

Bees in a landscape context – what do bees need and who needs them?

by

Ulrika Samnegård



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Summary

The interaction between plant and pollinator is generally mutualistic. The plant becomes pollinated or gets its pollen grains dispersed and the pollinator gets food rewards consisting of nectar or pollen. Many plants and crops are dependent on pollinators for fruit set and must therefore have efficient pollinators in their surroundings. There are many groups of animals that include pollinating species; however, bees are often referred to as the most effective pollinating group. Their effectiveness is partly because of their dependence on floral food resources both for larval development and adult survival. In addition to high abundance, high diversity of bees has been shown to be important for effective and stable pollination services of crops and wild plants. The importance of identifying what is affecting the bee composition and distribution in a landscape is therefore obvious. In addition to food resources, bees need suitable nesting habitats for reproduction and often external substrates for the construction of brood cells. On Earth, there are bees on every continent except Antarctica and 17,500 species are so far identified (Michener 2007). Despite the high diversity of bees with great variation in food and nesting requirements one factor has been found to frequently explain the diversity of bees; heterogeneity. In general, on a regional scale, bee diversity increases with higher heterogeneity in the landscape. Highly heterogeneous environments, provides high diversity of food and nesting resources, which can support more species. However, bee communities will differ in their response to changes in the landscape depending on species composition, habitat and continent. Therefore knowledge about the bees' basic ecology and life-history is important for interpreting results and planning conservation measures.

Sammanfattning

Interaktionen mellan växt och pollinator är oftast mutualistisk, dvs. både parterna drar fördel. Växten blir pollinerad eller får sina pollenkorn spridda och pollinatoren får en födobelöning bestående av nektar eller pollen. Många växter och grödor är beroende av pollinatörer för fruktsättning och måste därför ha effektiva pollinatörer i sin omgivning. Det finns många djurgrupper som innehåller pollinerande arter, men bin framhålls ofta som de mest effektiva pollinatörerna. Deras effektivitet beror bland annat på att de är helt beroende av blomresurser både för larvutveckling och för överlevnad som adult. Eftersom inte bara en hög abundans utan även hög diversitet av bin har visat sig vara viktigt för effektiva och stabila tjänster, i form av t.ex. säkrare pollination av grödor och vilda växter, är det viktigt att identifiera vad som påverkar bins fördelning i landskapet. För bins reproduktion behövs utöver födoresurser även passande habitat för skapandet av boplatser. På jorden finns bin på alla kontinenter förutom Antarktis och 17 500 arter är än så länge identifierade (Michener 2007). Trots denna mångfald av bin med variation i födo- och boplatsskrav har det visat sig att en faktor ofta förklarar mångfalden av bin; heterogenitet. Generellt sätt, över hela jorden, gäller att på en regional skala ökar bi-diversitet med högre heterogenitet i landskapet. Heterogena miljöer innehåller ett varierat utbud av föda och boplatser vilket kan stödja många arter. Det är dock skillnad mellan olika bisamhällen, och därmed deras respons på miljöförändringar. Skillnaderna beror bl.a. på habitat och kontinent, vilket måste tas hänsyn till både när man utvärderar landskaps inverkan på bin men också när man planerar stödåtgärder.

Contents

Introduction	5
What is pollination and who performs this kind of activity?	5
Little essential bee knowledge... ..	6
Why is pollination needed? Why are not all plants self-fertilized?.....	8
Pollination systems.....	8
What is affecting a plants reproduction success?	9
What can influence the pollinator community in a landscape?	11
Fragmentation of natural habitats and distance to source habitats	11
Landscape features important for bees	14
What types of habitats do bees want?	15
Mini review - What do bees want?.....	15
European temperate broadleaf forest.....	17
North America.....	19
Mediterranean region	23
The tropics and subtropics.....	25
Conclusions from mini review	29
Do we need to have a diverse pollinator community?.....	30
What about the landscape scale?	32
References	34

Introduction

In this essay I summarize how one of our most important pollinating group, bees, is distributed in the landscape and what could affect their distribution. In addition, I will touch upon how this or if this distribution connects with crops and wild plant communities. Due to the close interaction between pollinators and the plants which they pollinate, I start by summarizing different pollination systems and what could affect a plants reproductive success. Thereafter, the focus will be on bees. I discuss what role human disturbances play for the pollinator community and if there are special features important for a rich bees community; moreover, if it differs globally. Human activities affect bees in many ways; however, bees can affect human welfare as well. I go through why it is important with a diverse bee community and the possible consequences if the bee community gets too impoverished. In the end, I summarize how bees perceive the landscape; that different species respond differently to different spatial scales, which is essential knowledge for understanding local bee communities.

What is pollination and who performs this kind of activity?

Pollination is a noun referring to a “*transfer of pollen from anther (in angiosperms) or male cone (gymnosperms) to stigma or female cone respectively*” (Lawrence 2000). Pollination is in many plants facilitated by animals, which in general result in a mutualistic relationship where both the plant and the animal benefit. The plant get its pollen spread and its ovaries fertilized and the animal gets, in most of the cases, food rewards of pollen or nectar from the flowers. The animals that are transferring pollen between or within flowers are called pollinators. Since plants very likely benefit from having pollen vectors that are good dispersers, it is not surprising that the majority of pollinators are from animal groups that have evolved flight; insects, birds and bats (Pellmyr 2002). The number of vertebrate pollinators worldwide has been estimated to 1,200 species and invertebrate pollinators to around 290,000 species, where beetles, butterflies and bees are the major groups (Nabhan & Buchmann 1997). Many of the pollinating animals rely almost entirely on floral resources in certain periods, during one or several stages of their life. Among vertebrates the known

pollen vectors are mainly different species of bats and birds, though some additional vertebrates are also known (Bawa 1990; Fleming & Muchhala 2008). There are six phylogenetically independent groups of birds that contain nectar specialists, where hummingbirds, hermits and sunbirds are examples (Fleming & Muchhala 2008). Nectarivorous and frugivorous bats are also important flower-visitors in all tropical regions (Fleming & Muchhala 2008). There are also non-flying vertebrates for which a pollinator function in some instances has been documented, like for mice, possums, lemurs and primates (Carthew & Goldingay 1997). Long lived animals need food resources throughout the year; therefore, vertebrate pollinators are mostly found in tropical and subtropical areas (Sazima et al. 1995). However, for many plants the most important pollinators are different hymenoptera and lepidoptera species. Lepidopterans, which alone constitute for approximately 11% of all described species on Earth, includes species with coiling tongues making several of them very effective nectar consumers (Wilson 1992). Hymenopteran pollinator species, particularly bees, are in many cases known to be the most important and efficient pollinators (Fussell & Corbet 1992; Garibaldi et al. 2011; Michener 2007), whose visit will result in higher reproductive output for the plants compared to visits by other pollinating groups (Schemske & Horvitz 1984). One reason for the high efficiency of bees as pollinators is that they, in contrast to for example nectar feeding lepidopterans, are depending on flower resources both for larvae and adults stages and therefore need to visit and collect from many flowers during a life time (Michener 2007; Pekkarinen 1997). In addition, many species have pollen-trapping body hair which facilitates that pollen get stuck on their bodies, with the consequence that pollen easier get transferred to the next plant (Pitts-Singer & James 2008).

Little essential bee knowledge...

Like for most hymenopteran insects, bees' sex are determined by a haplodiploid system (Michener 2007). Males are coming from unfertilized eggs, i.e. they are haploid, while females come from fertilized eggs i.e. are diploid. The fertilized females store sperm in their spermatheca and can control the sex of each of their eggs by releasing or not releasing sperm to the eggs (Michener 2007). The sex ratio of the bee population is important because female bees are more effective pollinators than male bees (Pitts-Singer & James 2008). Females need to collect large quantities of pollen and nectar to feed their young as well as themselves and

will therefore visit more flowers. Males only need to feed themselves. Due to female bees restricted foraging range around their nests, bees are called *central place foragers* (Goulson 2003; Schoener 1979).

Bees have evolved different social systems; from highly eusocial systems to solitary lifestyles (Michener 2007; Pitts-Singer & James 2008). Eusocial means that there is a division of labour within the colony. The most common example of a highly eusocial system are honey bees (tribe Apini), but there are also the tropical bee tribe Meliponini (i.e. stingless bees) (Michener 2007). The eusocial colony system includes sterile female workers, only one or few reproducing perennial females (queens), overlapping generations and cooperative brood care. The eusocial queens' only task is to lay eggs while the workers forage, take care of the brood and guard the colony, for which the queens are incapable of doing. In solitary bees, females construct their own nest and collect food, like pollen and nectar masses, for each of their brood and then die or depart before the offspring completes their development (Fig. 1) (Michener 2007; Pitts-Singer & James 2008). In between these two systems there are bees that are primitive eusocial, like the bumblebees (Bombinae), some sweat bees (Halictinae) and some carpenter bees (Xylocopinae) with annual colonies where the queens are more similar to the workers (Michener 2007). These colonies are usually short-lived where only the new generation of mated females survives and go into hibernating until next season when they, themselves, start new colonies (Michener 2007). Some solitary bees sometime nest in aggregations, when that happens it is commonly among soil nesting bees. However, some cavity nesting bees could form aggregations if nesting sites are available (Michener 2007). In all type of different systems cuckoo-bees are found, which are species that parasitizes other bees by letting their own larvae feed on the food stored for their host's larvae (Michener 2007).



Figure 1. A nest by the solitary *Xylocopa californica arizonensis*. Photo: Ulrika Samnegård

Why is pollination needed? Why are not all plants self-fertilized?

Pollination systems

In nature a whole range of different pollination systems exist. There are very specialized systems including few actors, from figs that require a specific wasp for their pollination (Wiebes 1979) to wind pollinated or very generalized systems with as many as 70 insect taxa visiting the plant (Herrera 1988). A benefit with specialized systems could be that the plants are less likely to receive “wrong” pollen from other species and to get its pollen spread to wrong plants (Wilcock & Neiland 2002). A specialised pollinator might also fly longer distances to find the same plant species and thereby spread the pollen further than a more generalised pollinator would. Nevertheless, even generalized pollinators practice a behaviour called “floral constancy” which means that individual bees tends to collect pollen from the same plant species during a collecting trip (Michener 2007).

The drawback with very specialized systems is that these systems are more vulnerable; if one actor disappears, the other or others are at risk to meet the same fate (Wilcock & Neiland 2002). However, pollination systems including only a single species of bee and a single species of plant are rare; in most cases when a specialist is included, the other actor, either the bee or the flower, tends to be more generalistic (Michener 2007). Bees that are specialised on one or very few plant species are referred to as oligolectic bees. Specialized pollination systems seem to be more common in areas with very high diversity of organisms, like in the tropical region of the world (Johnson & Steiner 2000).

There is a diversity of reproductive systems in plants with different advantages and disadvantages under different conditions. Plants do not always need animals for pollen transportation; wind dispersal of pollen (anemophily) is also common in some plant groups. Plants with wind dispersed pollen are rare in tropical rainforest but increases in significance with increasing latitude (Regal 1982). Wind dispersal is also more commonly found in regions where trees drop their leaves, in regions with low floral diversity and in open landscapes like savannas (Regal 1982). Despite the importance of wind pollination for many plants, this essay will focus on insect pollination, and especially bee pollinators.

How come that many plant species want to exchange pollen with other plants? Why do they not save themselves the cost and trouble of producing high numbers of pollen grains to disperse when there is no guarantee for the plant that these pollen grains actually reaches a stigma and fertilizes the ovules of another plant? Many plants are to some extent capable of self-fertilization (selfing); these are called *self-compatible* (SC) plants. The range of sexual systems in plants is from closed hermaphrodite flowers that exclusively are selfing (cleistogamy) to plants that have evolved sexually polymorphism with separate male and female individuals (dioecy) (Goodwillie et al. 2005; Jarne & Charlesworth 1993). Some plants have evolved self-incompatibility genes that blocks pollen with the same self-incompatibility genes, these are obligate out-crossing i.e. *self-incompatible* (SI) plants (Igic et al. 2006). However, the sexual system found in the majority of the plant species is hermaphroditism with flowers having both male and female functions, capable of selfing to some extent (Goodwillie et al. 2005; Jarne & Charlesworth 1993; Silvertown & Charlesworth 2001). Even for plants capable of selfing, most hermaphrodite plants prefer mating with other individuals, which results in outcrossing (Goodwillie et al. 2005). Outcrossing is costly in many ways; the parental plant will be less related to its offspring (Goodwillie et al. 2005) and there is no guarantee for mating. For isolated populations or populations with few individuals the disadvantages of self-incompatibility is also obvious. However, the long term advantages may be the explanation for its existence. It has been shown that SI species have lower extinction rate than SC species (Goldberg et al. 2010; Takebayashi & Morrell 2001). With obligated cross pollination, inbreeding-depression is avoided and the progeny gets a more diverse set of genes which increases the chances that some will survive in a changing future; a force selecting against selfing (Jarne & Charlesworth 1993). However, many plants have a backup mechanism which is called delayed selfing, which causes movement by anthers to touch the stigma, to assure fertilization when no outcrossed pollen has reached the stigma in time (Goodwillie et al. 2005; Jarne & Charlesworth 1993).

What is affecting a plants reproductive success?

Of all the things plants' need (Fig. 2), the earlier common view was that the most limiting factors for plants' seed and fruit set were nutrients and water supply, because pollen is produced and spread in such a quantity. However, later research has revealed that pollen limitation occurs in many plant species and could be a major reason for lower fruit and seed

production (Burd 1994; Larson & Barrett 2000), especially for plants in fragmented landscapes (Aguilar et al. 2006). This indicates the essential roll pollinators have for many plants reproductive success. Pollination failure can occur at different stages; before, during and after pollen dispersal (Wilcock & Neiland 2002). Reasons for pollination failure can be pollen feeders depleting the pollen, not viable pollen, lack of pollinators or pollinator activity or suitable mates (reviewed in Wilcock & Neiland 2002). Moreover, breeding systems, floral traits and population size and density of the plants can affect the vulnerability to pollination failure (Wilcock & Neiland 2002). Unfertilized ovules in a flower could be a consequence of too few pollen grains arrived at the stigma or an excess of heterospecific pollen (Wilcock & Neiland 2002), which would be a result of too few pollinators or not efficient pollinators around.

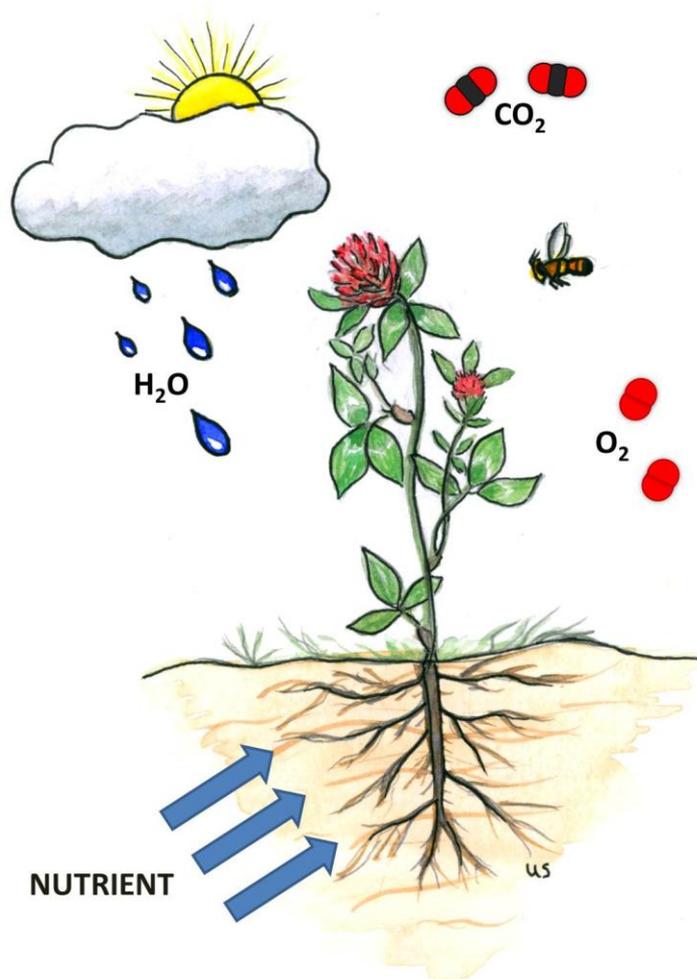


Figure 2. Different factors can affect a plants reproductive success. In addition to lack of water and nutrition, pollen limitation may be one of the major reasons for reduced seed set. By: Ulrika Samnegård.

From a plants point of view; the actual reproductive success is related to whether progeny will survive into the future or not. Unfertilized ovules must be the absolutely least beneficial scenario. Even though it has been found that selfed flowers can produce more seeds than cross-pollinated flowers, the seeds are often significantly smaller (eg. *Caladenia behrii* in Petit et al. 2009). Selfing can have a negative effect on germination; the reason seems not only be because of the smaller seeds, but also due to inbreeding depression (Petit et al. 2009).

What can influence the pollinator community in a landscape?

Fragmentation of natural habitats and distance to source habitats

It is well known that many bee species from all over the world have declined during the last half a century (Kearns et al. 1998; Murray et al. 2009; Potts et al. 2010). Researchers have even argued that we soon will be facing a global pollination crisis, if we are not already in it (Kearns et al. 1998; Kremen & Ricketts 2000; Steffan-Dewenter et al. 2005); however opinions have been divided over that matter (Ghazoul 2005). The major evaluated reasons for the decline of native, wild pollinators are the destruction and fragmentation of pollinators' natural habitats (Goulson et al. 2008; Hendrickx et al. 2007; Kearns et al. 1998; Steffan-Dewenter et al. 2002; Winfree et al. 2009). In addition, other factors known to negatively affect wild pollinators are agrochemicals, exotic species competing for resources and parasites and diseases often coming together with introduced exotic species or subspecies (Brown & Paxton 2009; Goulson 2010; Ings et al. 2006; Inoue & Yokoyama 2010; Kovacs-Hostyanszki et al. 2011; Meeus et al. 2011; Peng et al. 2011). Moreover, other interacting drivers are presumably also important for the declines (see eg. Brown & Paxton 2009; Potts et al. 2010). However, some of the expected driving factors for the decline have been hard to find. For example increased abundance of honey bees has not been found to negatively affect native bee abundance and diversity on watermelon farms in California (Kremen et al. 2002). Due to continued expansion and intensification of agricultural landscape and the rapidly growing human population, many of our pollinators will most probably continue to decline and become more and more displaced (Tilman et al. 2001). This can and has already been shown to lead to disrupted pollination of crops and wild plants (Aguilar et al. 2006; Kremen et al. 2002).

In 1700 approximately 95% of the earth's ice-free area was wild land and semi-natural human biomes (eg. woodlands with minor land use), by the year of 2000 this figure had declined to 45% (Ellis et al. 2010). The earth's ice-free land has been transformed into human biomes like rangelands, croplands, villages and densely settled areas (Ellis et al. 2010). Today, croplands together with pastures have become one of the largest terrestrial biomes on earth (Foley et al. 2005). The risk with this rapid conversion of natural habitats into agricultural land is that services from "the wild nature" like pollination of crops and wild plants by unmanaged bees could be impaired, which will lead to lower agricultural production (Foley et al. 2005; Kremen et al. 2002). Conversion of natural habitat is equal to loss of natural habitats and the remaining habitat is often left highly fragmented. Habitat fragmentation has been shown to have a strong negative effect on sexually reproductive plants; however, fragmentation affect species differently, self-incompatible plants are more negatively affected than plants able of selfing (Aguilar et al. 2006). In many regions, the constant pressure on increased agricultural production, leads to that already existing agricultural land gets increasingly intensified with more agro-chemicals and larger field and farm sizes. Even though many flowers, and therefore presumably also bees, should be able to thrive in agricultural landscape, high input of agro-chemicals is obviously negatively affecting the species richness and abundance of both plants and bees.

Despite the knowledge of the negative impact of fragmentation on many organisms, it is difficult to draw general conclusions on the effect of fragmentation on all pollinating organisms. This is due to the facts that groups differ in their responses and that fragmentation can lead to different types of new habitats. However, a recent review, addressing the effect of fragmentation on wild pollinators (mainly bees) that are visiting crops, has found some general patterns (Garibaldi et al. 2011). Even though the review included 29 studies from 15 different countries; the results were surprisingly consistent (Garibaldi et al. 2011). Mean richness of wild pollinators, visitation rate and fruit set declined with increased isolation from florally diverse natural and semi-natural areas; moreover, the stability of the services declined with isolation (Garibaldi et al. 2011). Contrasting the wild pollinators, honey bees visitation rate was not found to change with isolation (Garibaldi et al. 2011).

Fragmentation can sometimes give confusing results. Examples of that are Brosi's et al. (2008) study on bee communities in Costa Rica and Aizen and Feinsinger (1994) study from Argentina. Both studies found the abundance or visitation rate of bees to not differ between the natural and fragmented habitat. Brosi et al. (2008) did not either find the bee richness to differ. However, the bee species composition was found to change. More native bees were found in the natural habitat, and more honey bees were found in the fragmented habitat (Aizen & Feinsinger 1994; Brosi et al. 2008). These studies reflect the complexity in different species traits and demands. Results that only show pollinator abundance or richness may give understated results on the importance of natural habitats for many wild, native bees. Different pollinators perceive and utilize their surroundings differently which will be reflected in their response to fragmentation and isolation. There are bees that never cross fragmented areas, like male euglossine bee species that never cross 100 m of cleared forest between continuous forest and forest fragments (Powell & Powell 1987). In contrast, as seen in the above mentioned studies, generalistic bees, like honey bees, can successfully utilize many disturbed and fragmented habitats (Aizen & Feinsinger 1994; Brosi et al. 2008; Garibaldi et al. 2011).

Another reason for the often divergent effects of fragmentation is that "fragmentation" is a concept used under different circumstances, in different habitats and scales (Fahrig 2003). Nevertheless, a meta-analysis on bee responses to different kinds of anthropogenic disturbance found that both abundance and species richness of bees are negatively affected by disturbance, even if the effect generally is small (Winfree et al. 2009). Habitat loss and fragmentation were the only types of disturbance showing significant negative effects on bee abundance and richness, however; this was only found to be significant in systems that experienced extreme habitat loss (Winfree et al. 2009). Fragmentation variables such as patch area and isolation often fail to be strong predictors for species occupancy (Prugh et al. 2008). A suggested explanation is that many studies ignore the surrounding matrix (Prugh et al. 2008). The distinction between habitat islands and the matrix is not always as straightforward as it is for true islands. Matrix type has been shown to be an important predictor for the sensitivity of species to isolation and small patch area, for example, a matrix consisting of a forest clear-cut is more hostile for many organisms than a more semi natural matrix (Prugh et al. 2008).

Landscape features important for bees

The composition of pollinators can affect the plant community and vice versa (Biesmeijer et al. 2006; Fontaine et al. 2006), therefore it is good to know the driving factors for changes and shifts in communities. Many studies have been done to understand what affects the composition of pollinators, especially bees, in a landscape (Grundel et al. 2010; Potts et al. 2003; Potts et al. 2010; Potts et al. 2004; Potts et al. 2005). Important features that could explain bee community structure are for example flower abundance, pollen abundance, nectar resource diversity, site age, nesting substrate available, time since last fire, canopy cover and grazing intensity (Grundel et al. 2010; Potts et al. 2003; Potts et al. 2004).

Since pollinators are living organisms they are in need of energy for survival. Therefore, a positive association between food resources available and pollinator abundance is to be expected and has repeatedly been found (Grundel et al. 2010; Hagen & Kraemer 2010; Potts et al. 2004). The connection between species richness of flowers and nectar resource diversity and the pollinator abundance and diversity is also quite intuitive (Grundel et al. 2010; Hagen & Kraemer 2010; Potts et al. 2004). The more diverse food supply, the more different species can get their food request satisfied. Annual plant diversity seems to be especially linked to bee diversity (Potts et al. 2004). Since there is a strong dependence from both sides between flowers and their pollinators it may also be important to have a high diversity of pollinators to preserve a rich assemble of flowers. This has been suggested by the parallel decline in pollinators and insect-pollinated plants in Britain and the Netherlands (Biesmeijer et al. 2006). Specialist species with narrow habitat or dietary requirements seems to be more vulnerable and decline more than generalists and more mobile species (Biesmeijer et al. 2006).

In addition to food resources, bees need nest sites for survival and reproduction (Michener 2007; Osborne et al. 2008; Potts et al. 2005). Typically bees build their nests in soil, but bees could also nest in wood, narrow cavities or make external nests, all depending on species (Michener 2007). Most bees also need some kind of foreign material from the surrounding to build broad cells within the nest (Michener 2000). Therefore, availability of diverse nesting substrates is also important for high bee diversity (Potts et al. 2005). The diversity of nests

and nesting substrates might as well as food be a limiting factor for establishment or persistent of many bee species (Potts et al. 2005).

What types of habitats do bees want?

We can start by exploring what bees do not want. Ecological and life-history traits of bees have in a review been linked to different bee species' response to different kinds of disturbance (Williams et al. 2010). Disturbances that were included in the analyses were habitat loss, agricultural intensification, grazing, fire, tilling and pesticide use. In general, all bee species tended to be less abundant in all types of disturbed areas (Williams et al. 2010). However, when all bee species were merged in the analysis, only increased isolation from natural or semi-natural habitats was found to have a decreasing tendency on bees. Ecological traits were found to help predicting species sensitiveness; abundance of above-ground-nesting bees were on average six times more reduced by disturbance (all types) compared to below ground nesting bees; "renters" were more affected than excavators; and social species more strongly affected compared to solitary species (Williams et al. 2010). Above-ground nesting bees in the disturbance category "agricultural intensification" were even more strongly affected compared to below ground nesters. Above-ground nesters were also found, if honey bees were disregarded, to be proportionally more affected by isolation from semi-natural habitats, decreasing with 47% with isolation from 0 to 1 km. Social bees were more affected by isolation and pesticides use compared to solitary species, with abundance-reductions due to pesticides averaging 70% for social compared to 29% for solitary bees. On the other hand, solitary bees were more negatively affected by agricultural intensification in general (Williams et al. 2010). In conclusion, generally, bees do not like disturbances and bees ecological and life-history traits are important to know to be able to predict their responses to different types of disturbance.

Mini review - what do bees want?

If a bee pollinator community should persist it is obvious that their fundamental requirements like food and nesting places must be satisfied both in time and space. However, in a disturbed area, the limiting factors for the bee community could be difficult to identify. If actions are taken to increase bee abundance, there are some questions that need to be considered. Should

the bee community just be sustained as it is or should the bee richness increase? Are all bee species wanted or only native, wild bees? Is it the most efficient crop pollinating species the ones that should be targeted? Since bees are found in most regions in the world in very different habitats, we can suspect that the limiting factors for a diverse, indigenous bee community differ (Fig. 4). For example, even though hedgerows are known to increase bumblebee abundance and richness in agricultural landscapes in northern Europe (eg. Osborne et al. 2008), it is not sure that hedgerows will have the same effect on bee communities in agricultural systems in Indonesia. Likewise, the positive impact of indigenous forest on bee diversity often found in the tropics (Klein et al. 2003b; Ricketts 2004) might not be found, and not even expected to be found, from the indigenous boreal forests in the northern hemisphere.

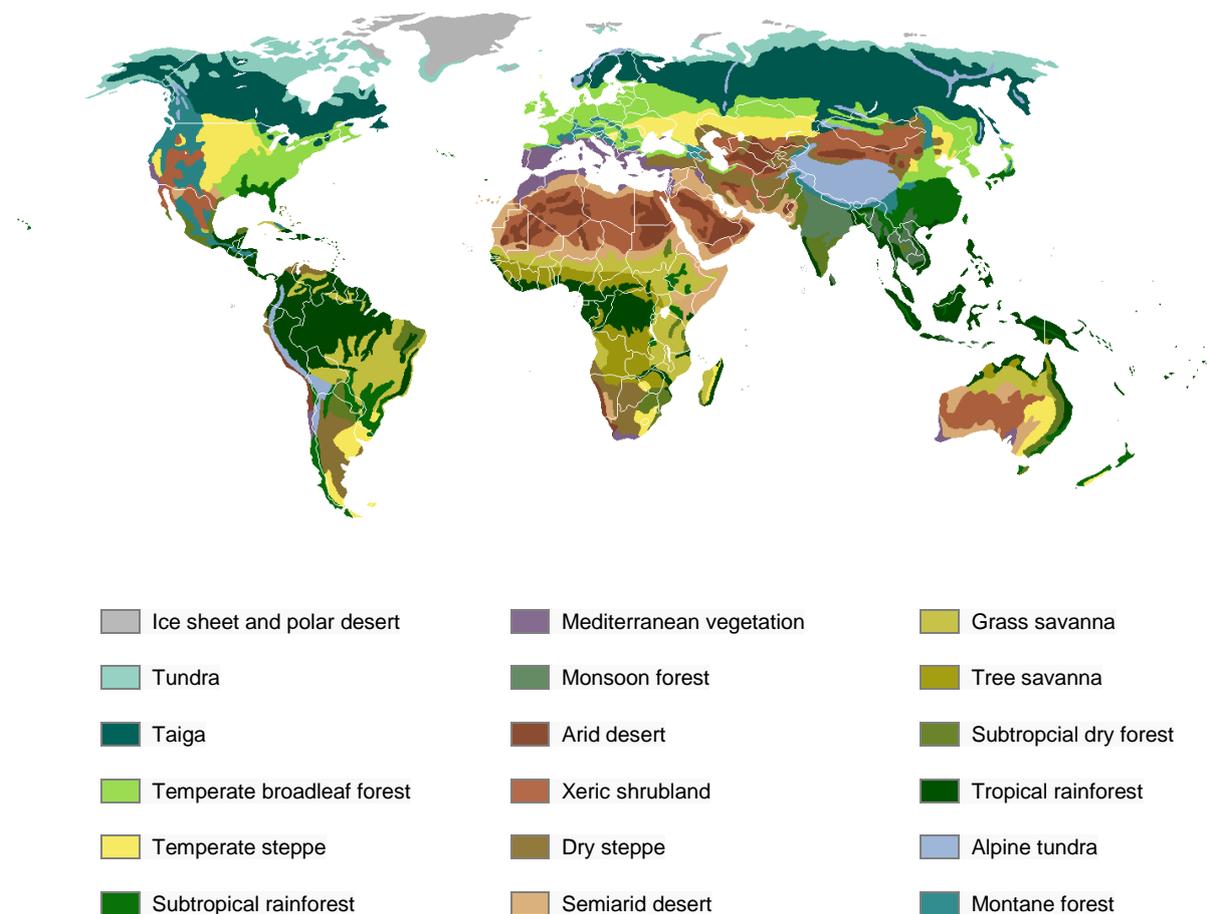


Figure 3. The biomes of the world. By Ville Koistinen, via Wikimedia Commons.

Here I made a short review of important features or limiting factors for bee abundance and/or diversity that has been found in different regions of the world. I started by exploring the 16 studies summarised in Murray et al. (2009) and added 17 more. Although there are bees with very specific needs, bee diversity and abundance are expected to some extent to be affected by similar structures in the different regions. The most desirable thing would be to describe the features and factors found to be important for bee abundance and richness for each biome separately. This is however not possible for this short review due to the high and variable number of biomes (Fig. 3) (Begon et al. 2006) and the few number of studies conducted in many of them. To be able to see patterns and draw conclusions from a region, a fair number of studies must have been done there. Therefore, after some selection and grouping, four categories were chosen: “European temperate broadleaf forest”, “North America”, “Mediterranean region” and “the tropics and subtropics”. These categories were chosen because they cover a large part of the world’s habitats but also because most studies have been done in these areas. Even though both the categories; “European temperate broadleaf forest” and “North America” cover to some extent the same biome, temperate broadleaf forest, their difference in history and conservation measures made them better suitable as separated categories. Some studies were difficult to classify, and can, in some respects have been misplaced or mentioned repeatedly. However, this will hopefully not affect the general conclusions.

European temperate broadleaf forest

Temperate forests, including mainly wind-pollinated forest trees, are presumably not a good habitat for most bees (Michener 2007). The larger part of European land, that is not forested or urbanized, has been under cultivation for a long time, therefore many species are adapted to agricultural habitat. Probably, it has been beneficial for many bees with deforestation in this part of the world, leading to more flower-rich habitats as pastures, waste lands, road and field margins and so on (Michener 2007). However, after the World War II agricultural land has been increasingly intensified, with more agrochemicals and simplified structures with larger farms and field sizes. This has in many places resulted in a rough, homogeneous habitat, not so friendly for biodiversity (Hendrickx et al. 2007).

Since pollinators are essential for many crops' fruit set (Klein et al. 2007), several studies have been done to find out about different kinds of habitats that could positively affect the species richness and abundance of pollinators in homogenous, agricultural landscapes in Europe. Many studies do find that habitats that were more common before the intensification of the farmland are important for a rich bee community in the landscape. Examples of habitats that have been shown to positively affect the diversity of flora, invertebrates and birds in the agricultural landscape are managed small, semi-natural habitats like hedgerows, field margins, road verges and other linear landscape fragments (reviewed in Benton et al. 2003; Svensson et al. 2000). Semi-natural (Sweden, Öckinger & Smith 2007) and calcareous grasslands (Germany, Steffan-Dewenter & Tschardt 1999), and also common gardens (Sweden, Samnegård et al. 2011), have been shown to act as sources for pollinating insects, to the surrounding more simple environment. This was shown by the higher richness and abundance of bees proximate these habitats. Likewise, Hendrickx et al. (2007) study that range over seven European countries also found bee species richness to increase proximate semi-natural habitats, where semi-natural habitats were defined as patches that were “unmanaged or managed to the extent that its natural production levels were not purposely increased” (Hendrickx et al. 2007). Abundance and diversity of solitary bees have moreover been found to be positively correlated with the proportion semi-natural areas in a radius up to 750 m, although the big social bees *Bombus* and *Apis* were not affected (Steffan-Dewenter et al. 2002).

Different farming practise has also been suggested to improve biodiversity (Bengtsson et al. 2005; Hole et al. 2005). Organic farming and other “friendly” management practices, like Agri-environmental management (AEM) (which is management practices aiming to support biodiversity), has been showed to positively affect species richness and abundance of pollinators (Batáry et al. 2011; Holzschuh et al. 2008). However, the effect of more friendly management practices seems to depend on the context. A study from southern Sweden found a significant positive effect of organic farming on species richness and abundance of bumble bees only in extremely homogeneous, simple landscapes, not in heterogeneous (Rundlöf et al. 2008). These findings are supported in a recent meta-analysis (Batáry et al. 2011). Similarly, the effect of AEMs on species richness and abundance of pollinators was found to differ between simple and complex landscapes (Batáry et al. 2011). The reason for the higher impact of more friendly management practise in homogeneous lands is presumably because it

decreases the distance between nesting and foraging sites (Kremen et al. 2007). Many pollinating species, like bees and hoverflies, needs several habitats for their survival, for example semi-natural habitats for nesting or hibernation and agricultural fields for foraging (Kremen et al. 2007). AEMs and organic compared to conventional management of fields often result in much higher floral abundance and thereby food resources for pollinators in the agricultural land (Holzschuh et al. 2008; Rundlöf et al. 2008). In complex landscapes, management practices might not be as important for bees, since there already are available forage and nesting resources in the vicinity of the agricultural fields which they could utilize.

North America

North American studies differ quite often from European studies in their expectation on what is beneficial for pollinators. This may not be without good reasons. Many European studies are studying the effect of amount or proximity to “semi-natural habitats” whereas most North American studies do similar kind of studies but with amount of or proximity to undisturbed “natural habitats”. The reason is probably that most of Europe has been under cultivation for many hundreds of years and do not have much pristine natural habitats left, and especially not much adjacent the most intensified agricultural lands. North America, on the other hand, is in comparison a continent that relatively recently became colonized with settlers using permanent agricultural plots for food production and have therefore still a lot of natural habitat remaining. As Winfree et al. (2007) themselves pointed out, the “semi-natural habitats” like grazed grasslands, orchards and gardens as for example Steffan-Dewenter et al. (2002) evaluated and found to be good habitats for wild solitary bees in Germany, would in their study from New Jersey have been considered as “agriculture” or “development”, not as “natural habitat”. It could be that North American pollinators are less adapted to old-fashioned agricultural management including what we today call semi-natural habitats than European pollinators, or that the same type of semi-natural habitats do not exist. I will not speculate on this, but in general it seems like semi-natural habitats are not valued as highly in North America as in Europe as a promoter of biodiversity.

In New Jersey, the relationship between bee richness and abundance and degree of human disturbance in forested ecosystems has been studied (Winfree et al. 2007). Contrary to

expectations, the bee abundance and species richness decreased with an increased amount of natural vegetation (Winfree et al. 2007). The study included sites across a gradient from 25 to 99% natural vegetation cover in a 1600 m radii, where the natural vegetation was pineoak heath (Winfree et al. 2007). The pineoak heath consisted of pitch pine (*Pinus rigida*) and oak (*Quercus*) trees and a shrub layer of ericaceous species on sandy soils, which were thought to be a good habitat for bees (Winfree et al. 2007). Agricultural fields were found to have the highest bee abundance and richness when compared to extensive forest and suburban and urban development (Winfree et al. 2007). Only 18 out of the 130 bee species found were positively affected by extensive forest, and these species were not more likely to show a specialised feeding habit compared to the other species (Winfree et al. 2007). Similarly, wild bee visitors to crops in New Jersey and Pennsylvania could not be predicted by the proportion of natural habitats (=woodland) or landuse intensity (organic vs. conventional) (Winfree et al. 2008). However, a positive association between the abundance of solitary bees and weedy flowers in the agricultural fields was found (Winfree et al. 2008). In this study natural habitats were scattered throughout their study system adding heterogeneity to the whole landscape (Winfree et al. 2008). Winfree et al (2008) argued that in other studies addressing similar questions, farms with different management systems differ more in field size, crop diversity and weedy flower diversity and these factors per se may be more important than management practice.

Different pollinators are often found to differ in their responses to surrounding land use. A study from northern California found that the two main pollinators of field grown tomatoes; *Anthophora urbana* and *Bombus vosnesenskii*, were affected differently by the surroundings (Greenleaf & Kremen 2006a). *B. vosnesenskii* was positively affected by proximity to and amount of natural habitats (orchard, row-crop, pasture), whereas none of the measured variables could explain *A. urbana* visitation rate (Greenleaf & Kremen 2006a). When studying another crop, watermelon, which is visited by a higher diversity of bees than tomatoes, pollination services by native bees were positively related to proportion of natural habitats (in terms of riparian forest, chaparral and oak woodlands) nearby the farm. In fact, the proportion of natural habitat was the only factor found to have an influence on native bee abundance; farm type, insecticide usage, field sizes and honey bee abundance were not found to have an influence (Kremen et al. 2004). There are additional studies from the Mediterranean biome in California that has found bee-pollinators of various crops to be

positively influenced by area of nearby chaparral and oak woodlands (natural habitats) (Kremen 2008). The effect of farming practices (organic vs. conventional), on the other hand, is often not found to affect the bees or at least to a much lesser extent than the amount of surrounding natural habitat (Kremen 2008).

Attempts have been made to evaluate how much natural habitats that actually is needed to ensure pollination of crops in agricultural landscapes. A study on bee abundance in canola fields, *Brassica napus*, from Alberta, Canada, found that bee abundance was greatest in fields that had more uncultivated land within 750 m from the field edges (Morandin & Winston 2006). By using the measured relationship between seed set and bee abundance a cost-benefit model for the system could be developed. This model showed that yields and profits could be maximized by allowing 30% of the surroundings to be uncultivated (Morandin & Winston 2006). The surrounding uncultivated land seems to consist mainly of aspen parklands. However, this 30 % suggestion was to maximize farmer yields, not bee abundance, which seems to increase with even more uncultivated surrounding land.

Even though one of the main causes of habitat fragmentation is clearing for agriculture, there are also other types of disturbances that can affect bee communities. Urbanization, for example, is also a process that could cause fragmentation of natural habitats. During the latest 80 years, the Tucson city in Arizona has expanded from 30 km² to 500 km². This urbanization has caused disruption in continuity between fragments of native desert shrubs, that earlier grew in a continuous desert (Cane et al. 2006). To see the effect of urban fragmentation on bees, bee visits to creosote bush, *Larrea tridentate*, which is known for its many bee species visitors, were recorded in different settings (Cane et al. 2006). Most species found in pristine desert habitats were also found in urban fragments. However, ground-nesting *L. tridentate* specialist species were fewer in smaller and older fragments (Cane et al. 2006). Contrary, cavity nesting bees were found to be positively affected by the fragmentation, maybe because of the diverse nesting supply a city could offer (Cane et al. 2006), that could be limiting in desert habitat. The authors conclude that bees' ecological traits, like their nesting and food demands and specialization, is the best predictor for bees responses to urban fragmentation (Cane et al. 2006).

Many studies of bees are carried out in agricultural landscapes, to connect bee abundance and richness to pollination of crops. This approach will more or less indirectly reveal habitats or structures important for bees. However, some studies do more directly address the question what is important for bees. In northwestern Indiana a study has been designed to investigate factors influencing bee distribution in an open-forest gradient (Grundel et al. 2010). Sites were classified into five different classes; open, savanna, woodland, scrub and forests. In these sites, different variables that could be valuable for bees were measured including possible bee nesting resources, floral resources, habitats structure, fire history and also the surrounding landscape composition (Grundel et al. 2010). Bee abundance, bee richness and bee composition were found to be influenced by different parameters. Bee abundance was negatively affected by canopy cover but positively affected by recent fire frequency; bee richness was positively affected by amount of dead woody vegetation and plant richness; and whole bee composition was related to plant richness, soil characteristics and canopy cover (Grundel et al. 2010). Proportionally more bees visiting open sites compared to forest sites where oligolectic bees (Grundel et al. 2010). This could explain the differences in bee community composition along the gradient (Grundel et al. 2010).

At first glance, it seems like the North American studies mentioned here differ substantially in some senses from each other. This may reflect the very diverse habitats found on the continent. Nevertheless, all of them indicate the same thing, even if the approaches differ in the studies; more heterogeneous landscapes will support more bee species to crop and in general. Sometimes fragmentation can lead to higher heterogeneity in a landscape providing new habitats for some bees (Cane et al. 2006; Winfree et al. 2007), in other cases fragmentation depletes and destroy the best habitats leading to a more homogeneous landscapes (Kremen et al. 2004; Morandin & Winston 2006). Many studies have also mentioned or shown the importance of knowing the bees' life-history and ecological traits since bee species will differ in their responses to the environment (Cane et al. 2006; Greenleaf & Kremen 2006a; Grundel et al. 2010) . Without this knowledge results could be difficult to interpret even in other places in the world.

Mediterranean region

“Bees appear to attain their greatest abundance, greatest numbers of species, and probably greatest numbers of genera and subgenera, not in the tropics, but in various warm-temperate, xeric regions of the world” (Michener 2007). Even though this has been difficult to prove, because of lack of documentation from all parts of the world, it seems like most studies and field experiences by experts point in favour of this statement (Michener 2007). An appropriate question to ask is why bee diversity is higher in these places. Even though there is not a definite answer to it, suggestions have been made. Due to the high diversity of many animals in the tropic, we would expect the tropics to also hold the highest bee diversity; however, this seems not to be the case. A suggested reason for lower bee diversity in the tropics is that the humid climate could facilitate fungal attacks in the bee-nests (Michener 2007). The yearly heavy rains could also be detrimental by flooding ground nesting bees’ nests. Other reasons suggested are for example that highly social bees like *Apis* and *Meliponini* bees has been very successful in the tropics to the detriment of solitary bees and that ant predation could be worse in tropical compared to temperate regions (Michener 2007). Michener has observed proportionally more oligolectic bees in the bee fauna in temperate compared to tropical regions, and that highest portion of oligolectic bees seems to be in the xeric regions of the world, at least in the Western Hemi-sphere (Michener 1954 in Michener 2007). Oligolectic and other solitary bees have sometimes very short adult flight seasons, synchronized with the time for flowering of their preferred plant (Michener 2007). Short flight seasons can give space and resources for more bee species resulting in a total higher species richness compared to places with more social and long-lived bees active throughout the flowering season.

In desert areas in Central Jordan rift valley in Israel both natural desert habitats and settlement gardens can be found (Gotlieb et al. 2011). The settlement gardens are a type of anthropogenic disturbance, they are irrigated and contains alien plant species blooming for an extended period compared to the native plants growing under nutrient and water poor conditions (Gotlieb et al. 2011). Altogether 81 bee species were found in the study and even though only a little more than one fourth (470 of 1778) of the bees were sampled in the desert habitat, there were more species compared to the settlement gardens (55 vs 50 species). Only 24 of the 81 bee species were sampled in both habitats, but note that 31 species were

singletons. Bees found in the desert habitat were mainly known from Middle East and North Africa, while most bees sampled in gardens had a more wide distribution (Gotlieb et al. 2011). Bee-plant networks differed between habitats with more generalized networks in gardens compared to desert habitats. No difference was found in the proportion plant- and ground-nesting bee species and the authors do therefore not think that there is a lack of nesting places (Gotlieb et al. 2011). In this type of habitat, anthropogenic disturbance like settlement gardens could actually add food resources instead of deplete it. More bees were found in the settlement gardens that contained larger amounts of flower resources during a longer time. However, proportionally fewer species were found in the gardens compared to the desert, especially rare or region specific species (Gotlieb et al. 2011).

In Mount Carmel National Reserve, Israel, foraging resources and nesting resources have been found to organize the bee community (Potts et al. 2003; Potts et al. 2005). Bee community structure and bee species richness has been found to relate to nectar resource diversity, floral diversity and post-fire age of the habitat (Potts et al. 2003). Bee communities were in addition dependent on floral abundance and the ratio of pollen to nectar energy. The abundance of the most common species were mainly linked to post-fire age, grazing intensity, and nesting substrate available (Potts et al. 2003). When more specifically addressing the impact of post-fire age of the habitat in relation to nesting resources available, the highest number of species was found in freshly burned sites (Potts et al. 2005). In mature sites that have not burned during the latest 55 years, species richness was lower compared to freshly burned sites and the lowest number of bee species was found in intermediated aged habitat (Potts et al. 2005). Bees with different nesting requirements differ to some extent in their responses. The nesting resources were linked to post fire aged, with more soil available in recently burned sites (Potts et al. 2005). Both the availability of bare ground and amount of cavities were found to affect the composition of the bee community (Potts et al. 2005). In addition, even though it did not affect the whole community model, stem nesting bees were most abundant in the 10-year post-fire habitats which included most suitable stems, and carpenter bees were found where most woody substrates occurred (Potts et al. 2005).

The importance of floral diversity, floral abundance, nectar energy availability and the diversity of nectar resources for structuring the bee community has also been found on

Lesvos, a Greek Island (Potts et al. 2006). Most bee species were found in “managed olive groves” followed by “mixed oak woodland”, “mature pine”, “freshly burned pine”, “intermediate age burned pine” and lastly “abandoned olive groves”. The habitat containing the highest bee diversity was also found to have the highest floral diversity. A more targeted in-depth study solely in olive groves on Lesvos, found that different sizes of bees were affected differently by landscape parameters and covers (Tscheulin et al. 2011). However, the abundance of all bees was positively correlated with the variable that was developed to include good bee habitats (for example amount of olive groves, phrygana and broad-leaved forest).

The studies from the Mediterranean region all show the importance of different structures for different bees. Bee abundance can be increased by more flowers during an extended period of time (Gotlieb et al. 2011); however, more flowers will not automatically increase the richness of bee species. Habitats that include both a high diversity of floral resources and nesting resources on the local scale, is most of the times inhabited by most bee species (Potts et al. 2003; Potts et al. 2006; Potts et al. 2005).

The tropics and subtropics

As mentioned in the previous section, experienced experts on bees have been surprised by the relatively low numbers of bees, both in species and abundance, found in the tropics compared to the warm-temperate regions (Michener 2007). However, the highly eu-social bees like Meliponini and Apini have been very successful in the tropics (Michener 2007). A reason for the success could be that most of them have evolved from nesting below to above ground, which seems to be beneficial in humid areas (Michener 2007). The tropics in America seems to be the richest tropical bee species area and could maybe in the future, when more surveys have been done, be found to have the same richness as warm-temperate regions (Michener 2007). However, the bee fauna from many countries in the tropics is relatively unknown and comparisons between regions are therefore difficult to do.

In the tropics and subtropics, many studies are focusing on bees’ response to degradation or fragmentation of forest and how bee communities change with isolation from the forests

(Blanche et al. 2006; Brosi et al. 2008; Klein et al. 2003a; Klein et al. 2002; Ricketts 2004). In fact, all studies included in this section are connected to forest habitats. There are many differences between temperate and tropical forests. Among others, two main differences are that tropical forests include much higher plant diversity and that a higher proportion of the plants, including trees, are animal pollinated (Ollerton et al. 2006; Ollerton et al. 2011). It has been estimated that as many as 98-99% of the flowering plant species in tropical lowland rain forests are animal pollinated (Bawa 1990). The proportion of animal-pollinated plants increases from temperate-zones to tropical communities, with proportions averaging 78% and 94%, respectively (Ollerton et al. 2011).

In the tropics it is possible to grow a lot of crops different from those in higher latitude areas; common cash crops are for example coffee and cacao. These are both perennial, shade loving plants that often are grown under shading trees; however, some varieties are grown in full sun. These kinds of system are called agroforests and differ quite a lot from the annual croplands in Europe. Different agroforestry systems differ in their intensity and thereby impact on forest; in some systems all trees are replaced by other more economically important trees and in others the native rainforest trees are preserved (Moguel & Toledo 1999).

Bees and especially bee diversity has in many studies been found to be negatively affected by isolation from tropical forest (Blanche et al. 2006; Hagen & Kraemer 2010; Klein 2009; Klein et al. 2003a; Klein et al. 2002; Ricketts 2004). This is sometimes also connected to higher fruit set close to forest (Blanche et al. 2006; Klein et al. 2003b). However, different bee groups are often found to be affected differently. The number and richness of social bees visiting coffee have been found to decline with increased distance from Indonesian old-growth rainforest (Klein et al. 2003a). Solitary bee richness and richness of all bee species merged together have been found to increase with less shaded conditions and with more blossoms (Klein et al. 2003a). An earlier study, concentrated on bee responses to land use intensity in coffee plantations found similar patterns (Klein et al. 2002). Abundance, not richness, of solitary bees increased with land-use intensity, while social bees, like the *Apis* and *Meliponini*, had the opposite pattern decreasing in abundance and also richness with increased land use intensity (Klein et al. 2002). Nesting sites for social bees were mostly

found in the less intensively managed forest systems, whereas nesting sites for solitary bees like vegetation free ground was found in the more intensively managed plantations (Klein et al. 2002). No significant relationship was found between number of plant species and bee species in this study (Klein et al. 2002). However, in a later study in Indonesian coffee and cacao agro-forestry systems species richness and abundance of bees were again negatively affected by increased forest distance but positively affected by available flower resources (Klein 2009). Proximate rainforest, bee species richness did vary less over time, giving more stable pollination services (Klein 2009).

In Costa Rica, eusocial meliponines and honey bees have, similar to Indonesia, been found to be the most common visitors to coffee (Ricketts 2004). In a gradient out from larger forest fragments (max distant 1.6 km), visitation rates by exotic honey bees to coffee were found to be constant, but honey bees increased in their proportion of all bee visits to coffee with forest distance (Ricketts 2004). Bee richness, overall visitation rate and pollen deposition were higher close to forest fragments, reflecting the native bees' limited distribution (Ricketts 2004). A study concentrating on the effect of forest fragmentation on bee communities, found similar patterns (Brosi et al. 2008). Although bee diversity and abundance were not affected by area or shape of different forest fragments, the composition of the bee community was (Brosi et al. 2008). Likewise, eusocial meliponines are highly connected to forest, and were found to be positively associated with larger forest fragments, smaller edge:area ratios and proportion of forest in the surroundings (Brosi et al. 2008). Honey bees on the other hand, had opposite responses. Pastures surveyed adjacent forest fragments were dominated by honey bees and lacked the orchid bees (euglossines) found in the near forest fragments and had a lower proportion meliponines (Brosi et al. 2008). Somewhat similar results have been found in Argentina, when the flower-visitor assemblage to two tree species (*Cercidium australe* and *Prosopis nigra*) was surveyed. The trees grew either in the forest or in fragments. The frequency of bee visits was not found to differ depending on whether the trees grew in forest fragment or continuous forest, but the species identity of visitors did (Aizen & Feinsinger 1994). The number of native visiting taxa decreased, whereas honey bees increased in abundance, from continuous forest to smallest fragment (Aizen & Feinsinger 1994).

Agricultural landscapes and forest edges in very heterogeneous flower rich landscapes, as in tropical forest-agriculture mosaic in Western Kenya can hold a higher abundance of bees than natural forest habitats (Hagen & Kraemer 2010) . The reason is presumably the less humid conditions and the high and diverse amount of food and nesting sites available in the forest edge and in the agricultural land compared to the forest (Hagen & Kraemer 2010). When honey bees were disregarded, the highest bee richness and abundance were found in the forest edge. The authors suggest that the forest edge and the heterogeneous agricultural land may support bee communities in the forest (Hagen & Kraemer 2010).

A synthesis of several studies investigating landscape effects on pollination services, found that both crop visitation rate and pollinator richness declines exponentially with distance from natural or semi-natural habitats (Ricketts et al. 2008). Interestingly, visitation rate decreases faster with distance in tropical regions compared to temperate regions (Ricketts et al. 2008). Additionally, social bee species were found to decrease faster with distance compared to solitary species (Ricketts et al. 2008). The reasons for these different bee responses between tropical and temperate regions may be many. However, when considering the earlier mentioned studies some general patterns may be found. In the tropics, especially in the tropical Americas, the eu-social Meliponines are common, dominating some habitats and are presumably the main pollinating groups for many native plants (Michener 2007). The Meliponines are mostly nesting in cavities and the nest is built by wax mixed with collected material found in the forest like resins and gums (Michener 2007). As found in some of the mentioned studies, Meliponines do not fly far from forest or forest fragments (Brosi et al. 2008; Ricketts 2004). When tropical social bees are compared to temperate social bees, the actual comparison, when honey bees are disregarded, will be between Meliponines and bumblebees (mentioned in Ricketts et al. 2008). Bumblebees are bigger, more mobile and do commonly build nests in rodent nests, bird nests or other cavities (Michener 2007). Bumblebee characters are better suitable for taking advantage of disturbed habitats like agricultural land compared to Meliponines characters.

Conclusions from mini review

From these studies carried out in different parts of the world, three general worldwide conclusions could be made. First, bee species richness and abundance seems to be highest in landscapes holding the highest heterogeneity (mentioned by Winfree et al. 2007). If the heterogeneity occurs naturally or is enhanced by anthropogenic disturbance, does not seem to matter. It is the total diversity of nesting and foraging resources that makes the difference. Second, wild native pollinators and honey bees are often not affected the same way by the surrounding landscape. Honey bees thrive in many disturbed habitats that many other bee species do not use and honey bees may to some degree compensate for the loss of other bee species. Third, bees' ecological and natural history is essential for understanding their distribution in a landscape and to make management plans (Greenleaf & Kremen 2006a). It is difficult to make good, general conclusion when bees differ substantially in their requirement and responses. Soil nesters will be affected more than cavity nesters if fields start to be tilled. Wood nesting bees will be more affected if all old trees are cut down. Although all bees' ecology are not known, some general knowledge about nesting requirement, floral preference and mobility should be thought through before making too general conclusions.



Figure 4. Even extremely fragmented and human used areas could significantly differ in their effect on bee populations. Compare agricultural land in southwestern Ethiopia (to the left) with southern Sweden (to the right). Photo: Ulrika Samnegård.

Do we need to have a diverse pollinator community? Will it affect the reproductive output of plants and crops?

The majority of higher plant species is directly dependent or get greatly enhanced pollination by insects, which either facilitates cross pollination or helps selfing by moving pollen within the flower (Klein et al. 2007). Since not even generalistic bees collect pollen from all types of flowers, a diversity of bees are needed to ensure pollination of a diverse plant community (Murray et al. 2009). Many plant populations (62–73%) are known to suffer from lower fruit and seed set if there is not enough pollinators, although this may vary markedly between sites and seasons (Potts et al. 2010). For example, in the Sichuan provinces in China, high amount of pesticides in apple and pear orchards, has destroyed the pollinator community; as a consequence, people need to hand pollinate their trees to ensure proper fruit set (Partap et al. 2001). Even plants that are not completely dependent on animal pollination are known to benefit from pollination in the form of higher fruit set (Larson and Barrett 2000; high-land coffee Klein *et al.* 2003; Klein *et al.* 2007; Mediterranean myrtle Gonzalez-Varo *et al.* 2009).

In many places honey bees have been and still are the most recognized pollinators. Orchard owners often rent bee hives when it is time for crop flowering to increase their yields. But since honey bee populations have markedly declined in many places, due to diseases, mites, pesticides among other things, people have realized that a system based solely on one species is very sensitive (Desneux et al. 2007; Martin 2001; Peng et al. 2011). In addition, it is well known that honey bees not always are the best pollinators for all crops and wild plants. Tomatoes, to give one example, will not release its pollen if the pollinator does not sonicates (buzz), and since honey bees do not perform sonic vibrations, another pollinator should be used. Most tomato plantations in greenhouses use bumblebees as pollinators instead. In wild plants like the native cactus, *Melocactus intortus*, in Puerto Rico, honey bees have been found to only be one fourth as effective pollinator of the plant compared to the native hummingbird *Anthracothorax dominicus* (Fagua & Ackerman 2011). Likewise, in habitats where honey bees are dominating the bee community, solitary bee species have been found to be the primary pollinators, contributing disproportionately more to the pollination services compared to honey bees (Potts et al. 2006). A recent study has actually found indications of that increased abundance of honey bees can affect coffee fruit production negatively (Badano & Vergara 2011).

The pollination services we receive from wild pollinators are free of charge in contrast to rented bee hives. If the surroundings of crop fields can be managed to support a diverse and rich pollinator community, beehives may not be needed or at least to a lesser extent (Isaacs & Kirk 2010). Honey bee abundance can vary substantially between years, while wild bees have been found to deliver more stable services. Coffee in Costa Rica received more wild bee visits when the honey bee population was low, compensating to some extent for the fewer honey bees, at least in sites close to forest (Ricketts 2004)

A rich pollinator community, with a high functional diversity makes the pollination more efficient and supports a higher diversity of plant species (Fontaine et al 2006). The variation in bees' morphology i.e. differences in size, hairiness, and tongue length, makes different bee species more or less specialized for different kinds of flower types. Bees will therefore differ in their pollination ability between different flowers. In other words, different species of pollinators can complement each other. A diverse pollination community could moreover increase seed set in single plants by complement each other with different within-flower and foraging behaviours (Hoehn et al. 2008). Both in Indonesia and Mexico, *Coffea arabica* has been found to increase fruit set with higher diversity, not abundance, of flower-visiting taxa (Badano & Vergara 2011; Klein et al. 2003a). Even a single visit from a rare solitary bee species led to higher fruit set compared to visits from common social species (Klein et al. 2003a). Even if honey bees in many cases are good pollinators, it has been shown that the presence of other bees can increase the effectiveness of honey bees since they get disturbed and therefore move more frequently between flowers (Greenleaf & Kremen 2006b).

Even though most studies find positive effects of bee visits on plant reproductive success, there are exceptions. Sometimes only a weak correlation is found between visitation rate and seed set (Steffan-Dewenter et al. 2001) and sometime a negative correlation for some bee families are found (Franzén & Larsson 2009). Clearly, all relationships between plants and bees are not mutualistic (Franzén & Larsson 2009; Lau & Galloway 2004; Thomson & Goodell 2001). Some pollen foraging bees have a low pollen deposition rate on the stigmas but a high pollen removal rate from the flower, resulting in less pollen left in the system for more efficient pollinators (Thomson and Goodell 2001). Some small bees can collect pollen and nectar without touching the stigmata, hence they do not pollinate (Michener 2007).

Moreover, some species of *Bombus* and *Xylocopa* and also honey bees can rob flowers of their nectar by open the sides of tubular flowers, without touching the anthers, making the flower less attractive for other pollinators (Michener 2007). Bees with parasitic lifestyles (social and cleptoparasitism) are often quite hairless, lack pollen collecting structures, and will therefore only disperse the pollen that happens to get stuck on them (Michener 2007). However, if parasitic bees are found, their hosts must be available, and their host is certainly a pollen collecting species. Although all bees differ in their pollination efficiency depending on morphology and behaviour; bees are generally very good pollinators and a diverse bee community is in many cases essential to maintain pollination services of wild flowers and many crops.

What about the landscape scale?

Because of the essential services bees provides for humans, in terms of pollination of crops and wild flowers, improvement of bee resources in highly intensified agricultural habitat is a hot topic to combat further pollinator declines. To do good conservation measures, knowledge about how bees perceive and use the landscape is important to perform actions on an appropriate scale. The knowledge is also needed to be able to estimate how far from a bee-rich area pollination services can be expected. Since bees differ in their mobility, different bees can find and utilize resources at different spatial scales (Greenleaf et al. 2007; Hirsch et al. 2003; Steffan-Dewenter et al. 2001). Body size and foraging distance is often correlated and larger bees are expected to have a disproportionately larger foraging range than smaller bees (Greenleaf et al. 2007). A recent study on three solitary bee species foraging distance (*Hylaeus punctulatissimus*, *Chelostoma rapunculi* and *Hoplitis adunca*) found that many bees' maximum foraging distance probably has been underestimated in earlier studies (Zurbuchen et al. 2010). Bees from the three species were found to be able to fly 1100 m, 1275 m and 1400 m from their nest respectively. However, most individuals did not cover that maximum distance; 50% of *H. punctulatissimus* and *H. adunca* did not forage further than 100-225 m and 300 m respectively from their nests. Depending on method used for estimation of foraging distance, results differ and could either be over or underestimated (Zurbuchen et al. 2010). The common honey bee has with mark and recapture techniques been found to have a foraging distance of approximately 1000 m (Gary et al. 1972).

However, when interpreting honey bees waggle dance (a dance that tells other workers where food can be found); it seems like honey bees are able to forage up to 14,000 m away from their nest (Beekman & Ratnieks 2000). Big carpenter bees from the species *Xylocopa flavorufa* have been marked with radio-transmitters, and were found to forage up to 6040 m from their nests, but most flight distances were shorter than 1000 m (Pasquet et al. 2008). Nevertheless, even if many bees can cover long distances, flying imposes energy and exposing costs for the bee and foraging close to the nest is presumably most desirable. This is indicated by Williams and Kremens study (2007) that found that females of *Osmia lignaria* in nests close to natural habitat produced enough offspring to replace themselves independent of the local management practice. However, *O. lignaria* nesting on conventional farms far from natural habitats, could not rear enough offspring to guarantee the same population size next year. Likewise, *Megachile rotundata* females have been found to produce more and heavier offspring if nests are placed close to their foraging site (alfalfa fields) compared to 150 m away (Peterson & Roitberg 2006). In addition, females produced proportionally more daughters when nesting near foraging sites. Since daughters are larger than sons, the female are required to gather more food for her daughters development than for her sons (Peterson & Roitberg 2006).

In many landscape studies, the proportion of “good bee habitats” in different radii is tested against bee richness or abundance to evaluate at what spatial scale bees are affected. This is a more indirect measurement, but seems to give quite clear results on the spatial scale affecting different bee groups. Solitary bees have in a German study been found to only be affected by the landscape structure at small spatial scales whilst bumblebees were positively affected by the landscape structure at very large spatial scale (Steffan-Dewenter et al. 2001), presumably reflecting their foraging range. The larger proportion (~47%) of the variation in bee community composition in northwest Indiana, USA, was explained by environmental conditions like, soil organic matter, canopy cover and flowering plant richness within 150 m from the transects (Grundel et al. 2010).

Despite the ability of many bees to fly long distances, nesting sites and foraging sites should not be separated too much in the landscape. If long-term survival of different bee-populations should be ensured, bees need to have both foraging and nesting sites at a small local scale

even if they sometimes could fly longer distances. There are bees, especially social, generalist bee species like honey bees and some bumblebee species, that can utilize short time mass flowering crops and thereby do quite well in intensified agricultural landscape (Holzschuh et al. 2011; Knight et al. 2009). Unfortunately, it seems like mass flowering crop can attract pollinators from wild flowers that are flowering simultaneously, leading to lower seed set of wild flowers growing close to mass-flowering crop (eg. *Primula veris* Holzschuh et al. 2011). However, even if mass-flowering crops benefit some bee species, the short flowering period cannot without additional plants support rich and diverse pollinator communities (Garibaldi et al. 2011).

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