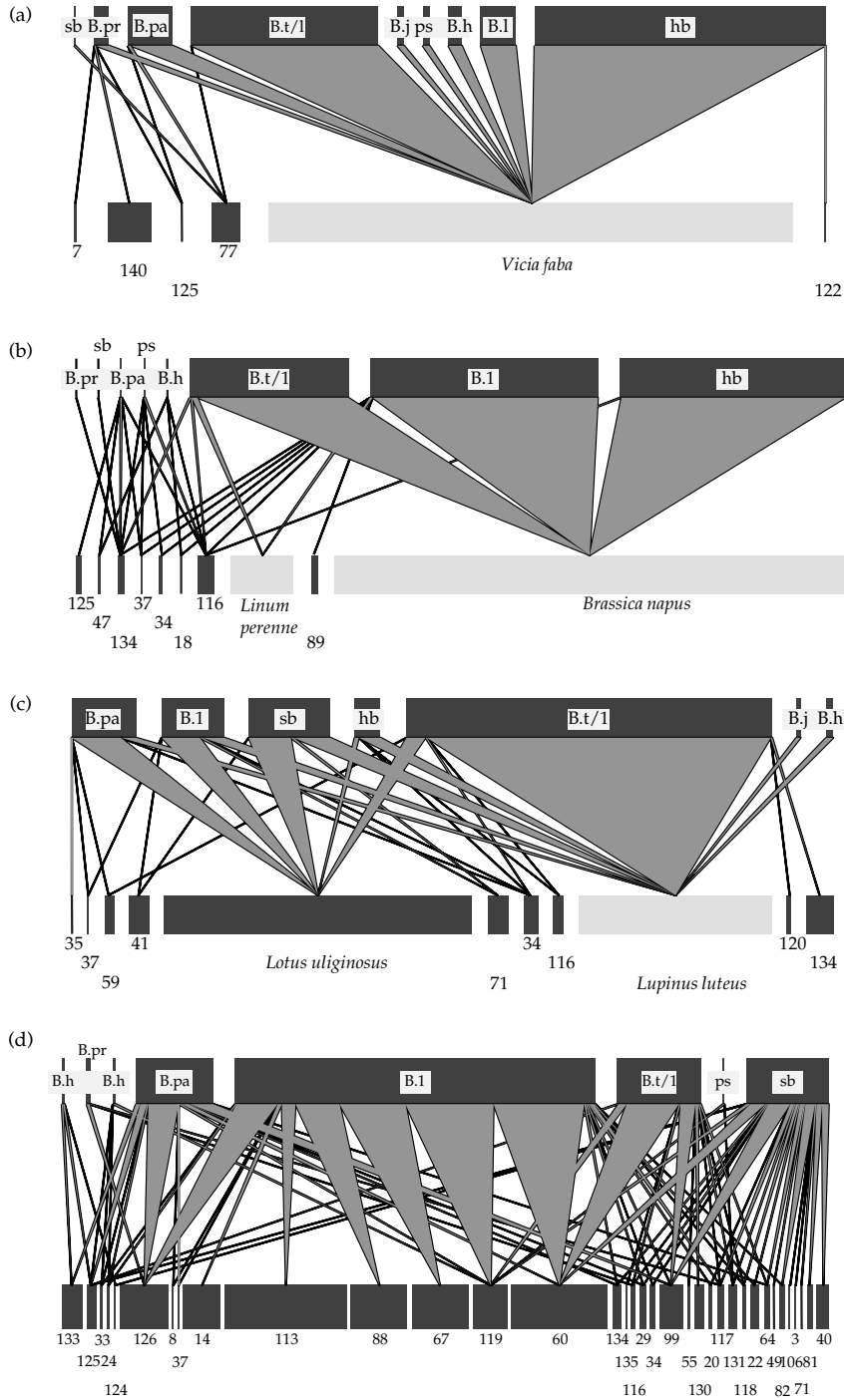


Figure 14.2 Quantified PfV webs in (a) bean, (b) oilseed rape, (c) lupine, and (d) calcareous grassland. The area sampled ranged between 10 and 13 ha and included a 10 m margin of flowering herbs around each crop field. Quantification was done by counting the specific interactions between a plant and a bee species over a sampling time of two to three hours on a sunny, windless day, except in the case of the grassland, where sampling was done repeatedly over the period of floral availability. All flowering plants were counted within one metre quadrates that were placed in a stratified manner over the area to estimate the

plant-flowering strips of the bean field to relatively rich plant strips of the lupine field. The oilseed rape field was adjacent to a linseed field which was at the end of its flowering period during sampling. The most abundant generalist bees were bumble bees, *Bombus terrestris/lucorum*, which were strongly attracted to the flowering crop, while more specialized bumblebees, such as *B. pascuorum*, *B. lapidarius*, *B. hortorum* and solitary bees appeared to prefer alternative flowering resources in the flowering strips. There was little attraction for solitary bees to either bean or oilseed rape, while lupine was visited frequently by leafcutter bees. In comparison, more evenly distributed interactions among plants and bees and a species-rich local community of solitary bees were found in calcareous grasslands where bees specialized on many different plant species (Fig. 14.2 (d)). Honey bees as generalist foragers were strongly attracted to mass-flowering crop and were not encountered in the grassland (non-crop) site.

The four quantitative PFv webs visualize the interaction between crop and wild plants and their flower-visiting species and can be used to identify whether the use of flowering strips adjacent to a crop field attracts several species to forage and interact via facilitation and complementarity to benefit the crop or divert flower-visiting species from the crop plants, which could lead to reduced flower visitation.

PFv webs are characterized by their highly nested structure. This indicates that flower-visiting specialists mainly interact with generalized plants that are visited by a whole array of other flower-visiting species. Specialist plants tend to be visited by gen-

eralist insects (Bascompte *et al.* 2003, Bascompte *et al.* 2006, Blüthgen *et al.* 2007, Montoya *et al.* 2006, May 2006). This nestedness leads to an asymmetry in plant–flower visitor interactions with strong dependence in one direction often linked to weak dependence in the reverse direction (Thompson 2006, Vázquez and Aizen 2004). Furthermore, mutualistic networks are dominated by a few extreme generalists, meaning only a few species build the core of the nested web and are much more connected than would be expected by chance (Jordano *et al.* 2003).

14.4.2 Species extinction and integration in PFv webs

Habitat loss or alteration, species extinction and addition of invasive species are the main factors disrupting PFv webs. Given the current, accelerated biodiversity loss, it becomes important to understand how whole networks of interacting plant and animal species are affected by extinction events and especially how extinction events might affect crop pollination services. The characteristic structure of PFv (nestedness and asymmetry) provides important alternative routes when species disappear and thus a certain insurance against biodiversity loss (Bascompte *et al.* 2006, Memmott *et al.* 2004).

Simulated progressive extinction models are currently only available for non-crop flower visitor webs. Memmott *et al.* (2004), for example, simulated flower-visiting species extinction to explore the resulting extinctions in plants depending on flower visitors for reproduction. The extinction scenarios

Figure 14.2 (continued)

abundance of floral resources per square metre. Bee counts were then extrapolated to the square metre unit. The upper represents bees and the lower bars plants. Each bar depicts a species and the length of the bar contains information about its abundance. The wedges depict interactions between plants and pollinating bees. The width at the basis of a wedge contains information about the interaction strengths. Honey bees (hb) did not occur in the grassland but were abundant on all three crop species. Bumble-bee groups consisted of *Bombus terrestris* and *B. lucorum* (B.tl: pooled because they were difficult to distinguish in the field), *B. lapidarius* (B.l.), *B. pascuorum* (B.pa), *B. pratorum* (B.pr), *B. hortorum* (B.h), *B. jonellus* (B.j) and parasitic *Bombus* species (ps; former *Psythirus*). Solitary bees (sr) were pooled because straight identification in the field was difficult. The flowering crop plants were labelled by name and bars were depicted in grey; the other plant species were: 3 = *Achillea millefolium*, 7 = *Anchusa arvensis*, 8 = *Anthyllis vulneraria*, 14 = *Bellis perennis*, 18 = *Buddleja davidii*, 20 = *Campanula glomerata*, 22 = *Campanula rotundifolia*, 24 = *Carduus nutans*, 29 = *Centaurea nigra*, 33 = *Cirsium acaulis*, 34 = *Cirsium arvense*, 35 = *Cirsium palustre*, 37 = *Cirsium vulgare*, 40 = *Crepis capillaris*, 41 = *Crepis paludosa*, 47 = *Digitalis purpurea*, 49 = *Echium vulgare*, 55 = *Eupatorium cannabinum*, 59 = *Galeopsis tetrahit*, 60 = *Genista tinctoria*, 64 = *Helianthemum nummularium*, 67 = *Hippocrepis comosa*, 71 = *Hypochaeris radicata*, 77 = *Lamium purpureum*, 81 = *Leontodon autumnalis*, 82 = *Leontodon hispidus*, 88 = *Lotus comiculatus*, 89 = *Lotus uliginosus*, 99 = *Odontites verna*, 106 = *Pilosella officinarum*, 113 = *Ranunculus repens*, 116 = *Rubus fruticosus*, 117 = *Scabiosa columbaria*, 118 = *Senecio jacobaea*, 119 = *Serratula tinctoria*, 120 = *Silene dioica*, 122 = *Sinapis*, 124 = *Stachys officinalis*, 125 = *Stachys selvatica*, 126 = *Succisa pratensis*, 130 = *Teucrium scorodonia*, 131 = *Thymus polytrichus*, 133 = *Trifolium pratensis*, 134 = *Trifolium repens*, 135 = *Ulex europaeus*, 140 = *Veronica persica*.

were either random extinction of flower-visiting species, extinction from least linked to most linked species, or *vice versa*. The webs were surprisingly robust towards flower-visiting species extinctions unless the most generalist (most linked) species were removed first. In this case, the extinction trajectory of plant species was tightly correlated to that of declining flower-visiting species richness following a relatively rapid (essentially linear) decline. Furthermore, some morphological features, such as body size, may make certain flower-visiting species more prone to extinction than others. Hence in systems where generalist flower-visiting species are large bodied, extinction would follow the worst-case scenario and pollination function would disappear as quickly as flower-visiting species (Larsen *et al.* 2005).

The opposite of extinction through habitat loss is the integration of alien species into existing mutualistic networks. In some ways, this occurs in crop systems when sudden appearance of abundant floral resources (the flowering crop) will change the behaviour of the flower-visiting species. Resident plants may either facilitate (increase) or compete with (decrease) visitation to the introduced (crop) plant. Experimental studies on such multi-species interactions typically have looked at the role of invasive plants on wild plant reproduction and have show various results from negative (Chittka and Schürkens 2001, Ghazoul 2002, Larson *et al.* 2006), to positive (Johnson *et al.* 2003, Moller 2004), to neutral (Aigner 2004). Community studies that investigate the impact of alien plant species on the whole mutualistic network show substantial integration of these plants into native PFv webs, with generalist flower-visiting species most likely to visit introduced plant species (Memmott and Waser 2002, Morales and Aizen 2006). Studies on the effects of one alien plant on an array of native plants find mixed results that depend on the species identity of native plants (Moragues and Traveset 2005) and on the stages of invasion (Aizen *et al.* 2008b). Despite increased visitation frequencies in plots with a highly rewarding invasive plant, pollination of native plant species is not necessarily facilitated by the co-occurrence of these high-rewarding alien plant species, possibly because of the large amount of alien pollen they receive (Larsen *et al.* 2006), as was shown by quantified pollen transport webs (Lopezaraiza-Mikel *et al.*

2007). By analogy, these studies suggest that flowering crop species will be visited by flower-visiting generalist species and will integrate reasonably well in existent interactions webs.

14.4.3 Higher trophic levels in PFv webs

A further aspect that can be examined using the food web approach is to elucidate the role of higher trophic levels such as natural enemies of pollinators like predators, parasites, and parasitoids. Because of habitat losses and modifications through agricultural practices, pollinator communities may become more susceptible to some dominant enemies (Klein *et al.* 2006). A well-documented case is the dramatic increase of managed (Downey and Winston 2001) and feral (Kraus and Page 1995) honey bees infested by the *Varroa* mites and the subsequent declines or losses of many colonies. PFv webs analyzed to date, however, exclude predators, parasitoids, and diseases. Higher trophic levels increase the connectedness and nestedness of food webs (Lafferty *et al.* 2006), but food web properties are affected by more than just the species present. Habitat modification through agriculture also affects food web properties. These properties may negatively affect species richness, composition of communities, and the diversity and strength of interactions. Tylianakis *et al.* (2007), for example, used 48 quantitative parasitoid–host (bee and wasp) webs and showed, although overall species richness were not affected by land-use intensity, that web properties, such as connectance, linkage density, compartment diversity, and interaction evenness, were all affected by land-use management. This can be explained by the high vulnerability of the interaction structure to the presence, identity, phenology, physiology, behaviour, and diversity of different species. Hence, parasitoid–host interactions might show changes before species loss becomes apparent (Tylianakis 2008).

14.4.4 Quantitative PFv webs and the management of crop pollination services

In summary, quantitative food web analysis visualizes the structure and links between trophic levels and provides more detailed views of entire communities when assessing management effects on

crop-flower visitor interactions. Nestedness, asymmetry, and interaction strength are PFv characteristics that might indicate stability in crop pollination services, meaning insurance for flower-visiting species losses and effects of added invasive species.

Quantitative analyses can be also used to assess crop pollination services of multi-cropping systems or to evaluate management or restoration plans using flowering strips. Here web analyses give detailed information to help selecting appropriate wild flowering plant species, which do not divert flower-visiting insects from the crop plant and provide additional resources for them. Conversely, quantitative webs can also help to understand whether crop flower resources benefit certain wild flower-visiting insect species and/or their enemies, species of the higher trophic level. In this respect, statistical analyses using replicated networks to show, for example, degrees of specialization and generalization of the enemy species, the flower-visiting species, and plant species and the number of shared species in different management conditions will help to understand management effects on the flower-visiting community and its services for crop and wild plants (Forup *et al.* 2008, Tylianakis *et al.* 2008).

14.5 Consequences of pollinator decline for the global food supply

Both wild and managed pollinators have suffered significant declines in recent years. Managed *Apis mellifera*, the most important global source of crop pollination services, have been diminishing around the globe and particularly in the USA, where colony numbers are now at < 50 per cent of their 1950 levels (NRC 2006). In addition, major and extensive colony losses have occurred over the past several years in North America and Europe, possibly due to diseases and other factors (Cox-Foster *et al.* 2007, Stokstad 2007), causing shortages and rapid increases in the price of pollination services (Sumner and Boriss 2006). These recent trends in honey bee health illustrate the extreme risk of relying on a single bee species to pollinate the 75 per cent of crops that rely to some degree on insect visitation.

At the same time, although records are sorely lacking for most regions, comparisons of recent

with historical records (pre-1980) have indicated significant regional declines in species richness of major pollinator groups and the plants they pollinate (bees and hover flies in Britain, bees alone in the Netherlands) (Beisemeijer *et al.* 2006). Despite the alternative routes in PFv webs when species disappear, a recent meta-analysis on effects of habitat fragmentation on plant reproduction demonstrated that the reproductive success of self-incompatible (i.e. typically pollinator-dependent) but not self-compatible plants is strongly negatively influenced by habitat fragmentation, and that effects on both pollination and reproductive success were strongly correlated (Aguilar *et al.* 2006). These results strongly implicate pollinator loss as a major causative factor for the susceptibility of plant reproduction to one major disturbance, habitat fragmentation.

Large reductions in species richness and individual numbers of bees have also been documented in regions of high agricultural intensity in California's Central Valley (Kremen *et al.* 2002, Klein and Kremen unpublished). Traits associated with bee and hoverfly declines in Europe included floral specialization, slower (univoltine) development, and lower dispersal (non-migratory) species (Beisemeijer *et al.* 2006). In the most well-known taxon, bumble bees in Europe, declining species are long-tongued specialists on Fabaceae, and their increasing rarity may be due to the loss of unimproved grasslands that are rich in their food resources (Goulson *et al.* 2008). Specialization is also indicated as a possible correlate of local extinction in flower-visiting communities studied across a disturbance gradient in Canada. It could be shown that communities in disturbed habitat contained significantly more generalized species than those associated with pristine habitats (Taki and Kevan 2007). Large-bodied bees were more sensitive to increasing agricultural intensification in California's Central Valley, and ominously, bees with the highest per-visit pollination efficiencies were also most likely to go locally extinct with agricultural intensification (Larsen *et al.* 2005).

Thus, in highly intensive farming regions such as California's Central Valley that contribute comparatively large amounts to global food production (e.g. 50 per cent of the world supply of almonds), the supply of wild bee species is lowest in exactly the regions where the demand for pollination services is

highest. Published (Kremen *et al.* 2002) and recent studies (Klein and Kremen, unpublished) clearly show that the services provided by wild bee flower-visiting species are not sufficient to meet the demand for pollinators in these intensive regions. These regions are instead entirely reliant on managed honey bees for pollination services. If trends towards increased agricultural intensification continue elsewhere (e.g. as in Brazil, Morton *et al.* 2006), then pollination services from wild species are highly likely to decline in other regions, based on a recent comprehensive analysis across 16 crops on five continents that showed how wild bee pollinators decline in species richness and individual numbers with distance from natural habitats (Ricketts *et al.* 2008). At the same time, global food production is shifting increasingly towards production of pollinator-dependent foods (Aizen *et al.* 2008a), increasing our need for managed and wild pollinators yet further. Global warming, which could cause mis-matches between flower-visiting species and the plants they feed upon, may exacerbate pollinator decline (Memmott *et al.* 2007). For these reasons, more serious shortages of pollinators in the future may indeed be faced.

A recent global assessment of the economic impact of pollinator loss (e.g. total loss of pollinators worldwide) estimates our vulnerability (loss of economic value) at (153 billion or 10 per cent of the total economic value of annual crop production (Gallai *et al.* 2008), a much larger figure than previous global estimates (e.g. Costanza *et al.* 1997). Although total loss of pollination services is unlikely to occur and to cause widespread famine, they potentially have both economic and human health consequences. For example, some regions of the world produce large proportions of the world's pollinator-dependent crops. Such regions would experience more severe economic consequences from the loss of pollinators, although farmers and industries would undoubtedly quickly respond to these changes in a variety of ways, passing the principle economic burden on to consumers globally (Gallai *et al.* 2008, Southwick and Southwick 2002). Measures of the impacts on consumers (consumer surplus) are of the same order of magnitude ((195–310 billion based on reasonable estimates for price elasticities, Gallai *et al.* 2008) as the impact on total economic value of crop production.

Nutritional consequences may be more fixed and more serious than economic consequences, due to the likely plasticity of responses to economic change. The 75 per cent of crop species that are pollinator-dependent supply not only up to 35 per cent of crop production by weight (Klein *et al.* 2007), but also provide essential vitamins, nutrients, and fibre for a healthy diet (Gallai *et al.* 2008, Kremen *et al.* 2007). The nutritional consequences of total pollinator loss for human health have yet to be quantified. However, food recommendations for minimal daily portions of fruits and vegetables are well known and already often not met in diets of both developed and underdeveloped countries.

14.6 Conclusions and future directions

Pollination is a critical step in the reproduction of many plant species and can significantly reduce primary production in natural communities and crop fruit set and quality in agricultural systems if not provided or provided in adequate supply. Some landscapes promote high flower-visiting species richness and frequency offering adequate crop pollination services because they offer season-around foraging and nesting resources (Kremen *et al.* 2002, Winfree *et al.* 2008). Simple landscapes with low proportion of natural and semi-natural habitats can negatively affect flower-visiting species richness and frequency, which sometimes affect fruit set (Ricketts *et al.* 2008). Consequently, in intensively managed agricultural landscapes where pollinator-dependent crops are grown, farmers are managing bees for pollination services, as for example in alfalfa, almond, watermelon, and sunflower production in California. The effect of isolation from natural habitats on crop pollination in 23 studies is summarized by Ricketts *et al.* (2008), but more studies using fruit set and production data are needed to produce key synthetic results.

Can high numbers of just one species like the honey bee substitute for flower-visiting species richness? Californian's farmers are producing high yields and the honey bee pollination strategy seems to be successful. The examples discussed in this chapter indicate that in some situations managing for one pollinator species will not only result in higher pollination insurance but also result in optimal pollination success. Different mechanisms

lead to these effects, such as niche complementarity for resources, facilitation among species, or sampling to reach highest pollination frequency.

What further research is needed for a holistic understanding of the role of flower-visiting species richness for crop pollination? To predict in which crop-flower-visiting system and under which conditions species or functional group richness can be a limiting factor for pollination services, research in experimental settings to separate for the effects of functional group richness, species richness, and individual numbers *per se* are needed. Flower-visiting community composition needs to be experimentally set up to separate out the effects of aggregate abundance and species richness on pollination services. Such experiments are frequently carried out for plant communities to understand plant productivity. For pollination services, it is important to understand how much a species-rich, but individual-poor flower-visiting community can buffer pollination services loss of an abundant species like the European honey bee.

Mechanisms of species richness–pollination services relationships are complex, particularly when considering whole PFV webs including different

trophic levels. These complex interactions outside the crop-flower visitor network itself have received little attention to date. Quantitative PFV webs can be used to (1) assess crop pollination services of multi-cropping systems or to evaluate crop pollination management or restoration plans using flowering strips, (2) and help to understand whether crop flower resources benefit certain wild flower-visiting insect species or their enemies.

Studies in real systems need to include the complex spatio-temporal multitrophic interactions among pollinating species, their mutualistic partners, and their enemies. Ideally, all production limiting factors and services per crop production system should be studied to calculate the exact value of pollination services to crop production (Bos *et al.* 2007). As many farmers will only adopt restoration activities on their properties when recognizing an economic advantage, opportunity cost for restoration and conservation programs needs to be calculated (Ghazoul 2007). Estimating the costs and benefits of restoring pollinator habitat for increasing wild pollination services are also needed to assess the economic potential for conservation-incentive markets for pollination services.

Box 14.1 Economic value of bees as crop pollinators – the case of alfalfa seed production

Commercial pollination services are mainly provided by managed honey bees through a standing and organized market between beekeepers and farmers. At the global scale, alfalfa seed production depends on the services of managed honey bees (mainly in California) and other managed species like alkali bees and leafcutter bees (mainly in Canada, western USA), and managed bumble bees (in Turkey), but also on diverse wild insect communities, because seed production and quality is extremely low (4 per cent) if pollinators are excluded (Cecen *et al.* 2008).

Alfalfa or Lucerne, *Medicago sativa* L., is the most important forage crop in many parts of the world (FAOStat 2006). Economic markets for pollination services for the Californian alfalfa industry developed between 1949 and 1951 (Sumner and Borris 2006). Commercial pollination for alfalfa started with honey bee pollination experiments in 1947 followed by increased renting of honey bees for alfalfa seed production. At the same time, research to use alkali bees and leafcutter bees for alfalfa seed production was

carried out, as it was noted already in 1940 that a high diversity of insect species are visiting alfalfa flowers. Some solitary bee species were also noted to forage under different environmental conditions (Bohart 1947, Olmstead and Wooten 1987, Mueller 1999). Even for California with the honey bee as the cheapest and most important pollinator, farm advisers recommended a combination of leafcutter bees and honey bees to reach high seed production (Mueller 1999). Experimental testing, however of whether the honey bee alone or a combination with other bee species results in higher seed set or quality is missing.

Although bumble bees and solitary bees access the alfalfa blossoms in a more effective way, resulting in higher per visit seed numbers relative to honey bee visits (Delaplane and Mayer 2000, Cecen *et al.* 2008), honey bees are dominant in alfalfa seed production. In California, farmers usually prefer short-term honey bee colony rental because these portable pollination units are cheap and beekeepers usually take the responsibility to provide strong units during bloom.

Continues

Box 14.1 (*Continued*)

The establishment of solitary bee nests is expensive and farmers need additional training for successful long-term establishment. Losey and Vaughan (2006) estimated the value of wild bees (excluding pollination by managed bees) for alfalfa seed production. They assigned an annual amount of \$5.45 million to wild pollinators. This is 5 per cent of the annual average US gross yield for alfalfa seed production, assuming that 5 per cent of this production is provided by wild bees. This upper-bound value represents the contribution of wild pollinators to gross production. Such a calculation does not consider future adaptive responses by farmers and consumers to pollinator decline (Muth and Thurman 1995). Such responses, like adopting alternative crops or farming techniques that reduce the dependence of farmers on pollinators, will lower the value of pollination services from wild pollinators, as would consideration of net rather than gross revenues (Olschewski *et al.* 2006).

Another approach to assess pollination services by managed bees is to estimate how many bee workers will be needed to fully pollinate a given area of crop production (Robinson *et al.* 1989). Here, such a lower-bound value based on production and cost per area of alfalfa seed production in Montana (USDA-NASS 2008) is calculated for pollination services provided by rented honey bees and by managed leafcutter bees (table below). Mean honey bee colony rental numbers and mean renting cost for the blooming period of alfalfa were used to calculate farmers' costs for renting honey

bees (Sumner and Boriss 2006). The cost to manage leafcutter bees on alfalfa-growing land is available and was calculated for a management period of 15 years (British Columbia Ministry of Agriculture and Food 1998). Management costs of leafcutter bees to pollinate alfalfa are similar to those of honey bee renting during alfalfa bloom. This is only the case when managing leafcutter bees over a longer time period, as the main expenses are covered in the first year of leafcutter bee establishment (bee cocoons, nesting blocks, nesting shelters). In other words, only long-term management of solitary bees is economically reasonable.

The average annual value (gross yield) of the total alfalfa seed production in Montana is \$4,729,400 (USDA-NASS 2008). The state-wide farmer's cost and value for the pollination services of honey bees was calculated to be \$1,220,550 and for leafcutter bees \$1,394,620 (see table below). Thus pollination service values (farmer's cost) represent about 25.8–29 per cent of the value (gross yield) of this crop.

Relying on a single pollinator species is a risky strategy and this chapter highlights that in at least some cases different species can complement each other to achieve the best pollination results. An equivalent economic evaluation approach to estimate the pollination services provided by wild flower-visiting communities is to calculate replacement costs for honey bees by wild insects (Kremen *et al.* 2007). For this approach a calculation of the costs to restore agricultural landscapes for crops to get full pollination services by wild insects is needed, but to date not available.

Annual value of bee pollination of alfalfa seed production in Montana, based (a) on farmer's mean annual cost of renting honey bees; or (b) managing leafcutter bees, to fully pollinate alfalfa for seed production based on 1997–2007 production and yield data.

| | Area in production (ha) | Stocking rate (hives/ha or bee cells/ha) ¹ | Rental, management cost (\$/hive, \$/10,000 cells) ² | Cost/ha | State-wide cost (\$) |
|-----------------|-------------------------|---|---|---------|----------------------|
| Honey bees | 5150 | 7.9 | 30 | 237 | 1,220,550 |
| Leafcutter bees | 5150 | 74,100 | 36.6 | 270.8 | 1,394,620 |

¹ average number calculated by Delaplane and Mayer (2000)

² HB= average annual value considering the years of 1996–2005 (Sumner and Boriss 2006); LCB = average annual value for bee management of 15 years (British Columbia Ministry of Agriculture and Food 1998).