Chapter 8
Indicators of Pollinator Decline and Pollen Limitation

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Abstract  Pollination is a crucial process for maintaining plant reproduction, and is responsible to the yield of about two third of the world’s crops. In recent years, there are growing concerns over pollinator declines and global pollination crisis. A decrease in pollinator populations also affects plants’ reproductive success, and alters the composition of wild plant communities. The main drivers for pollination decline are agriculture intensification and the subsequent fragmentation and loss of habitats, as well as introduction of non-native species and indirect effects of global climate change. Specialist pollinators and self-incompatible plants are seemingly in higher vulnerability. Our current knowledge of environmental effects on pollination processes is limited by the relatively little knowledge of the ecological requirements of pollinators and plants, and by the shortage of studies on the response of populations and communities to changes in land use. In this chapter we provide indices for estimating pollinator decline in both local and landscape scale, and discuss the relative efficiency of taxonomic and environmental indicators and indicators for estimating pollination services. We propose that future research should include developing and testing cost-effectiveness of indicators for patterns of pollinators’ diversity and of indicators for pollination services. These indicators should be tested in various ecological and spatial scales.

Keywords  Biodiversity decline • Ecological services • Ecosystem function • Plant-pollinator interactions • Pollen limitation • Taxonomic index

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8.1 Introduction

8.1.1 What Is Pollination?

Pollination is the transfer of pollen grains to the stigma of a flower. Pollen grains are the male germ line cells of the plant, and once they arrive at the stigma, they imbibe water and germinate, producing a pollen-tube that penetrates the stigma surface, growing through the style to the ovary (Proctor et al. 1996). There, the gamete (haploid nucleus) unites with the female gamete in the ovule and this fertilized ovule creates the zygote. The zygote develops into an embryo, which matures to become a seed. The process is totally dependent on the movement of pollen from the male organs (stamens) to the female organs (pistils). This movement can be spontaneous, or, as in many plant species, mediated by animal pollinators (Ollerton et al. 2011).

8.1.2 What Are Pollinators?

Of the ~300,000 animal species that visit plant flowers (Kearns et al. 1998) only a subset are true pollinators that actually transport the pollen grains to the stigma. Pollinators are flower visitors that transfer pollen sequentially to the stigma of conspecific flowers while collecting rewards, usually pollen and nectar as food (Willmer 2011).

8.1.3 A-biotic Pollination

Some plants have evolved a dependency on non-biotic media for pollination, namely wind or water. The main characteristics shared by these plants are small inconspicuous flowers with reduced perianths and exposed anthers and stigmas, as well as diverse adaptations for exploiting the properties of the mediating media for efficient delivery of pollen (Willmer 2011).

8.1.4 Insects

Insects comprise the great majority of pollinators, including some generalist food-foragers, such as beetles, carrion and dung flies, wasps and ants, as well as various unusual flower visitors, such as cockroaches and thrips. Other insects, including mainly bees, hoverflies (Syrphidae) and bee-flies (Bombylidae), moths and butterflies, are floral specialists, showing morphological, sensorial, and behavioral adaptations for collecting and carrying nectar and pollen (Willmer 2011). Members of these groups can provide more reliable and frequent pollination.
services, and bees in particular are considered the most important pollinators in many ecosystems due to their total reliance on flowers for both adult and larval nutrition (Minckley and Roulston 2006; Wcislo and Cane 1996).

### 8.1.5 Vertebrates

The most common vertebrate pollinators are birds and bats. Both groups had evolved less specialized interactions with flowers as compared to those of insects (Willmer 2011), with some exceptions, such as the Caribbean hummingbird species (e.g., Temeles and Kress 2003). Other, unusual, pollinators include arboreal marsupial and eutherian mammals from all southern continents, and several lizards and geckos typically found on islands (Willmer 2011). Plants pollinated by vertebrates often have large and robust conspicuous flowers, with sufficient nectar to provide the energy requirements of the animals.

### 8.1.6 Importance of Pollination for Nature and Agriculture

Animal pollination is crucial for the persistence of natural ecosystems, as more than 87% of the world’s angiosperm species require animal pollination for sexual reproduction (Ollerton et al. 2011). A decrease in pollinator populations can affect the reproductive success of these plants, and alter the composition of wild plant communities (Ashman et al. 2004; Christian 2001). Animal pollination is critical also for maintaining agricultural ecosystems. Animal pollination, provided mainly by bees (Delaplane and Mayer 2000), is required for more than two thirds of the world’s leading fruit and seed crops, and collectively accounts for 35% of the global food production (Klein et al. 2007). The demand for pollination services increases continuously with the increasing need for agricultural products due to human population growth (Aizen and Harder 2009). Without adequate pollination, the human diet would be greatly diminished, both nutritionally and culturally (Klein et al. 2007; Steffan-Dewenter et al. 2005). Hence, pollinators play a key role in maintaining both natural ecosystems and human food supply.

### 8.2 Environmental Threats

Growing anthropogenic disturbance in natural ecosystems directly threatens plant–pollinator interactions via several environmental stressors, commonly including habitat degradation and loss, fragmentation, agricultural intensification, and the introduction of non-native species, as well as indirect effects, such as climate change (Potts et al. 2010a). A quantitative synthesis of 54 studies showed that habitat fragmentation and loss is the most important disturbance factor having a
significant negative effect on the richness and abundance of pollinator bees (Winfree et al. 2009). A comparable negative effect of habitat fragmentation has been demonstrated also among flowering plants and was found to be particularly strong among self-incompatible plant species (Aguilar et al. 2006). Studies on the effects of herbicides and insecticides (Brittain et al. 2010; Holzschuh et al. 2007), cattle grazing (Sjödin et al. 2008; Yoshihara et al. 2008), and fire (Potts et al. 2003) reported varying effects on pollinators that were dependent on the disturbance intensity, sampling period, and pollinator taxon studied. In addition, the changes in pollinator richness and abundance in these studies were largely mediated by the diversity and abundance of the flowering plants. The introduction of non-native invasive plant species can either facilitate or reduce pollinator visitation through competition with native plants for pollination services, but their effects on the local pollinator communities are not yet clear (Bartomeus et al. 2008).

Also in debate is the extent to which the introduction of the European honeybee (Apis mellifera), the most important managed pollinator and an exotic species in most ecosystems, affects native bee species (Paini 2004). There is already an indication of competitive suppression of native bumble bees by non-native honey bees in North America (Thomson 2004). In addition, an indirect effect of honey bees, through faster and more efficient pollen removal, was shown to reduce pollination of the endangered plant Iris atropurpurea by native longhorn bees (of the genus Eucera; Watts et al. 2013). The honeybee, A. mellifera, being a habitat generalist opportunistic species, largely benefits from anthropogenic disturbance (Carré et al. 2009). It is, however, more susceptible to other factors, namely infestation by pests and pathogens (Genersch 2010).

Finally, multiple global change pressures are currently impacting animal-mediated pollination (González-Varo et al. 2013). For example, climate change is a factor that has been commonly associated with latitudinal shifts in the distribution ranges of butterflies (Chen et al. 2011). A particularly large effect of climate change on butterfly populations has been demonstrated in lower elevation areas that also comprised a disturbed habitat (Forister et al. 2010), emphasizing the importance of interacting disturbance factors. Global warming was found to shift phenology in both plants and insects (e.g., Calinger et al. 2013; Ovaskainen et al. 2013). Plants are more likely than insects to advance phenology in response to springtime warming (Forrest and Thomson 2011), and a mismatch of flowering and the emergence of the pollinators may cause population declines if the plants flower at times when effective pollinators are unavailable (Rafferty and Ives 2012).

8.3 Pollinator Decline

8.3.1 Evidence for Pollinator Decline – Pollinators Diversity

In recent years, there are growing concerns over pollinator declines and global pollination crisis (Potts et al. 2010a). However, scarcity of long-term data on the status of domesticated and wild pollinators, in particular bees hampers attempts to
evaluate trends in wild pollinators’ abundance and diversity (National Research Council 2007). In the last few decades, the number of domesticated honey bee colonies declined in some central European countries, but increased in other countries (Potts et al. 2010b). Overall, the global stock of domesticated honey bees is growing more slowly than the agricultural demand for pollination, stressing the global pollination capacity (Aizen and Harder 2009). As for native pollinators, studies have shown declines in populations of some bumble bee (Bombus) species (Cameron et al. 2011; Colla and Packer 2008; Goulson et al. 2006), while other bumble bee species have shown stability or even expansion in range (Williams et al. 2009). Studies on long term trends in the status of pollinator species other than honey bees and bumble bees are scarce. Among these few studies are that of Biesmeijer et al. (2006), who demonstrated significant declines in native bee populations, other than bumble bees, in Britain and the Netherlands, and of Burkle et al. (2013) who found an extinction of 50% of the native bee species in Illinois forests, as well as subsequent degradation in bee-plant interactions in these communities. However, a comparable study by Bartomeus et al. (2013) did not find such significant declines in other regions of the northeastern United States. The status of wild pollinators in most other regions around the world is largely unknown.

8.3.2 Evidence for Pollination Decline – Pollen Limitation

Limited female success due to inadequate pollen receipt appears to be a common phenomenon in plants (Ashman et al. 2004; Burd 1994). This pollen limitation can be the result of one of two components. First, pollen quality can reduce fruit-set and seed-set due to genetic factors, even when pollinator services are sufficient (Aizen and Harder 2007; Sapir and Mazzucco 2012). For example, Segal et al. (2007) showed that reduced fruit-set and seed-set in Iris bismarckiana occurs in crosses within population, relative to crosses between populations, suggesting that genetic similarity within a population reduces reproduction. Similarly, the plant Hymenoxys herbacea showed reduced reproductive success because of mate limitation, despite sufficient pollination services (Campbell and Husband 2007). In addition, a plant’s mating system also affects its fecundity and intensifies the pollen limitation in plants that rely on cross pollination, as compared to self-pollinated plants (Larson and Barrett 2000).

Second, pollen limitation can be the result of reduced pollen quantity, due to reduced pollinator services. Pollinator decline reduces fruit-set due to reduced pollen transfer to stigmas. To assess the effect of pollinator decline on pollen limitation, it is important to partition the effects of pollen quality and quantity (Aizen and Harder 2007). The recent development of a standardized modular approach to measure pollinator effectiveness and efficiency (Ne’eman et al. 2010) is an important step toward assessing the effect of pollination decline on pollen limitation and plant’s reproductive success.
Although pollen limitation is a relatively common phenomenon in natural ecosystems, it is accelerated by anthropogenic disturbance, such as habitat loss, grazing, logging, and agriculture. For example, habitat fragmentation led to a decline in pollination and subsequent fruit set in wild plant populations and an even stronger decline in cross-pollinated species (Cunningham 2000; Winter et al. 2008). The anthropogenic decline of natural areas results in the decline of pollinator populations, leading to a collapse of pollination webs and to seed production failure in specialized plants (Cunningham 2000; Klank et al. 2010; Pauw 2007).

8.4 Methods to Detect Pollinator Decline

The direct assessment of pollinators’ diversity, and even more so, the assessment of pollinators’ function requires large investments of time, money and expertise. Hence, there is a need for surrogate measures (indicators) that will provide the necessary data inexpensively, quickly, and reliably (Mandelik et al. 2010). The two main categories of surrogates used to assess patterns of species diversity are environmental indicators, which are the physical characteristics of the environment that are expected to affect species distribution, and taxonomic indicators, which are the assessment of a taxon or a subset of taxa that are expected to reflect a wider range of taxa in the ecosystem (Mandelik et al. 2012a; Rodrigues and Brooks 2007).

8.4.1 Environmental Indicators

8.4.1.1 Local-Scale Environmental Indicators of Pollinators

Many studies have found a strong positive relationship between the abundance and species richness of flowers and bees at a given site (e.g., Gotlieb et al. 2011; Grundel et al. 2010; Persson and Smith 2013). This may be especially true during periods of limited availability of bloom (Mandelik et al. 2012b). Similar positive relationships were found between the number and diversity of nesting sites and substrates and wild bee richness (Grundel et al. 2010) and bee community structure (Lonsdorf et al. 2009; Murray et al. 2012; Potts et al. 2005). Hence, the overall amount and diversity of the main limiting resources of bees, foraging plants and nesting sites and substrates, may be used to assess diversity patterns of bees at local (field) scales.

8.4.2 Landscape-Scale Environmental Indicators of Pollinators

Spatial characteristics of the landscape, such as patch size, land-use distribution, and degree of fragmentation, were found to affect the richness and abundance of
wild bees (e.g., Grundel et al. 2010; Hinners et al. 2012; Potts et al. 2010b; Winfree et al. 2009). Accordingly, spatial indices of land-use intensification and fragmentation may be used to evaluate the number and diversity of bee populations in different landscapes (Sheffield et al. 2013a).

### 8.4.3 Taxonomic Indicators

Subsets of pollinators, e.g., a single species or a few functional groups, may be used to reflect the diversity patterns of additional pollinators. Cleptoparasitic bees, in particular, hold promise as representatives of the status of bee communities and as indicators of environmental disturbances (Sheffield et al. 2013b).

Diversity patterns of high taxonomic levels, such as genus, sub-families etc., may reflect species-level diversity patterns of pollinators. The efficiency of genus level data in reflecting species patterns of wild bees is variable (Van Rijn 2012) and depends on community characteristics and sample size (Neeson et al. 2013). Such genus and even subgenus level-based analyses should be made with caution considering the high ecological diversity found within some groups of pollinators, for example among members of the bee tribe Osmiini (Müller 2013).

Overall, knowledge about the efficiency of the different possible indicators of pollinator patterns is very limited. Much of the current knowledge is based on speculative assessments rather than direct tests of the efficiency and cost-benefit ratio of the different indicators. Studies of the relative efficacies of the different indicators are urgently needed in order to develop reliable monitoring programs and allow better conservation of pollinator communities.

### 8.5 Pollination Services Indicators

#### 8.5.1 Pollination Measurement

Pollination rates can be used to assess the decline of pollinator communities indirectly. Pollination rates are assessed either by pollinator(s) behavior indices or by indices of pollination success. Pollinator activity on flowers includes visitation rate per plant/inflorescence or per flower, duration of stay in the flower, and foraging type (Dafni et al. 2005). The most common foraging behavior is food collection, usually nectar or pollen, but other behaviors exist, such as night sheltering (Sapir et al. 2005), mating (Fishman and Hadany 2013), or behaviors associated with deception (Schiestl 2005).

The comparison of historical data on pollination rates with current pollination rates is a tool for assessing pollination decline in an ecosystem over time. For example, Pauw and Hawkins (2011) estimated the reduction in visitation rates to
orchids using estimates of pollinia removal from herbarium specimens as compared to current pollinia removal in the same region, and showed through time-series analysis that pollination services to these orchids have declined. On a larger scale, Biesmeijer et al. (2006) showed a concerted diversity decline of both bees and animal-pollinated plant species, based on a multi-year database from Britain and the Netherlands.

A different approach, replacing space with time, compares pollination rates in disturbed or destructed areas with that in nearby areas that are still relatively natural and undisturbed (e.g., Aizen et al. 2008; Lopes and Buzato 2007). However, this approach has been criticized on the basis of the high spatial variation of pollination rates, suggesting that the results may be confounded with spatial comparisons (Pauw and Hawkins 2011).

8.5.2 Post-Pollination Measurements in Plants

The pollen deposition on a stigma measured after a single visit can estimate the relative efficiency of pollinators in transporting pollen (Watts et al. 2013; Winfree et al. 2007). This way, not only the pollination services can be assessed, but also the integration of such services for different types of pollinators that may differ in their relative efficiency (Conner et al. 1995).

Fruit-set can be measured in the level of inflorescence, plant, or population (e.g., González-Varo et al. 2009; Gonzalez-Varo and Traveset 2010). To quantify pollen limitation in natural populations, pollen supplementation experiments are conducted, in which the reproductive success of control plants is compared with that of plants receiving supplemental pollen. If more fruits or seeds are produced when pollen is supplemented, then it is usually concluded that reproduction is limited by pollen receipt (Ashman et al. 2004; Knight et al. 2005). Pollen limitation can be quantified by the Pollen Limitation Index (PLI; Campbell and Husband 2007):

\[
PLI = \frac{\text{fruit-set}_{\text{Suppl.}} - \text{fruit-set}_{\text{Open}}}{\text{fruit-set}_{\text{Suppl.}} - \text{fruit-set}_{\text{Open}}}
\]

Or:

\[
PLI = \frac{\text{seed-set}_{\text{Suppl.}} - \text{seed-set}_{\text{Open}}}{\text{seed-set}_{\text{Suppl.}} - \text{seed-set}_{\text{Open}}}
\]

In this index, the excess fruits or seeds produced with supplementary hand pollination as compared to those of open-pollination flowers is divided by the reproductive success when pollen is not limited, i.e., with supplementary hand pollination. The cumulative pollen limitation is achieved when the probability of
a flower to set a fruit and the number of seeds are multiplied (González-Varo et al. 2009):

\[
PLI_{\text{cumulative}} = \left( \frac{\text{fruit-set}_{\text{Suppl.}} \times \text{seed-set}_{\text{Suppl.}} - \text{fruit-set}_{\text{Open}} \times \text{seed-set}_{\text{Open}}}{\text{fruit-set}_{\text{Suppl.}} \times \text{seed-set}_{\text{Suppl.}}} \right)
\]

Pollen limitation measurements with supplementary pollination treatment may be a cheap and quick surrogate for the tedious and time-consuming pollinators’ observations, because a plant’s reproduction is determined by an integration of pollination events throughout the plant’s flowering season. However, special caution should be taken when the mating system or the genetic structure of the plant population may affect reproductive success (Aizen and Harder 2007).

### 8.6 Summary and Prospective

Recent studies found empirical evidence for the decline of pollinator-plant systems, particularly in intensified regions of Western Europe and the US. The main drivers for pollination decline are agriculture intensification and the subsequent fragmentation and loss of preexisting habitats. Some studies indicated the higher vulnerability of specialists, such as self-incompatible plants, and mutual obligates, such as many bee species. Our current understanding of environmental effects on pollination processes in both natural and human-dominated ecosystems is limited mainly by two factors. One is the relatively little knowledge of the ecological requirements of pollinators and plants, and the other is shortage of studies on the response of populations and communities to landscape change. Future research should include not only long-term monitoring schemes for pollinator-plant systems but also manipulation experiments in order to elucidate potential mechanisms of decline. For example, manipulating nesting-associated variables of various pollinators can contribute new insights into pollination processes, such as limitation in pollination services. For the conservation of pollinators and plants in disturbed human-dominated ecosystems, comprehensive solutions should be explored that improve not only the dominant attractive pollinator and plant species but also rare and less enchanting species. Finally, there is a great need to develop and test the cost-effectiveness of possible indicators of pollinators’ diversity patterns and their pollination services. These indicators will enable the execution of long-term monitoring programs to detect patterns and changes in pollinator communities.

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