5

Services from Plant–Pollinator Interactions in the Neotropics

Lucas Alejandro Garibaldi, Nathan Muchhala, Iris Motzke, Liliana Bravo-Monroy, Roland Olschewski and Alexandra-Maria Klein

Introduction

The Neotropics, with its large expanses of rainforests, forests and woodland savannas, includes some of the most diverse places on Earth (Kricher, 1999; Myers et al, 2000). A large proportion of plant and animal species in Neotropical communities are unique, including several pollinator species, which provide essential services to human welfare. In general, pollinators are known to enhance the sexual reproduction of the majority of angiosperms (Kearns et al, 1998) and can be important for the production of many crop species (McGregor, 1976; Klein et al, 2007; Aizen et al, 2009a). There is a wide array of arthropod and vertebrate pollinator species in the Neotropics, although we know little about their natural history and contribution to pollination (Kevan and Imperatriz-Fonseca, 2002; Freitas et al, 2009).

This chapter reviews studies on pollination services in the Neotropics, with an emphasis on crop pollination. We briefly describe the main taxa involved in pollination, followed by a list of the main crops grown in the Neotropics and a description of how many they rely on biotic pollination. Because methods vary across studies, key methodologies to determine pollination services are summarized. Finally, we discuss management options to improve pollination services at the farm and landscape scale, and socio-economic drivers affecting pollination.

Major Pollinator Taxa

Pollination by animals plays a vital role for plant reproduction in the tropics, where it is estimated that more than 98 per cent of plants are animal pollinated (Bawa, 1990). However, in general, information on pollinator communities and the diversity of taxonomic guilds in the Neotropics is incomplete (Freitas et al, 2009). In this section we give examples of the major pollinator taxa in comparison to other regions.

Similar to the Old World, bees play a major role in pollination of Neotropical plants (Roubik, 1995). Around 5000 bee species are thought to occur in the Neotropics, including 391 eusocial stingless bee species (Meliponini), an important pollinating bee taxa (Slaa et al, 2006). The invasive Africanized honey bee, *Apis mellifera scutellata* Lepeletier, is widespread throughout the Neotropics. Although presumed to compete with native bees, evidence is still controversial (Roubik, 2009). Other important invertebrate pollinators are wasps (Hymenoptera), beetles (Coleoptera), moths and butterflies (Lepidoptera) and flies (Diptera).

Pollinators in the Neotropics seem to be as diverse as in other tropical areas (Roubik, 1995); but species composition and identity are highly distinct. For example, in South America, coffee (*Coffea arabica* L.) is predominately visited by the non-native Africanized honey bee, but also by a high diversity of stingless bees (Klein et al, 2008a). In contrast, coffee-visiting bee species in Southeast Asia include the native eastern honey bee (*Apis cerana* Fabricius), the giant honey bee (*A. dorsata* Fabricius), the honey bee (*A. nigrocincta* Smith), a close relative of the eastern honey bee, few stingless bee species, and a high diversity of solitary species (Klein et al, 2008a; Klein, 2009).

Among vertebrate pollinators, birds, especially hummingbirds, followed by bats play the most important role for many wild flowers in the Neotropics. There are more than 300 hummingbird species confined to the Neotropics (Bawa, 1990). In agricultural systems, hummingbirds visit papaya (*Carica papaya* L.) and banana (*Musa* sp.) flowers (Free, 1993); but their role in crop pollination is not well documented. In other areas of the world, sunbirds (Palaeotropical and Pacific), sugarbirds (South Africa) and honeyeaters (Australasia) fill the ecological niche of hummingbirds in the Neotropics (Roubik, 1995; Ortega-Olivencia et al, 2005). Nectar-feeding bats are the second most widespread vertebrate pollinators in Neotropical rainforests, especially for many wild trees and epiphytes, but also for locally important crops (see Box 5.1).

Biotic Pollination and Crop Production

Biotic pollination is important for many crop species in the Neotropics. Altogether 44 crops and 4 commodities (method as in Klein et al, 2007) represent 99 per cent (98 and 1 per cent, respectively) of the total crop production in the Neotropics in 2007 (FAOSTAT, 2009). Of these, 29 (70 per cent) crops

Box 5.1 Bat pollination in the Neotropics

Bat pollination is restricted to the tropics and subtropics; plant-visiting bat species do not occur in temperate regions (Koopman, 1981; Fleming and Muchhala, 2008). Bats adapted to a nectarivorous diet occur in two distantly related families: the Phyllostomidae in the Neotropics and Pteropodidae in the Palaeotropics. Of these, bat species of the sub-family Glossophaginae are the most morphologically and ecologically specialized; they possess elongated snouts, highly extensible tongues and the ability to hover in front of flowers like hummingbirds (Helversen, 1993; Winter and Helversen, 2003).

In the Neotropics, nectar bats are known to pollinate flowers from 360 species of plants in 159 genera from 44 families (Geiselman et al, 2002; Fleming et al, 2009). The majority of these are trees and epiphytes, including many conspicuous members of local ecosystems, such as canopy-emergent Bombacaeae trees in rainforests and large columnar cacti (e.g. saguaro, organ pipe cacti) in arid regions. Although numerically a relatively small proportion of total angiosperm diversity, bat-pollinated plant species cannot be serviced as effectively by other pollinator taxa because specialized floral adaptations are required to attract, fit and reward bats: chiropterophilous flowers typically are physically robust and well exposed beyond the foliage, have wide bell-shaped flowers or a 'brush' morphology, open nocturnally, and produce a strong odour and copious nectar (Helversen, 1993; Muchhala, 2007; Fleming et al, 2009). Although such adaptations require large investments in floral structures compared to other pollination systems, bats provide two important advantages as pollinators. First, they can carry large amounts of pollen in their hairs (Law and Lean, 1999; Muchhala and Thomson, 2010). Second, they can disperse this pollen over extremely long distances. For instance, paternity analyses reveal that pollen was transferred up to 18km between individuals of the bat-pollinated kapok tree (*Ceiba pentandra*) (Dick et al, 2008). Such long-distance pollen dispersal improves gene flow, as evidenced in low genetic subdivision for bat-pollinated plant species (Roesel et al, 1996; Hamrick et al, 2002).

A number of bat-pollinated plants in the Neotropics provide economically important products. The kapok tree, which is pantropical and bat pollinated throughout its range (Elmqvist et al, 1992; Gribel et al, 1999; Nathan et al, 2005), produces silky fibres which are used in bedding and cushion materials. Many bat-pollinated cacti throughout the Americas produce edible fruits that are sold in local and international markets, often as jellies or jams (Anderson, 2001). Bat-pollinated dragon-fruit and other fruits of the cactus genus *Hylocereus* are now cultivated worldwide, both as food and as ornamental plants (Valiente-Banuet et al, 2007). Fruits of *Stenocereus griseus* (Haw.) Buxb. are harvested by indigenous communities, which also use the cacti for construction materials and as living fences (Nassar et al, 1997; Villalobos et al, 2007). The seed set of agaves, from which the well-known liquor tequila is derived, drops to less than 5 per cent in the absence of bat pollinators (Howell and Roth, 1981; Molina-Freaner and Eguiarte, 2003). Finally, many ornamental plants rely on bat pollination, such as *Cobaea scandens* Cav. and *C. trianae* Hemsl. (Polemoniaceae) (Vogel, 1969).

Figure 5.1 Anoura geoffroyi *Gray, 1838 pollinating* Cleome anamola *Kunth* (left) *and the ornamental* Cobaea trianae *Hemsl.* (right)

Source: N. Muchhala

increase their seed or fruit production in the presence of animal pollination. In the following discussion we highlight the leading animal-pollinated crops in terms of cultivation area, and give further examples of highly pollinator-dependent crops.

The most important pollinator-dependent crops exotic to the Neotropics are coffee, coconut, citrus, mango, and soybean (Table 5.1; see Box 5.2 for details on coffee pollination; FAOSTAT, 2009). For example, soybean is the second most cultivated crop in the Neotropics. Primarily self-compatible, flower-visiting insects, such as honey bees, have been shown to increase soybean production, measured in kilograms per hectare (kg ha^{-1}), between 38 and 58 per cent for some varieties in Brazil (Chiari et al, 2005, 2008). Given the importance of this crop, more research on its pollination system across countries and varieties is urgently needed.

The most important native Neotropical crops dependent totally or to certain degrees on insect pollination are cocoa, common bean, guava and cashew (see Table 5.1). Cocoa, for example, is generally highly self-incompatible and depends heavily on insect pollination, although a few self-compatible varieties exist (Falque et al, 1996). Tiny midges of the Ceratopogonidae and Cecidomyiidae families are predominantly responsible for pollination of the cocoa varieties that depend on insect pollination (Entwistle, 1972; Young, 1994). The cashew nut, native to Brazil, has both bisexual and male flowers on the same plant. This crop is frequently cultivated in the Neotropics (Roubik, 1995; Kevan and Imperatriz-Fonseca, 2002) and has two main pollinating species: the honey bee (*Apis mellifera* L.) and the native oil bee (*Centris tarsata* Smith) (Freitas and Paxton, 1998).

Many crops that depend on animal pollination are of high economic importance at a more local, country- or state-wide scale. For some of these crops, such as Brazil nut, melon, passion fruit, pumpkin, squash, vanilla and watermelon, animal pollination was found to be essential (Klein et al, 2007). Furthermore, a high number of crops depend partly (to certain degrees or under certain conditions) on animal pollination, such as agaves, annatto (or achiote), avocado, chayote, chilli pepper, common bean, dragon fruit, eggplant, guayule, jojoba, mesquite, papaya, peanut, pepper, pimento, rubber, quinine, sisal, soursop (or *guanábana*), star apple (or *caimito*), sunflower, tobacco and tomato (Roubik, 1995). Here we highlight two locally important native crops: passion fruit and avocado. Passion fruit (*Passiflora edulis* Sims) is cultivated throughout the Neotropics and has self-incompatible, large hermaphroditic flowers. It is mainly pollinated by large carpenter bees of the genus *Xylocopa*, as other frequent flower-visiting species are too small to touch the stigma during nectar and pollen collection (e.g. Benevides et al, 2009). Wind pollination is ineffective because pollen is heavy and sticky. Another important native crop is avocado (*Persea americana* Mill.), a variable and poorly understood species with respect to its pollination system. Avocado varieties vary between self-compatible to self-incompatible; but cross-pollination through bees, bats, flies and wasps improves fruit production

Table 5.1 *Pollinator dependence of the most cultivated crops in the Neotropics*

Species	*Crop*	*Pollinator dependence*	*Cultivated area (ha)*	*(%)*
Zea mays	Maize	None	26,314,959	24.6
Glycine max, *G. soja*	Soybean	Modest	24,124,332	22.6
Saccharum officinarum	Sugar cane	None	9,825,691	9.2
Phaseolus sp., *P. vulgaris*, *P. lunatus*, *P. angularis*, *P. aureus*, *P. mungo*, *P. coccineus*, *P. calcaratus*, *P. aconitifolius*, *P. acutifolius*	Bean dry like kidney bean, haricot bean, lima bean, azuki bean, mungo bean, string bean	Little	6,457,637	6.0
Coffea arabica, *C. canephora* (syn. *Coffea robusta*), *C. liberica*	Coffee	Modest	5,667,250	5.3
Oryza sp. (mainly *O. sativa*)	Rice, paddy	None	5,262,464	4.9
Triticum sp. (mainly *T. aestivum*, *T. durum*, *T. spelta*)	Wheat	None	3,236,071	3.0
Sorghum guineense, *S. vulgare*, *S. dura*	Sorghum	None	3,155,116	3.0
Manihot esculenta (syn. *M. utilissima*, *M. palmata*)	Cassava	Only breeding	2,791,040	2.6
Musa sapientum, *M. cavendishii*, *M. nana*, *M. paradisiaca*	Banana, plantain	Only breeding	2,128,586	2.0
Gossypium hirsutum, *G. barbadense*, *G. arboreum*, *G. herbaceum*	Cotton	Modest	1,735,189	1.6
Theobroma cacao	Cocoa	Essential	1,490,461	1.4
Citrus trifoliata	Orange	Little	1,442,261	1.4
Anacardium occidentale	Cashew nut, cashew-apple	High	1,354,993	1.3
Cocos nucifera	Coconut	Modest	672,713	0.6
Hordeum disticum, *H. hexasticum*, *H. vulgare*	Barley	None	667,234	0.6
Elaeis guineensis	Oil palm	Little	611,211	0.6
Nicotiana tabacum	Tobacco	Only sowing	545,856	0.5
Mangifera indica, *Garcinia mangostana*, *Psidium* spp.	Mango, mangostan, guava	High	458,435	0.4

Notes: Harvested area data given for each crop are extracted from the FAO dataset for the year 2007 (FAOSTAT, 2009). Argentina, Chile and Uruguay were excluded; but examples from these countries are discussed in the chapter when appropriate (e.g. Chacoff and Aizen, 2006). Listed crops accounted for 93 per cent of the total cultivated land in the Neotropics in 2007. Pollinator dependence data obtained from Klein et al (2007). Pollinator dependence: *none* = yield not dependent on animal pollination; *little* = yield reduction > 0 but < 10 per cent without pollinators; modest = 10–40 per cent reduction; *high* = 40–90 per cent reduction; *essential* = reduction >90 per cent; *only breeding* = pollinators increase seed production for breeding (in commercial farming, the plants are propagated from vegetative organs and the vegetative parts are harvested); *only sowing* = pollinators increase seed production to produce the vegetative parts that are harvested.

(Roubik, 1995). The flower is bisexual and opens twice; it functions as a female during the first opening, and functions usually as a male and releases pollen on the following day upon the second opening. Commercially grown avocado plantations are therefore planted with two complementary flowering groups to ensure the spatio-temporal availability of female and male openings for adequate pollination (Delaplane and Mayer, 2000).

In summary, 70 per cent of the leading crops in the Neotropics depend to some degree on animal pollination. This number is similar to that estimated for the global scale (74 per cent) (Klein et al, 2007), and also similar to tropical regions, in general (70 per cent: Roubik, 1995), to Argentina (74 per cent: Chacoff et al, 2010), Mexico (85 per cent: Ashworth et al, 2009) and the European Union (84 per cent: Williams, 1994). The latter two studies include many crops of minor importance in terms of production and total cultivated area, whereas the other calculations include major crops only. In general, however, few studies have evaluated pollination services in the Neotropics (Freitas et al, 2009); consequently, we know little about the pollinator relevance for many widely cultivated crops or about the variability of pollinator requirements among varieties.

Determination of Crop Pollination Services

Pollination can be important for agricultural and non-domesticated plants; however, the actual impact of these services is difficult to estimate. To better understand pollination services, it is important not only to measure the interaction between a pollinator and a certain crop or plant species, but to identify biophysical and socio-economic drivers in an interdisciplinary approach (see Figure 5.3; Bayon and Jenkins, 2010).

Pollinators can provide direct benefits by increasing the amount and inter-annual stability of crop yield quantity (kg of product ha^{-1}) and quality (e.g. fruit size, shape, weight), and indirect effects such as maintaining plant and animal biodiversity and their associated benefits for human welfare. These services can be promoted by either pollinator abundance or diversity (Hoehn et al, 2008; Klein, 2009; Klein et al, 2009; Vergara and Badano, 2009). We would like to note that some flower visitations may be a disservice to crops, as has been demonstrated for flowers in the wild. This can occur in the form of nectar or pollen robbery where a 'pollinator species' takes nectar or pollen without pollinating the plant (Irwin et al, 2001; Thomson, 2003; Hargreaves et al, 2009). However, we have found no studies showing that the exclusion of flower visitors has positive effects on crop pollination. The exclusion of wild visitors commonly reduces or does not significantly affect pollination services (Klein et al, 2007).

Many studies have measured pollinator abundance, pollinator richness/diversity, flower visitation rates, pollen deposition, pollen tube growth, and/or seed/fruit set (Klein et al, 2007). Fewer studies, however, have determined direct production variables (e.g. yield quality or quantity) at a farm (plot) scale. These calculations are also relevant at the socio-economic scale where decisions on land use are made (see the section on 'Socio-economic drivers affecting pollination services') (Ghazoul, 2007; Klein et al, 2008b; Veddeler et al, 2008). When estimating pollination services, the following processes and methods should be considered:

- *Biotic pollination* can be evaluated by comparing crop yield of pollinator exclusion (only self + abiotic pollination) and free pollination (self + abiotic + biotic pollination) treatments (e.g. Klein, 2009; Vergara and Badano, 2009).
- *Abiotic pollination* can be estimated by comparing an abiotic plus biotic pollination exclosure treatment with a pollinator exclosure treatment.
- *Self-pollination:* by preventing any outcross pollen from reaching the flower (abiotic plus biotic pollination exclosure), the degree of self-pollination can be evaluated.
- *Pollen limitation:* pollen addition (hand pollination) and control treatments are useful to understand the degree of pollen limitation (see review by Wesselingh, 2007).
- *Self-incompatibility:* the addition of pollen from the same individual versus addition from other individuals (out-crossing) can be used to quantify the degree of self-incompatibility.

Other considerations when studying the above processes are:

- *Natural history and field censuses:* knowledge on pollinators' natural history and censuses of flower visitation helps to understand plant–pollinator interactions and to identify key pollinator species and their requirements (e.g. for habitat) (Kevan and Imperatriz-Fonseca, 2002).
- *Number of replicates:* the estimation of the number of (independent) replicates needed given an expected variability and a required precision is critical for obtaining useful information from experiments.
- *Relevant production variables:* from an applied perspective, it is important to measure the quantity and quality of yield, and the spatial and temporal stability in both variables (Ghazoul, 2007; Klein et al, 2008b).
- *Spatial and temporal scale:* when possible, treatments should be applied to plots, which are usually the scale of interest when measuring pollination services (or sometimes entire plants). Special attention should be given to perennial plants, in which plant resource allocation strategies can involve years (e.g. high allocation to vegetative growth during one year, but higher allocation for reproduction in the following year). Therefore, experiments should ideally be followed during the whole plant productive cycle and over consecutive years.
- *Variability in pollen and pollinator limitation:* the impact of pollen limitation on crop production may vary greatly depending on other environmental factors such as resource availability (water, nutrients and radiation), abiotic conditions (e.g. frosts) and pests (Bos et al, 2007; Ghazoul, 2007; Klein et al, 2008b). Pollen limitation may also vary with crop variety, and the magnitude of pollinators' exclusion effects may greatly depend on the resident pollinator community. Studies over multiple seasons and years are useful to account for periodic weather perturbations and temporal variation in pollinator communities (Klein, 2009).

Box 5.2 Pollinators and coffee production in the Neotropics

Coffee is one of the most important cash crops in the Neotropics. It is traded at the global market and accounts for nearly 5.7 million hectares of land in 2007 (see Table 5.1). For many years, coffee has been the second leading export product of developing countries (ICO, 2009), providing income and employment for millions of people.

Since the 1950s, many studies have shown that pollinators promote coffee yield (production per plant or hectare) by increasing fruit set and/or berry weight (see reviews by Free, 1993; Klein et al, 2007). Pollinators have also been shown to reduce the frequency of 'peaberries' – that is, small misshapen seeds (Free, 1993; Ricketts et al, 2004). The magnitude of the positive effects on yield can vary greatly, between 10 and 40 per cent among studies using different methodologies and environmental conditions (see Table 5.1) (Klein et al, 2007). Studies finding positive effects on coffee yield include those performed at the plant scale (therefore not biased by resource allocation patterns within the plant) (Free, 1993) and those performed for more than one year (Ricketts et al, 2004). Positive effects of pollinators on both seed number and weight have also been found simultaneously, without the confounding effects of seed number versus size compensation (Ricketts et al, 2004). In most studies, the honey bee was found to be the most frequent visitor to coffee flowers, followed by stingless bees, and some semi-social and solitary bee species (see the previous section on 'Major pollinator taxa').

Research addressing the effects of habitat and landscape scale on coffee pollination began only during the last decade. They include studies in Panama (Roubik, 2002a), Venezuela (Manrique and Thimann, 2002), Costa Rica (Ricketts, 2004), Brazil (De Marco and Coelho, 2004), Ecuador (Veddeler et al, 2006) and Mexico (Vergara and Badano, 2009). These studies considered variables such as distance between coffee plants and adjacent forests or cultivation variables such as shade versus sun coffee. All studies found more bee species, higher visitation frequency, higher fruit set and/or higher berry weight on coffee plants bordering forests.

Other studies highlighted the monetary value of coffee pollination services, such as Roubik (2002b) in Panama; Ricketts et al (2004) in Costa Rica, and Benitez et al (2006), Olschewski et al (2006) and Veddeler et al (2008) in Ecuador. For example, the extrapolation of data gained from pollination experiments in Costa Rica estimated that the value of pollination services for two forest fragments (46ha and 111ha) in a single farm (480ha) was US$60,000 annually (Ricketts et al, 2004). Veddeler et al (2008) calculated that a fourfold increase in bee density would translate to an 800 per cent increase in net revenues for coffee farms in Ecuador. Certainly, wild habitats are providing important pollination services for this crop.

Figure 5.2 *Coffee production in Manabi, coastal Ecuador: From left to right are the Africanized honey bee,* Apis mellifera scutellata *(Lepeletier), foraging on coffee flowers; ripe coffee berries at harvest; traditional harvest with mules*

Source: D. Veddeler (bee and berries); A. M. Klein (traditional harvest)

- *Socio-economic assessments:* it is important to understand the value of pollination services for different aspects of a society (e.g. cultural and economic; see the section on 'Socio-economic drivers affecting pollination services').

Depending on the focus, other measurements and treatments can be included. Examples are the exclusion of vertebrate but not invertebrate pollinators to understand their interactions and relative contribution to pollination, or the study of niche complementarity among invertebrate pollinator species (Hoehn et al, 2008). Here, we emphasize methods to quantify the degree of overall pollination and pollinator limitation on crop production at a farm (plot) scale.

Management to Improve Pollination Services at the Landscape and Farm Scale

In the previous sections we described how lack of animal pollination can limit the yield of certain crops. There is also evidence that wild pollinator species are decreasing locally (Ricketts et al, 2008) and regionally (Biesmeijer et al, 2006; Brown and Paxton, 2009; Freitas et al, 2009) due to land-use changes and the application of agrochemicals, among other factors. A recent review suggested that the effects of habitat loss on flower visitation rates should be higher in the tropics compared to temperate zones (Ricketts et al, 2008). Therefore, it is increasingly important to understand the drivers affecting pollinator abundance and diversity for adequate pollinator management and conservation. Management for wild pollinators usually implies decisions at the landscape and farm level to provide floral resources, breeding areas and nesting habitats within the flying range of pollinators (Kevan and Imperatriz-Fonseca, 2002; Kremen, 2008).

Landscape and habitat management

Pollination services can vary widely depending on the quantity, quality and spatial arrangements of habitat types in the landscape. Because flying has energy costs and many pollinators have fixed nest sites, pollinators prefer flower visits close to their habitat. Recently, Ricketts et al (2008) reviewed 23 studies representing 16 crops on 5 continents to evaluate the effects of distance from natural or semi-natural habitats on pollination services. They found that visitation rates by wild pollinators and pollinator richness decreased exponentially with distance from natural habitat, reaching half of its maximum at 0.6km and 1.5km, respectively. However, they found no evidence of effects on fruit and seed set, although such effects were only measured by half of the studies and most of them did not measure the size, quality or stability of yield (see the previous section on 'Determination of crop pollination services'). Among the reviewed studies, only four were performed in the Neotropics. Decreases in native visitation rates with distance from natural habitat was observed for highland coffee in Costa Rica (Ricketts, 2004; Ricketts et al, 2004) and grapefruit in northwestern Argentina (Chacoff and Aizen, 2006); but no effect was found for passion fruit in eastern Brazil (Ricketts et al, 2008) or for oil palm in southern Costa Rica (Mayfield, 2005; Ricketts et al, 2008). Overall, these studies suggest that the conservation of natural habitats close to agriculture can be important to enhance wild pollinator diversity and flower-visiting frequency, although the effects of habitat conservation on pollination services needs to be further evaluated. Moreover, most of these studies use either distance or proportional area of natural habitat as the landscape variable; future studies should also consider the effects of the spatial arrangement of habitat patches in terms of distance, number, size and quality (Olschewski et al, 2010).

The magnitude of positive effects from natural habitat proximity can vary greatly among pollinator species. It is proposed that species with high dispersal abilities will be less affected by habitat degradation at relatively short distances. For example, a review concerning tropical crops found that small cavity-nesting bees and generalist beetles required natural forest near their foraging areas, whereas insects with large body sizes explored larger areas and were therefore less sensitive to isolation from forest (Klein et al, 2008a). Overall, taking into account the biology of species and considering different spatial scales will improve our understanding of the effects that land-use change has on habitat quality for pollinator species (Steffan-Dewenter et al, 2002; Tscharntke et al, 2005).

Habitat quality involves the abundance of appropriate floral resources, nesting places and the possibility to escape from natural enemies and diseases. Managing habitat quality requires detailed knowledge of the species' natural history. When the habitat is highly degraded, active management may be required (e.g. sowing or transplanting native species as well as constructing suitable habitat).

A matrix of agricultural and natural patches can be beneficial to pollinators because of a higher diversity of resources (Tscharntke et al, 2005; Winfree et al, 2007, 2008). Enhanced diversity and abundance of pollinators in these complex landscapes may also provide services to a wider spectrum of crops (Kremen, 2008). Pollination services should be greater when agricultural field sizes are smaller because of greater habitat complexity within the flying range of pollinators. Unfortunately, there is a trend towards increasing field size and homogenization of agricultural landscapes in the Neotropics and many other regions (Tscharntke et al, 2005; Aizen et al, 2009b). These landscape variables also interact with decisions at the farm scale because crop management influences the quality of habitat for wild pollinators.

Farm and pollination management

There are several agricultural practices that can improve the visitation of wild pollinators to flowers, such as small-scale farming, polycultures, sowing of diverse flower resources in edge habitats (e.g. field boundaries) and reduced use of agrochemicals (Tscharntke et al, 2005, Brosi et al, 2008). In general, farming practices that increase habitat diversity (and, thus, pollinator diversity) should promote pollination services because of:

- species complementarity, when species use different resource parts or promote positive intra-guild interactions;
- sampling effects, when higher biodiversity increases the probability of including species that provide important services; and
- redundancy, when different species provide a similar pollination service in highly diverse habitats, which is important for reorganization after disturbance (insurance hypothesis) (see reviews by Tscharntke et al, 2005; Klein et al, 2009).

For example, rustic shade coffee managed under native forest in Veracruz (Mexico) showed higher pollinator diversity and fruit production than less diverse sun coffee systems where native forest was removed (Vergara and Badano, 2009).

Although several thousand species contribute to pollination, only a few are managed. Examples include stingless bees as pollinators for tomatoes in Mexico (Cauich et al, 2004) and Brazil (Del Sarto et al, 2005) greenhouse production, and also for other crops such as cucumber and sweet pepper in the Neotropics (see reviews by Cortopassi-Laurino et al, 2006; Slaa et al, 2006). However, most managed pollinators are honey bees (Kevan and Imperatriz-Fonseca, 2002). This reliance on a single pollinator species seriously threatens the stability of pollination services. Indeed, higher incidence of pests and diseases in the US decreased the number of managed honey bee colonies during the past years, and raised several problems for the pollination of important crops such as almond in California (Oldroyd, 2007). In the Neotropics, for example, there has been an increase in the reproductive ability of the mite *Varroa destructor* Anderson & Truemann in the widely spread Africanized honey bee in southern Brazil (Carneiro et al, 2007). Furthermore, *Apis mellifera* L. is not the most efficient pollinator species for many crops (Freitas and Paxton, 1998; Greenleaf and Kremen, 2006). The temporal and spatial stability, as well as the rate of pollination services, can be improved by pollinator diversity (Greenleaf and Kremen, 2006; Klein, 2009; Klein et al, 2009).

Hand pollination is a difficult and laborious task that is currently performed only in expensive crops under intensive farming. This is the case for vanilla (*Vanilla planifolia* L.), an orchid native to Mexico and a highly pollinator-dependent crop species (Davis, 1983; Klein et al, 2007). In general, species with large flowers are easier to hand pollinate than species with small flowers. However, pollinators provide not only quantity of pollen, but also pollen quality (e.g. cross-pollination) and special techniques of pollen transfer (e.g. vibration). Performing such tasks by hand at the proper production scale is both challenging and expensive.

For many pollinator-dependent crops, there are some varieties that are non-dependent so that farmers have the choice to choose varieties that do not need pollinators. However, despite genetic engineering and crop breeding advances, many of the most important crop species depend on pollinating animals (see Table 5.1) (Klein et al, 2007).

Socio-Economic Drivers Affecting Pollination Services

Land-use decisions affecting pollination services are made at the household or farm scale in response to several environmental and socio-economic variables (see Figure 5.3) (Lambin et al, 2001). Crop production often depends on environmental drivers such as resource availability (e.g. water and radiation), abiotic conditions (e.g. temperature), incidence of pests and weeds, and pollination services (see Figure 5.3). Several socio-economic drivers interact with environmental variables to affect land-use decisions, such as markets, demog-

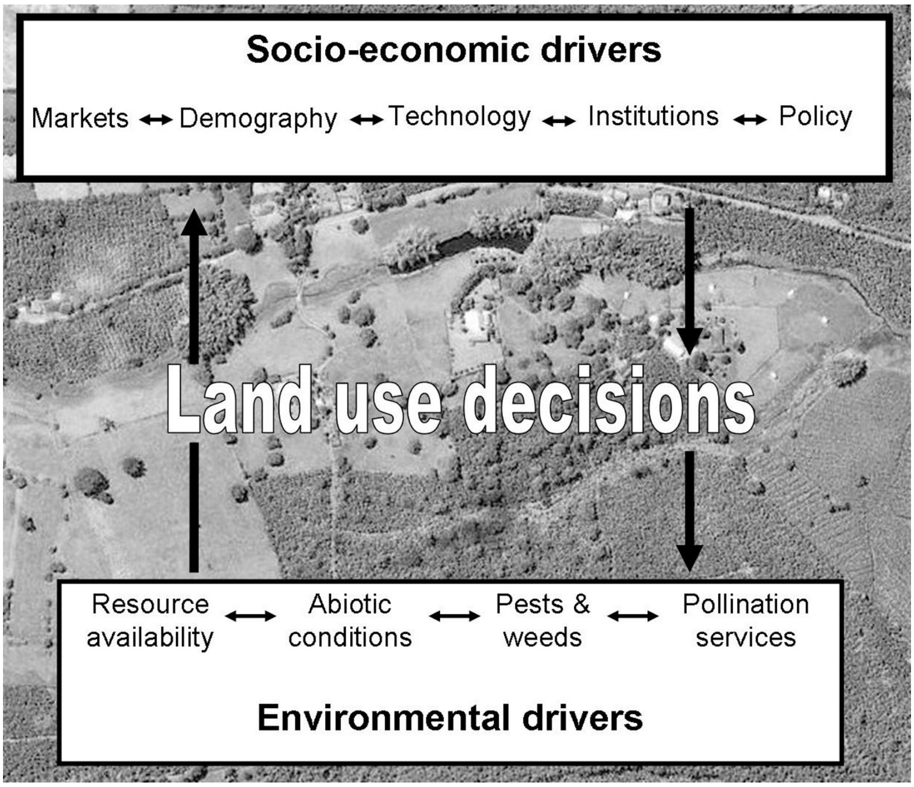

Figure 5.3 *Socio-economic and environmental drivers of land-use decisions and crop productivity*

Note: See explanations in the chapter.
Source: chapter authors

raphy, technology, institutional settings and public policy. This section briefly describes the socio-economic drivers of farmers' decision-making that influence the landscape and habitat management of pollination services (see previous section).

Relevant socio-economic drivers of land-use decisions are established markets, and the participation in trade. Besides income generation, participating in trade might have further advantages, such as access to credit, information, technology and urban centres. However, the importance of markets for small-scale producers depends on the type of land use considered, such as production of food (subsistence) versus cash crops (Cronon, 1985; Burgi and Turner, 2002; Black et al, 2003; Guhl, 2008). Supply and demand determine the market price and, thus, the profitability of crop species. The structure and functioning of markets allows us to understand how small-scale agricultural systems are connected to trade and market relationships. In general, pollinator-dependent crops achieve higher market prices (Gallai et al, 2009), thereby generating incentives to increase their production. However, a lack of pollinators might hinder the producers from doing so, and might force them to switch to less attractive non-pollination dependent crops.

Small-scale farmers' land-use decisions are often based on a comparison of net revenues. They depend on the product price, the quantity of the harvest and on the production costs. A case study in coastal Ecuador included these factors and assessed the impact of forest areas providing bee habitats and thereby enhancing pollination services for adjacent coffee production. It was shown that the impact on net revenues was significantly positive (Olschewski et al, 2006). However, alternative crops such as maize were more attractive from an economic point of view in that landowners had a strong incentive to convert forests into cropland. As a consequence, payments for single ecosystem services such as pollination are hardly sufficient to preserve bee habitats. Payment schemes should comprise further forest ecosystem services (e.g. carbon sequestration, soil and water conservation) in order to be effective.

Demography and other social criteria, such as gender, age and education, are common elements that influence land-use strategies (Mazvimavi and Twomlow, 2009). Institutional aspects such as landownership and tenure rights might be another powerful determinant (Wunder, 2000; Burgi and Turner, 2002; Black et al, 2003) – for example, owners are supposed to make different production decisions than tenants. Furthermore, it is important to consider underlying cultural beliefs and social perceptions of different land-use types (Nyerges and Green, 2000). Taking these into account might help to explain why families in the Neotropics often maintain small-scale farming despite modest income-generating opportunities.

Further important drivers of land-use change are agricultural knowledge and available technology (Angelsen and Kaimowitz, 1999; Burgi and Turner, 2002; Anastasopoulou et al, 2009). Among others, the inclusion of machinery may promote the cultivation of larger and more homogeneous fields. Additionally, the development of new crop varieties may affect pollination requirements and pollination service rewards. Little knowledge or experience on cultivation practices for a particular crop may also induce farmers to avoid the cultivation of that specific crop. Finally, public policies are crucial because they can establish incentives and recommendations regarding the adoption of specific land-use systems through their influence on several other drivers mentioned above (Burgi and Turner, 2002; Di Falco and Perrings, 2006; Anastasopoulou et al, 2009).

The variety of socio-economic drivers and their interactions show that simple explanations hardly provide adequate understanding of land-use change (Lambin et al, 2001). Various human and environmental conditions lead to specific land-use decisions, and policy recommendations aiming at habitat or landscape conservation should take these interactions into account.

Conclusions

We have shown that pollination services by wild pollinators are important for crop production in the Neotropics. However, our knowledge of the services that pollinators provide in terms of the amount, quality and stability of crop production is still deficient. It is also critical to understand how multiple socio-economic drivers influence the selection of particular management systems and, thus, the environmental services delivered. Land-use decisions based on short-term revenue calculations can lead to unsustainable results. Despite the high potential of social benefits, sometimes the net revenues obtained from pollination services through the preservation of a natural habitat are lower than other uses of that land, such as deforestation and crop cultivation. Future evaluations should also consider ecosystem services other than pollination and their interactions to reliably estimate the ecological and social benefits of conserving natural habitats. It is important to determine the value (monetary and non-monetary) of these services in order to raise awareness of ecosystem services when making decisions on particular land-use systems, and to support the design of appropriate conservation policies that benefit farmers and their environment.

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