The impact of forest on pest damage, pollinators and pollination services in an Ethiopian agricultural landscape

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Abstract

The distribution of wild biodiversity in agroecosystems affect crop performance and yield in various ways. In this thesis I have studied the impact of wild biodiversity, in terms of trees and forest structures, on crop pests, pollinators and the pollination services provided in a heterogeneous landscape in southwestern Ethiopia.

Coffee, *Coffea arabica*, is a forest shrub native to Ethiopia and is grown in most wooded areas in the landscape where I conducted my studies. Wild coffee is still found in remote parts of the forests in the landscape. For my first paper, I surveyed pest damage on coffee in coffee forest sites, where some sites were situated in continuous forest and some in isolated forest patches. I found the variation in pest damage frequency to mainly be among coffee plants within a site, rather than among sites, which indicates the importance of local processes. However, some pests were clearly connected to the forest habitat, such as the olive baboon.

In my second study, I surveyed pollinators visiting coffee flowers across a gradient of shade-tree structures. I found the semi-wild honeybee to be the dominating flower visitor. The abundance of the honeybee was not related to shade-tree structures, but to amount of coffee flower resources in the site. On the other hand, other pollinators, which included other bee species and hoverflies, were positively affected by more shade trees in the site.

In my third study I investigated how the forest cover affected local bee communities in the agricultural landscape. Moreover, I investigated if this relationship differed between the dry and rainy season. The distribution of food resources for bees changes between the seasons, which may affect the bees. Most trees, fruit trees and coffee, which are patchy resources, flowers in the dry season, whereas most herbs and annual crops, which are more evenly spread resources, flowers during the rainy season. I found a clear turnover in bee species composition between the dry and rainy season, with more mobile species in the dry season. Increased forest cover in the surrounding landscape had a positive impact on bee abundance and species richness. However, the impact did not change between seasons.

In my fourth study I evaluated the pollination success and pollen limitation of a common oil crop in the landscape in relation to forest cover. I found severe pollen limitation across the landscape, which may be related to the observed low bee abundances. The pollen limitation was not related to surrounding forest cover.

In conclusion, I have found the forest and wooded habitats to impact several mobile animals and pathogens in our study landscape, which in turn affect people. However, there is large complexity in nature and general relationships between forest structures and all crop related organisms may be unlikely to find. Various species are dependent on different resources, at different spatial scales and are interacting with several other species. To develop management strategies for increased pollination services, for reduced pest damage or for conservation in the landscape, more species-specific knowledge is needed.

List of papers

This thesis is based on the following papers, referred to by their Roman numerals in the text:

I. Samnegård, U., Hambäck, P.A., Nemomissa, S., & Hylander, K. (2014). Local and regional variation in local frequency of multiple coffee pests across a mosaic landscape in *Coffea arabica*'s native range. *Biotropica*, 46: 276-284.
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II. Samnegård, U., Hambäck, P.A., Nemomissa, S., & Hylander, K. (2014). Dominance of the semi-wild honeybee as coffee pollinator across a gradient of shade-tree structure in Ethiopia. *Journal of Tropical Ecology*, 30: 401-408.
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III. Samnegård, U., Hambäck, P.A., Eardley, C., Nemomissa, S., & Hylander, K. (2015). Turnover in bee species composition and functional trait distributions between seasons in a tropical agricultural landscape. *Agriculture Ecosystems & Environment*, 211: 185-194.
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IV. Samnegård, U., Hambäck, P.A., Lemessa, D., Nemomissa, S., & Hylander, K. A heterogeneous landscape does not guarantee high crop pollination. *Submitted*

Paper **I** and **II** are reprinted with permission from the publishers Wiley (paper **I**) and Cambridge University Press (paper **II**).

Contents

Introduction

Background

The terrestrial biosphere has experienced major land-use changes during the latest centuries (Ellis *et al.* 2010). From being about 50% "wild" or "semi-wild" in year 1700 to domination by agricultural and settled anthropogenic biomes in the year 2000 (Ellis *et al.* 2010). The destruction and fragmentation of natural or semi-natural habitats has a major influence in determining which species that can survive and thrive in a landscape. The occupancy of species in habitat fragments depends on, for example, habitat size, edge effects, quality, isolation and connectivity to other patches with source populations (Ewers *et al.* 2007; Hanski 1994, 1999; Prugh *et al.* 2008). However, the quality and composition of the converted land, i.e. the matrix, between habitat fragments is also important (Prugh *et al.* 2008; Tscharntke *et al.* 2012; Watling *et al.* 2011). The matrix may facilitate the movement of organisms between fragments and some organisms may also spillover and persist in the matrix (Tscharntke *et al.* 2012). Moreover, some species may utilize resources found in areas of different land use, e.g. both fragments and the matrix, so called "landscape complementation" (Dunning *et al.* 1992). For example, some bats and bee species roost or build nests in forest trees, but forage in more open, altered land (Ethier & Fahrig 2011; Klein *et al.* 2003b). The presence of high quality habitat can therefore have a positive influence on species occurrence and abundance found in the landscape surrounding the fragment, such as in farmland.

In agro-ecosystems, the distribution and abundances of species are affecting agricultural yields and other agro-ecosystem functions in many ways. Therefore, the habitat composition and configuration of the landscape – which are both most often driven by anthropogenic activity – have large impact on local farmers. Service-providing organisms, such as pollinators and natural enemies of crop pests, often disperse from natural and semi-natural habitats into farmland, which may increase yields (Bianchi *et al.* 2006; Garibaldi *et al.* 2011b; Macfadyen *et al.* 2015; Ricketts *et al.* 2008). However, natural or semi-natural habitats could also be sources of disservice-providing organisms like weeds, pathogens and pests (Lavandero *et al.* 2006; Lemessa *et al.* 2013; Zhang *et al.* 2007). Besides presence of natural and semi-natural habitats, the agricultural management practice influences species distributions (Hendrickx *et al.* 2007; Rundlöf *et al.* 2008). The large-scale intensification of farmland,

which started in the middle of the 20th century, with for example larger field sizes, removal of non-cropped areas and high agrochemical input, has caused major decline in farmland biodiversity (Benton *et al.* 2003; Tilman *et al.* 2001; Tscharntke *et al.* 2005). The decline in biodiversity affects humanity in many ways (Cardinale *et al.* 2012). For example, the decline in service providing organism, such as pollinators, has raised concern about food security and stability of the food production, since many crops are pollinator-dependent (Klein *et al.* 2007; Kremen *et al.* 2002; Potts *et al.* 2010a; Steffan-Dewenter *et al.* 2005).

In the developed, temperate parts of the world, accumulating studies on species distributions, landscape ecology and ecosystem services (see Box 1) have increased our knowledge about the impact of management and landscape composition on service and disservice providing organisms in agricultural landscapes (Batáry *et al.* 2011; Bianchi *et al.* 2006; Potts *et al.* 2010a; Steffan-Dewenter *et al.* 2002; Tscharntke *et al.* 2012; Veres *et al.* 2013; Williams *et al.* 2010). There are still many knowledge gaps, but we can now roughly predict how species may respond to, for example, habitat loss and changes in the management practice. In contrast, comparably fewer studies have been done on similar topics in most parts of the tropics and sub-tropics. This lack of targeted studies, in combination with different species compositions, climate, and in many cases management practice, means that we know far less about what affects the distribution of service and disservice providing organisms in those parts of the world. The lack of research is especially pronounced in sub-Saharan Africa (Eardley *et al.* 2009). To address this knowledge gap, I have in my thesis investigated how different landscape parameters affect organisms important for agriculture in a heterogeneous landscape in southwestern Ethiopia.

Box 1. Ecosystem services
Ecosystem services are the free services that ecosystems provide to humans. Ecosystem services can be divided into different types; supporting, provisioning, regulating and cultural services. Supporting services involves soil formation, nutrient cycling and primary production. Provisioning services comprise the production of renewable resources such as food, fresh water, fuelwood, fiber, biochemical and genetic resources. Regulating services involve water purification, pollination and regulation of climate, diseases and water. Cultural services includes recreation and ecotourism, spiritual and religious values, aesthetic and cultural heritage. Key ecosystem services in agriculture are for example nutrient cycling, pest and disease regulation and pollination (http://www.fao.org).

Tropical Forest and coffee production

The forested areas of the world are steadily declining and have been converted to mainly crop or rangelands (Achard *et al.* 2002; Ellis *et al.* 2010). Tropical and sub-tropical forests hold high species richness, and many species are dependent on the forest habitat for survival (Schipper *et al.* 2008). There is a large pressure on the remaining forests in the tropics, and this poses a great threat to the remaining forest species (Schipper *et al.* 2008; Turner 1996). Coffee plantations in tropical or sub-tropical forests are one way of preserving and at the same time utilizing the forest instead of converting it to farmland (Hylander *et al.* 2013). Shaded coffee plantation has been suggested to function as a refuge for forest dependent biodiversity (Borkhataria *et al.* 2012; Perfecto *et al.* 2003; Perfecto *et al.* 1996). However, there are debates regarding their conservation values since the forests also get disturbed and degraded (Aerts *et al.* 2011; Hundera *et al.* 2013).

Coffea arabica, commonly called high-land coffee, is the most widely used and also the most valuable cultivated *Coffea* species (Figure 1). It has its origin in the understory of moist Afromontane forests in Ethiopia and is thus a shade-tolerant species (Anthony *et al.* 2001; Anthony *et al.* 2002). Today, improved varieties of *C. arabica* are grown in most tropical countries, and coffee is grown under many different management systems, ranging from cultivation of sun-coffee, without any shade, to rustic or semi-forest coffee systems where coffee is grown in forest habitats (Hundera *et al.* 2013; Moguel & Toledo 1999). In many regions, coffee is grown by small-holder farmers that get their main income from their coffee production. In Ethiopia alone, more than 15 million people are dependent on coffee production, directly or indirectly, for income generation (Labouisse *et al.* 2008). Coffee yield therefore affects the livelihood of many people. Among the many parameters that affect coffee yields, the pest levels and the pollination success are important contributors. Coffee is attacked by various pests, and since coffee contains a lot of toxins, like caffeine, pests of coffee are generally specialists that can cope with the toxins (Frischknecht *et al.* 1986). The main pests differ between regions, but for example the coffee berry borer (*Hypothenemus hampei*), coffee rust (*Hemileia vastatrix*) and blotch miners (*Leucoptera* spp.) are present in most coffee growing regions (Vandermeer *et al.* 2010). The levels of pest and pathogen damage vary not only with region, but also with management, landscape contexts and interacting species (Avelino *et al.* 2012; Soto-Pinto *et al.* 2002; Teodoro *et al.* 2009a; Teodoro *et al.* 2009b; Vandermeer *et al.* 2010).

In southwestern Ethiopia coffee is grown in different landscape settings. Coffee is found in isolated forest patches surrounded by open agricultural land, in homegardens (see more information regarding homegardens in the method section) and in the edge of continuous forest, which is the more natural habitat for *C. arabica*. Since coffee has its longest evolutionary history in continuous Afromontane forests, I expected coffee to be included in many inter-

Figure 1. *Coffee plants in bloom (top) and ripening coffee berries (bottom).*

actions with other organisms in this habitat. I also expected the pest damage levels to be lowest in the continuous forest since most natural enemies of the pests would be present in the original habitat of coffee. In the first chapter of this thesis (paper **I**), I investigated if and how the levels of pest damage change when coffee is grown isolated from its original habitat. Furthermore, I investigated edge, area and isolation effects on pest damage levels.

C. arabica is self-compatible, and the degree of pollinator-dependence appears to vary among different varieties and regions. However, coffee yield generally increases with animal pollination (Klein *et al.* 2003a, b; Roubik 2002; Veddeler *et al.* 2008). Social bees, especially honeybees but also stingless bees, are reported to be the most common visitors of coffee flowers in areas where coffee has been introduced (Figure 2) (Badano & Vergara 2011; Boreux *et al.* 2013; Klein *et al.* 2003b; Ricketts 2004; Roubik 2002; Vergara & Badano 2009). However, the effectiveness of honeybees as coffee pollinators is under debate, and other species may be more efficient pollinators of coffee (Badano & Vergara 2011; Klein *et al.* 2003b). Fruit set of coffee increases with higher species richness of flower visitors, probably since species complement each other or increase the pollination effectiveness through species interactions (Albrecht *et al.* 2012; Brittain *et al.* 2013). High species richness of flower visitors are associated with low-impact management systems (Vergara & Badano 2009), proximity to natural forests (social bees) and high light intensity (solitary bees) (Klein *et al.* 2002; Klein *et al.* 2003b; Ricketts 2004). In Ethiopia, not only *C. arabica* is native but also the honeybee, *Apis mellifera*. The region is interesting for investigating the main pollinators of *C. arabica* in its native setting. Moreover, my study region allows for surveys of pollinators under different management intensities. The shade-tree structures in the coffee areas ranges from forests with nearly intact canopy structure, to coffee shaded by only one or two species of shade trees. In the second chapter of this thesis (paper **II**), I surveyed coffee flower visitors on coffee grown under different shade-tree structures in southwestern Ethiopia.

Bees and crop pollination

Globally, the area of pollinator-dependent crops has increased disproportionately compared to other crops and the trend is more pronounced in the developing compared to the developed world (Aizen *et al.* 2008, 2009). Simultaneously, there are reports of declining bee populations, among both domesticated honeybees and wild bees (Burkle *et al.* 2013; Potts *et al.* 2010a; Potts *et al.* 2010b). Bees, as a taxonomic group, are considered to be the most effective pollinators of most crops, and consequently, concerns have arisen about a global pollinator crisis that may affect food security and stability of food production (Potts *et al.* 2010a; Steffan-Dewenter *et al.* 2005). Indeed, there are

indications for pollen limitation to lower the expected yield growth and to decrease the stability of the yield from pollinator-dependent crops (Garibaldi *et al.* 2011a). However, the warning of a global pollinator crisis has been questioned, partly because the available data on bee abundances and declines is heavily skewed towards certain taxonomic groups and geographical areas (Ghazoul 2005). Even though pollinator and pollination studies conducted in the developing world are accumulating, there are still large knowledge gaps in many regions, among them sub-Saharan Africa, where we know very little about the status and trends of most pollinators (Eardley *et al.* 2009).

In many agricultural landscapes, proximity to florally diverse natural or semi-natural habitats has a positive influence on richness of wild pollinators and visitation rate and fruit set of pollinator-dependent crops (Garibaldi *et al.* 2011b; Kremen 2008; Williams *et al.* 2010). Pollination services are also more stable close to natural or semi-natural habitats compared to more isolated areas (Garibaldi *et al.* 2011b). In addition to the amount of – and proximity to – natural or semi-natural habitat, the resources in the landscape, in terms of flower abundance, pollen abundance, nectar diversity and nesting sites, have a positive impact on the pollinators, and especially the bee community present (Grundel *et al.* 2010; Hagen & Kraemer 2010; Potts *et al.* 2004). Which habitats are important for the local pollinator community depends on the region and the species that occur there, as well as on the history of the landscape. For example in Europe, in which large parts of the land has been under cultivation for a long time, many species are adapted to the heterogeneous, low intensity managed farmland common before World War II. The historical conversion of forest into flower rich, low intensity managed grazing land may actually have been beneficial for many bees in temperate Europe where trees are mainly wind-pollinated (Michener 2007). Even though not fully "natural" in the traditional sense, the presence of semi-natural habitats, like semi-natural and calcareous grasslands, hedgerows, field margins and road verges, do have a positive effect on flora, invertebrates and birds in Europe (Benton *et al.* 2003; Steffan-Dewenter & Tscharntke 1999; Svensson *et al.* 2000; Öckinger & Smith 2007).

In the tropics, on the other hand, isolation from the forest habitat often has a negative effect on bee and bee diversity (Blanche *et al.* 2006; Hagen & Kraemer 2010; Klein 2009; Ricketts 2004), and higher fruit set has been found in crops closer to the forest (Blanche *et al.* 2006; Klein *et al.* 2003c). However, in some tropical areas, heterogeneous, flower rich agricultural landscapes may hold higher abundances of bees than natural forest habitats (Hagen & Kraemer 2010; Klein *et al.* 2003b). Bee species vary in their sensitivity to different anthropogenic disturbances, and their sensitivity is linked to various traits, like food preferences (generalists, specialists), size (foraging rang), nesting substrate (above ground or soil nesters), sociality etc. (Williams *et al.* 2010). Wild bees (females) may be more sensitive to their surroundings than other pollinators such as hoverflies are, since they are central place foragers and need to

return to their nests. Additionally, since bees vary in size, which is correlated with mobility, they perceive the landscape at different spatial scales (Greenleaf *et al.* 2007; Tscharntke *et al.* 2012). Small bees are affected by the landscape on smaller scales than large bees are, and each species must get its resources needs satisfied on its own specific scale (Steffan-Dewenter *et al.* 2002). In contrast to many wild pollinators, the honeybee, which is a very

Figure 2. *Pollinators in Ethiopia. A honeybee,* Apis mellifera, *visiting a coffee flower (top left). A colonized traditional bee hive (top right). A stingless bee,* Meliponula *sp., visiting rapeseed (middle left).* Lasioglossum *sp. visiting rapeseed (middle right).* Xylocopa *sp. visiting* Caesalpina decapetala *(bottom left). Resting* Xylocopa *sp. male (bottom right).*

mobile species, is less affected by distance to natural or semi-natural habitats, and can be abundant in disturbed habitats (Aizen & Feinsinger 1994; Brosi *et al.* 2008; Garibaldi *et al.* 2011b). Even though homogeneous, simplified landscapes hold few species, the species existing may reach high numbers (Ghazoul 2005; Kleijn *et al.* 2015). Hence, abundance and species richness are not always correlated.

Many solitary bees are connected to specific floral resources and are only active for a short time frame (Cane *et al.* 2006; Michener 2007). The species richness and abundance of bees may therefore not only vary spatially with the landscape structure and management, but also temporally with changes in the vegetation and food resources (Tylianakis *et al.* 2005). The amount and type of resources a habitat offers may change over a year; consequently the importance of that habitat for local bee abundance and diversity may also change. In southwestern Ethiopia, as in many other parts of the tropics, the changes in precipitation over the year have marked effects on the landscape, as well as on the distribution of floral resources (Figure 3). Most forest trees, fruit trees and many shrubs have their main flowering time during the dry season, whereas most annual crops and herbs have their main flowering time towards the end of the rainy season (Fichtl & Adi 1994). Consequently, the distribution of floral resources changes from patchy resources (flowering trees) to more evenly spread resources (herbs and crops). Many studies from the tropics have indicated the importance of nearby forest for bee diversity (Klein 2009; Ricketts 2004). However, few studies have addressed the possible temporal change of its impact. In the third chapter of this thesis (paper **III**) I surveyed the bee species community and bee traits in contrasting seasons to assess if the impact of forest cover on bee abundance, richness and composition changes between seasons. To further investigate if the forest cover may in turn affect local pollination success, I also conducted a manipulative pollination experiment on a common oil crop in the same sites as for the bee species community (paper **IV**).

Aim of the thesis

The main aim of this thesis was to study the impact of wild biodiversity, in terms of trees and forest structures, on crop pests, pollinators and the pollination services provided in a heterogeneous landscape in southwestern Ethiopia. Since coffee is a very important and valuable crop in the studied landscape I dedicated the first two chapters of my thesis (paper **I** and **II**) to studies of this perennial crop. I investigated how the level of pest damage on coffee was related to the specific setting the coffee plants was grown in, like the contrast edge vs interior habitat, the size of the forest habitat and the isolation from larger continuous forest, which is the natural habitat for coffee (paper **I**). Furthermore, I surveyed the pollinator community visiting coffee under different shade-tree structures, ranging from very simplified forests dominated by one shade-tree species, to multi-strata forests with a high diversity of shade-tree species (paper **II**). In the second part of the thesis I investigated the distribution of bees (paper **III**) and pollination services (paper **IV**) across the more open agricultural landscape. In two contrasting seasons, I surveyed the bee community in sites with varying amount of forest in the surroundings. I analyzed the relationships between the bee community, abundance and species richness and the spatial variation in forest cover. Finally, I investigated the possible temporal changes of these relationships (paper **III**). In a subset of the same sites, I experimentally evaluated the pollen limitation and pollination success of a common oil crop, in relation to both forest cover in the surrounding landscape and the local bee abundance and richness (paper **IV**).

Methods

Study area

All studies included in this thesis were conducted in Gera and Gomma Woreda, Jimma zone, in southwestern Ethiopia (7°40' - 7°56' N; 36°13' - 36°38' E, Figure 4) on altitudes between 1500 and 2100 m.asl. The landscape is heterogeneous and composed of a mixture of moist Afromontane forests, agricultural land, homegardens, grasslands, woodlots and wetlands. In the western part of the landscape, there are still some larger remnants of continuous forest, whereas the forests in the eastern part of the landscape are highly fragmented (Figure 4). The density of trees varies across the landscape and can sometimes be high even outside the larger forest remnants, for example in woodlots of Eucalyptus, shaded coffee stands, live fences (composed of different shrub and tree species) and homegardens (Ango *et al.* 2014). The annual precipitation varies between 1480 and 2150 mm per year (Ethiopian National Meteorological Service Agency, unpubl. document). Most rainfall is between June and September (rainy season) and the driest time is between December and February (dry season) (Figure 3). During and following the rainy season, the landscape is green and flourishing, with plenty of flowering herbs and a lot of food for the livestock. Most annual crops flower during and following the rainy season. In contrast, at the end of the dry season, the landscape is dusty, few herbs are flowering, and skinny cows are seen on the sometimes overgrazed grasslands. At this time, many trees and perennial crops, like coffee, have their main flowering time.

Coffee in Ethiopia

My study area is located in one of the main coffee-growing regions in Ethiopia. *C. arabica* has its origin in Ethiopian moist Afromontane forests and wild coffee plants are still found in the remote parts of the region's larger forests. The common coffee management in the region, as well as in other parts of Ethiopia, is to grow coffee under shade from trees. The most common coffee production systems in the study area are recognized as semi-forest or semi-plantation coffee, which one is depending on the forest management intensity and plant diversity (Hundera *et al.* 2013). Planted coffee is found in most wooded habitats; it is grown at the edges of continuous forest, in isolated

Figure 3. *The appearance of the landscape changes a lot between the dry (top) and the rainy season (bottom).*
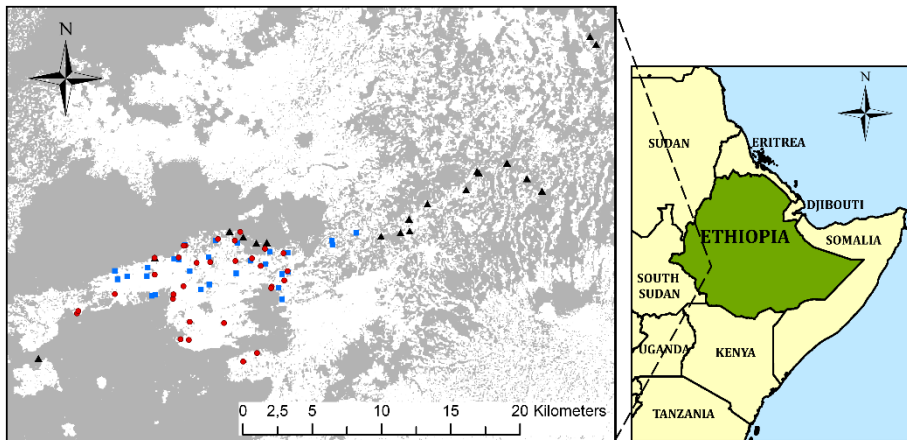
Figure 4. The landscape in southwestern Ethiopia where I conducted the field work for this thesis. The gray parts are wooded areas and the white parts are open land such as farmland, wetland and grasslands. The red dots are the position of the sites where I surveyed coffee pests (paper *I*), the black triangles indicate the sites where I surveyed coffee flower visitors (paper *II*), and the blue squares are the position of the homegardens where I surveyed bees with pan and vane traps (paper *III*) and grew rapeseed for evaluation of pollination services and pollen limitation (paper *IV*).

woodlots and in homegardens. *C. arabica* is the only *Coffea* species that occurs in this region and many varieties are bred from the wild ancestors found in the remote forests. The management of coffee is often organic without any chemical fertilizers or pesticides. Understory vegetation is repeatedly removed, mainly by hand, to reduce competition for the coffee plants and to facilitate picking of berries from the ground (Schmitt *et al.* 2010). Additional management such as irrigation and pruning of shade trees and coffee plants is uncommon. Instead, larger trees are removed and old or sick coffee plants are occasionally replaced with coffee seedlings. The coffee blooms after the first heavy rains in the mid of the dry season.

Homegardens and crops

In the study area, subsistence farming is the main land use outside the wooded habitats. Crops are grown either in homegardens or in open fields. Homegardens are the compounds of individual households where the family often rears livestock and grows vegetables, root crops, spices, fruit trees, coffee and other stimulant plants (Lemessa *et al.* 2013) (Figure 5). The homegardens as well as connected crop fields are often enclosed by live fences. Among the most common crops and fruits grown in homegardens are cabbage, coffee, avocado, enset (false banana), jackfruit, rapeseed, sugarcane,

taro and banana (Lemessa *et al.* 2013). Khat, which is another stimulant plant, is also commonly grown (Lemessa *et al.* 2013). In the larger fields, which are separated from the homegardens, the most common crops are teff, which is an indigenous cereal species, maize and wheat (Lemessa *et al.* 2013). The overall use of agro-chemicals is low.

Figure 5. *The compounds of individual households are called homegardens. Within the homegarden area the family often grow vegetables, root crops, spices, fruit trees, coffee and other stimulant plants and has livestock rearing.*

Field sampling

The data for paper **I**, **II** and **III** are based on inventory data whereas the data for paper **IV** are mainly from an experiment. All data was collected between September 2010 and November 2012.

Coffee pest damage across the landscape (Paper **I**)

To evaluate the effect of different forest habitat on coffee pest damage I selected 31 coffee sites, of which 10 were in continuous forest and 21 were in forest patches embedded within the agricultural landscape (Figure 4). Within each site I established an edge plot, 10 x 20 m, bordering the edge of the forest or forest patch. In sites with a diameter larger than 100 m, a second plot, was established 50 m towards the interior of the site. In each plot I surveyed pest damage on 90 leaves, divided among five plants. In addition I picked 40 ripe coffee berries that were checked for pests. I also asked the coffee owners if they had experienced any problems with mammal pests such as baboons. The forest patch areas and the distances between continuous forest and the forest patches were measured in Google Earth. With this setup, I could analyze if pest damage levels differed 1) between edge and interior habitats, 2) between continuous forest and forest patches and 3) depending on site area and isolation from its natural habitat, i.e. continuous forest.

Coffee flower visitors on coffee grown under different shade-tree structures (Paper **II**)

Before the onset of the coffee bloom in 2011, coffee sites that varied in shade tree structure were located. The location of very simplified coffee plantations, with mainly one or two shade tree species and relatively low shade provisioning were identified, as well as forest coffee sites with high and intermediate species richness of shade trees. I could not á priori determine which sites to visit since coffee is in bloom for a very short period (1–2 days) and I had a large area to cover and keep track of. Instead, I went to the sites that were flowering each day with the aim to visit as many sites as possible and to cover the full gradient of shade tree species diversity. In sites with flowering coffee, I established a 40 x 40 m plot where I counted number of trees and number of tree species and estimated the canopy cover, coffee flower abundance and other floral resources. Within the plot, three surveyors sampled all insects landing on coffee flowers in three 15-min trials. The sampling ended with 15 min catching of pollinators visiting other flowering plants. One site was visited before noon and one after noon. Altogether, I managed to visit 19 sites during the two events of coffee flowering (Figure 4). The different forest variables were correlated, and I therefore chose the variable with the longest gradient, which was the number of trees, to be included in my analyses. I also

developed a forest index, which included the measured and estimated forest variables, to ensure that I captured the shade-tree structural complexity. My three response variables; abundance of honeybees, other pollinators and surrounding pollinators (not on coffee), were analyzed separately in relation to the number of trees or forest index, coffee flower resources, other flower resources, time of the day and presence of beehives.

Bee community and pollination success in relation to surrounding forest cover (Paper **III** and **IV**)

To survey the bee community over seasons (paper **III**) and to evaluate pollination success and pollen limitation of a crop (paper **IV**), I established more permanent, protected sites. I cooperated with 28 homegarden owners, who let me rent land and place traps on their property. The homegardens were selected to cover a gradient with homegardens surrounded by low to high forest cover (Figure 4). In a hectare surrounding the central house of the homegarden I mapped the land-uses, identified and counted the trees and conducted flower surveys twice per season.

For the bee survey (paper **III**), I placed three pan traps, yellow, white and blue respectively, a couple of cm above the ground in protected fields and I hung two yellow vane traps in trees or on fences. The traps were continuously active for 67±6 days at the end of the dry season and for 86±1 days at the end of the rainy season. The traps were emptied three times per week, with the exception of the first month in the rainy season when the traps were emptied twice per week. All bees were identified to species or morphospecies (Eardley *et al.* 2010). I analyzed differences in bee composition, richness, abundance and traits between seasons and in relation to forest cover.

To evaluate pollination services and pollen limitation in the same homegardens as I surveyed bees, I planted rapeseed, *Brassica napus*, and applied three treatments to the plants; control, pollinator exclusion and pollen addition (paper **IV**). The rapeseed flowered at the end of the rainy season. Each treatment was applied to five plants per homegarden. The pollinator exclusion plants were covered with a mesh bag (tulle, mesh size: 1 x 1 mm) prior to flowering, and the bags stayed on the plant until harvest time. The pollen addition plants received extra pollen by hand two times per week, from when the first flowers opened, until all flowers had wilted. The control plants were left untouched. When all fruit capsules, also called siliques, on a plant were ripe, the plant was harvested. All fruit capsules were counted and ten randomly selected fruit capsules were individually harvested for separate length measure, seed count and seed weight. Due to crop failure and grazing, I could only harvest rapeseed in 23 of the 28 sites. The three treatments enabled us to analyze the pollination services (control compared to pollinator exclusion plants),

and the pollen limitation (pollinator exclusion compared to control plants) in the landscape and in relation to local and landscape variables.

Landscape classification

To investigate the impact of the surrounding land use on bee composition and pollination success for paper **III** and **IV**, I first classified a satellite image into three main classes: open area, forest and other wooded habitats (Figure 6). I chose to classify an area with a radius of 700 m around each homegarden, since this area covers the appropriate scale on which most bees perceive and interact with their environment (Steffan-Dewenter *et al.* 2002). The satellite image was a pan-sharpened high resolution [0.5m] big world view2 image taken in October-November 2011, projected in UTM WGS 84. I used the program ChorosLandCover 0.9.0.2 (Izolde and Choros Cognition Company 2012) to execute an unsupervised classification of the image. The advantage of this program is that it in addition to evaluating each pixel's own value, it also considers the values of surrounding pixels to recognize combinations of pixels. This facilitates the recognition of specific land-uses. However, when I compared the classified picture with the satellite image I found that the area of forest was underestimated. Therefore I designed a more generous forest variable, designated "wooded habitats", which included both forest and other wooded habitats (Figure 6). Since the land use in the nearest surroundings
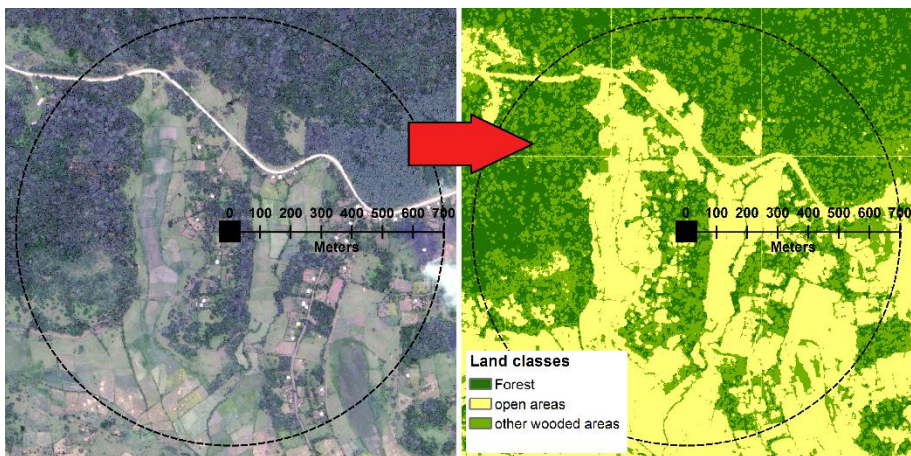

Figure 6. *An example of a satellite image that I classified using the program Choros-LandCover 0.9.0.2. Around each homegarden an area with a radius of 700 m was classified into three main classes: forest, open area and other wooded habitats. Since the variable "forest" was found to underestimate the real amount of forest, "other wooded habitats" and "forest" were merged into the more generous forest variable "wooded habitats". The square in the center of the image is the location of the homegarden.*

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probably has the largest impact on insects, I included weights together with the land-use variable. In this way I could give the land-uses in the nearest surroundings of the homegarden a larger impact in the analyses compared to land uses further away.

Results and Discussion

Overall results

The results from the studies included in this thesis suggest that several mobile animals and pathogens are affected by the amount, composition and configuration of forest and wooded habitats in our study area. However, I found no uniform response to forest, and the impact of forest structure and cover on surveyed organisms was generally weak. In the coffee pest study (paper **I**), I found each surveyed species to have specific responses to variation in local attributes. The only general result found, for the majority of the surveyed pest species, was that the variation in damage level was larger on the very local scale (within the plots) than on the regional scale (among plots). When it comes to coffee flower visitors (paper **II**), it was clear that "other pollinators", which included hoverflies and bees except for honeybees, were positively affected by more complex shade-tree structures (i.e. less management). On the other hand, the honeybee, which was the main coffee flower visitor, was not affected by the shade-tree structures. Bee abundance and richness in homegardens were positively affected, although weakly, by higher forest cover in the surroundings (circle with 700 m radius) (paper **III**). The positive impact of forest cover on bee abundance and richness did not result in higher pollination success of rapeseed in the more forested areas (paper **IV**). Instead, I found pollen limitation throughout the landscape.

Paper **I** – Coffee pests

The main insect coffee pests in my study landscape were a leaf skeletonizer (*Leucoplema dohertyi*), a blotch miner (*Leucoptera caffeine* / *L. Meyricki*), a serpentine miner (*Cryphiomystis aletreuta*) and fruit flies (Diptera: Tephritidae). Coffee leaf rust (*H. vastatrix*) was a wide-spread fungal pathogen. The pathogens coffee berry disease (*Colletotrichum kahawae*) and coffee wilt disease (*Fusarium xylarioides*) were also present, but due to unreliable identification their distributions in the landscape were not analyzed. The coffee growers also reported that olive baboons (*Papio anubis*) raid the coffee plantations when the berries are ripe. The main insect pests and the coffee leaf rust were found in the majority of the surveyed sites, i.e. in continuous forest as well as

in larger and smaller forest patches. I hypothesized that the level of pest damage on coffee would be lower in the continuous forest, which is the natural habitat of *C. arabica*. The long evolutionary history of coffee may also have resulted in more links in the food web including more natural enemies that protect the coffee. However, I found no such general pattern. Each surveyed species showed species-specific responses to environmental conditions and the variation in damage levels for the four leaf pests/pathogens was larger on the local scale (within the plots) than on the regional scale (among plots). The high within plot variation indicated the importance of local processes on pest damage. The aggregation of pest damage could be due to different mechanisms depending on species. For example, the spores from the coffee rust disperse with wind or water splashing, therefore, the risk of receiving spores is highest for leaves adjacent to already infected leaves (Rayner 1961; Waller 1982). Similarly, the leaf skeletonizer larvae feed externally on the leaves and can probably move between leaves and feed on several nearby leaves before pupation. Variation in local pest damage levels could also be affected by the distributions of the species that the pests interact with. In Latin America, ants have been found to protect the coffee plants on which they rear scale insects, which results in low pest damage from other pests (Philpott *et al.* 2008; Vandermeer *et al.* 2010). The impact of ants in coffee forests in Ethiopia is less studied. I conducted the pest damage survey during the rainy season. At that time, ant activity was low and I hardly saw any ants on the coffee plants. However, a survey conducted in the same landscape in the dry season, recorded lower pest damage on coffee growing less than 3 m away from trees with an ant nest compared to coffee plants 5 m away (Rudolphi *et al.* unpublished), indicating that ants may affect coffee pest damage also in Ethiopia. Since the lifespan of a coffee leaf may cover several seasons, the conditions during other parts of the year may impact the surveyed pest damage levels (Kushalappa & Eskes 1989).

Despite the high within plot variation, I did uncover certain regional patterns for the coffee pests. The frequency of coffee blotch miner on coffee leaves decreased with larger patch size and the occurrence of fruit flies in ripe coffee berries increased in sites closer to continuous forest. The baboons were clearly connected to the continuous forest habitat, as baboon visits were reported in all sites in the forest and in the vicinity of the forest, while sites > 400 m away from the forest edge rarely had any baboon visits. That is, some coffee pests, like the baboon and the fruit flies where more problematic on coffee in or closer to more "natural" conditions, whereas other pests, like the blotch miner had lower damage levels in larger patches (compared to smaller patches), which are similar to natural conditions.

Paper **II** – Coffee pollinators

The contradictory reports from areas where coffee has been introduced, about the effectiveness of honeybees as coffee pollinators, together with the observations of other bee species being more effective pollinators, raised my question whether the honeybee is the main pollinator of *C. arabica* also in its native range (Badano & Vergara 2011; Klein *et al.* 2003b; Roubik 2002; Vergara & Badano 2009). I can now confirm that the honeybee, *A. mellifera*, is the main day-time pollinator of *C. arabica* in its native range. The honeybee was the most common visitor in all surveyed sites, independent of shade-tree structures. The honeybee alone accounted for 96% of my collected specimens, which is an even higher proportion of the pollinator community than in surveys from the introduced range of coffee (Klein *et al.* 2003b; Ricketts 2004). My result seems robust since Berecha *et al.* (2015) found similar proportions of honeybees visiting coffee in the same study region. Additional to honeybees, I found six hoverfly species and 16 bee species that visited coffee flowers. The abundances of these other pollinators were low, but increased in sites with more complex shade-tree structures. However, honeybees were present even in the most complex sites. Even though I did not evaluate pollination effectiveness, the very low abundance of other pollinators suggest that they have low impact on the pollination of coffee.

The number of honeybees increased with the amount of coffee-flowering resources in the sites. Honeybees have the ability to recruit workers from their colony and are therefore very efficient users of mass-flowering crops like coffee (Jha & Vandermeer 2009; Krishnan *et al.* 2012; Veddeler *et al.* 2006). Since the honeybee is a very mobile species it can utilize resources several kilometers away from the nest and is not as dependent on nearby resources as many other tropical social bee species (Beekman & Ratnieks 2000; Brosi *et al.* 2007; Brosi *et al.* 2008). In the studied landscape the honeybees are provided with artificial nests in the form of traditional beehives, which are made from split logs where the core has been carved out (Figure 2; top right picture) (Ango *et al.* 2014). These traditional beehives are tied to branches in the canopy of larger trees and are colonized by semi-wild honeybees. Traditional beehives are normally established in the coffee areas before the coffee bloom. The reason for establishment at this specific time is not yet understood, but is probably due to that the beekeepers want to take advantage of the available nectar from either coffee or flowering forest trees like *Syzygium guineense* and *Schefflera abyssinica*. Either way, these beehives may facilitate the occurrence of honeybees on coffee flowers. However, in 2013, the coffee-bloom started unusually early, and there were very few traditional beehives in the coffee areas (personal observation). I observed surprisingly few insects visiting coffee, and the flowers stayed open for a much longer period than in the two years before. Such delayed flower senescence may indicate inadequate pollination (Oneill 1997). This observation supports my suggestion that other

pollinators have low impact on the pollination of coffee, but also raises question regarding where the honeybees are. Traditional beehives are not found in the landscape throughout the year, meaning that honeybees are, at some periods, dependent on the existence of "natural" nest sites. The forests in southwestern Ethiopia are continuously changing, with deforestation and simplification of coffee forests (Hundera *et al.* 2013; Hylander *et al.* 2013). Besides that other pollinators benefit from more complex forest structures, also semi-wild honeybees may be dependent on nesting sites and food resources from trees in the forests.

Paper **III** – Bee species composition and functional trait distributions

In the third chapter of this thesis (paper **III**), I investigated if the impact of forest cover on bee composition, abundance and richness changes between dry and rainy season. I hypothesized that if food resource availability is the main limiting factor for the bee abundance and richness, the impact of forest should be strongest in the dry season when most forest trees are flowering. In the rainy season flowering herbs are abundant, and more evenly spread across the landscape than food resources from trees. On the other hand, if the availability of above-ground nests is the main limiting resource, forests may be more important in the rainy season when the soils are wet. My collection of bees with pan and vane traps revealed a clear turnover in bee species composition between the dry and rainy seasons. The turnover in bee species composition between seasons was related to bee traits such as size and nesting preferences. The species richness of small bees was higher in the rainy season whereas big bee species had a tendency to be more abundant in the dry season (rarefaction of individual based species accumulation curves, EstimateS, Colwell (2013)). More bees were also trapped at tree height in the dry compared to the rainy season. Even though these findings indicate that the bee fauna may be adapted to scattered tree resources in the dry season (larger, mobile bees foraging at tree height), I did not find the bee species composition to be related to forest cover in any of the seasons. On the other hand, increased forest cover had a general, positive impact on bee abundance and richness, which is in accordance with some previous studies (Garibaldi *et al.* 2011b; Klein 2009), even though there are studies where no effect was found (Brosi *et al.* 2007). However, I found no interaction effect with season, which indicates that the impact of forest does not change over the year. Contrary to our hypothesis, I found more below compared to above ground nesters in the rainy season (rarefaction of individual-based accumulation curves). In the dry season the numbers of below- and above-ground nesters were similar. Thus, nest construction in soils

with high moisture may not be problematic for the bee species that occur in the area.

With this study I could not disentangle why forests are important to bees or what type of limiting resources they provide. Beyond food and nesting places, trees could provide other important resources, such as resins and wood, for nest construction in the soil (Michener 2007), which may be valuable in both dry and rainy seasons. The forest may also offer a more stable habitat, with less trampling and human disturbance (Williams *et al.* 2010). I did not find support for the hypothesis that the forest habitat varies in its importance for bees between seasons. However, my finding of a clear shift in species composition highlights that such a temporal variation might occur. Different species have different resource needs, and since both the bee species composition and flower resources in a habitat changes over the year, the importance of that habitat may also change (Persson & Smith 2013; Tylianakis *et al.* 2005). Pollination services to crops and wild plants are needed for an extended period of time, longer than the individual flight time for most solitary bee species. Therefore, not only spatial but also temporal variation in the pollinator community should be considered.

In general the catch rates in the traps were low, 0.084 and 0.035 bees per day and trap when honeybees were excluded (with honeybees included: 0.10 and 0.05) in the dry and rainy season respectively. This raised my concern about pollination services in the landscape, which I examined in paper **IV**.

Paper **IV** – Pollen limitation and low bee abundance

In correspondence to the findings from paper **III**, with higher bee abundance and richness in sites with high forest cover in the surrounding, I hypothesized in paper **IV** that also the pollination success and thereby relative yield would be higher in sites located in more forested surroundings. However, when evaluating my pollination experiment with rapeseed, I found severe pollen limitation across the whole landscape. Extra pollinated plants developed one more seed per fruit capsule and 88% more fruit capsules compared to control plants. In total, the seed set increased with 91% for the plants where the flowers had been hand-pollinated, compared to the control plants that were not hand-pollinated. In other words, the farmers could get a 91% yield increase if the pollination services were optimal. The plants where pollinators had been excluded developed similar number of seeds per fruit capsule and marginally more fruit capsules compared to the control plants. No interaction was found between treatment and the measured local and landscape variables, such as forest cover, flower abundance, area of annual crops or altitude. Thus pollen limitation, which is the difference in seed production between extra hand-pollinated plants and control plants, was not connected to any of these variables.

No significant relationship was found between pollen limitation and local bee abundance or richness.

The appearance of the landscape, with mixed land-uses, low management intensity and low input of agro-chemicals, indicates generally good bee habitats where pollination services could be expected to be high. This then raises the question of why pollination services are, in fact, lacking. There may be several explanations for this, for example, there could be a general lack of pollinators in the landscape, or the rapeseed plants are not attractive to the present pollinators. I found a weak negative relationship between local floral abundance and the seed set for rapeseed, which may suggest local competition between rapeseed and other co-flowering plants, or dilution of pollinators (Holzschuh *et al.* 2011; Veddeler *et al.* 2006). Other studies have found higher blossom cover and flowering plant diversity to instead increase pollinator species richness and frequency and stability of flower visits (Ebeling *et al.* 2008). However, the identity and the attractiveness of the co-flowering plants may affect the outcome (Ghazoul 2006). If the rapeseed flowers are not as rewarding as other co-flowering plants they may not attract enough pollinators.

While I cannot exclude that the pollen limitation in rapeseed occurs because it is unattractive to the local pollinators, my other data indicate low bee abundance in the landscape. Beyond high pollen limitation of rapeseed, the catch rate in my traps (paper **III**) was very low compared to other regions (eg. Kimoto *et al.* 2012; Kovacs-Hostyanszki *et al.* 2011; Westphal *et al.* 2008). Additionally, when I observed pollinators on coffee, the abundance of wild pollinators was very low, although the abundance of honeybees was sometimes high (paper **II**). Moreover, in a year with very few traditional beehives in the coffee forests at the time for coffee flowering, I observed extremely few individuals of both the wild and semi-wild pollinators on the coffee. Bees are present, and I have found quite high species richness, but the overall impression is that the abundance of bees is low. I do not know if bee abundance has decreased, similar to other areas, since there is a lack of long term monitoring of bees in my study landscape, as well as in other parts of sub-Saharan Africa (Eardley *et al.* 2009). A study conducted on Mount Kilimanjaro in northern Tanzania, found similar bee abundance levels on comparable altitudes which suggest that the elevation may affect bee abundance (Classen *et al.* 2015). Other possible negative factors could be presence of various predators and different types of anthropogenic disturbances. However, high pollen limitation seems not to be general in sub-Saharan Africa (Otieno *et al.* 2015; Otieno *et al.* 2011).

Conclusion and final remarks

The main objective for my thesis was to study the impact of wild biodiversity, in terms of trees and forest structures, on crop pests, pollinators and the pollination services provided in a heterogeneous landscape in southwestern Ethiopia. I found the amount, composition and configuration of the forest and wooded habitats to affect several mobile animals and pathogens in my study area. Many organisms are directly or indirectly important for the livelihood of local people, both in positive and negative ways, as for example pests on crops (direct negative effect), pest suppressors of crop pests (indirect positive effect) or pollinators of crops (direct positive effect). Since humans constantly affect the land-uses, humans also have a large impact on the distributions of mobile animals and pathogens. However, the results of this thesis demonstrate the complexity of the natural world and that straightforward relationships are rare. Habitats that are beneficial for some species may be unfavorable for others (paper **I**). And specific habitats could support populations of animals that provide services to humans but also support animals that provide disservices (paper **I** and **III**). To develop management strategies for increased pollination services, for reduced pest damage or for conservation of specific species in the landscape, more species-specific knowledge is needed. A search on "Web of Science" for the species causing the most widely found coffee leaf damage in the study area: the "coffee leaf skeletonizer" or its scientific name "*Leucoplema dohertyi*", showed zero records. If the basic ecology of the species is poorly understood, actions to successfully suppress or enhance a species will be impossible. Moreover, out of the 1206 bees collected in the homegardens for paper **III**, 1112 could not be given species identities, whereof 39 could not even be determined to genera by a taxonomic expert. The lack of species knowledge is problematic. When species identification is not possible, specimens are given a morphospecies name. Morphospecies are morphologically distinct species without a proper species identity e.g. "*Lasioglossum* A". These morphospecies are not comparable between studies, which results in the impossibility to evaluate trends and distributions of these species from the literature.

The studies included in this thesis are to a large extent basic research, investigating patterns of species distributions, which have provided a platform for new and better targeted questions. I have many more questions now than I had when I started my PhD-studies. There are two issues that stand out as especially puzzling. The first issue regards the semi-wild honeybees. They are

provided with traditional beehives during parts of the year, and these beehives seem to be colonized quite successfully. However, there are not always traditional bee-hives available in the landscape, and I have not observed more than a few "homeless" honeybee colonies. Where do they retreat? How important is the forest habitat for these semi-wild bees during periods when beehives are not available? My second question is broader and more troublesome. I have found strong indications for low bee abundances in parallel with low pollination success of rapeseed in the landscape I worked in. Why is it so? Is it common with low pollination successes for other pollinator-dependent crops, and in other parts of the year? Does the bee abundance vary between years and would I get the same low abundance if I used other surveillance methods? The areas of pollinator-dependent crops are expanding globally, and especially in the developing world (Aizen *et al.* 2008, 2009). Pollen limitation in these pollinator-dependent crops hinders yield growth and leads to global yield instability (Garibaldi *et al.* 2011a). To compensate for lower and fluctuating yields, more land is being converted to agricultural land (Garibaldi *et al.* 2011a). If the abundance of bees and other pollinators are low in many Afro-tropical landscapes, these landscapes may not be suitable for expansion of pollinator dependent-crops since high pollen limitation is then expected.

May it be possible to increase pollinator abundances in the study landscape? The main purpose of the traditional beehives, according to local beekeepers, is to collect honey, but would it be possible to use them in a way to increase pollination services in the landscape? Kleijn *et al.* (2015) recently reported that the majority of pollination services in agricultural landscapes are provided by a small subset of the pollinator species available. The dominant crop-visiting species are often common and relatively easy to enhance with simple conservation measures (Kleijn *et al.* 2015). The conservation measures evaluated in their study to enhance the dominant crop-visiting species; organic farming, planting of wild flowers and establishing grass margin strips, may not be as helpful in my focal landscape since most elements are already present. However, the identification of the dominant crop-visiting species and investigations of their ecologies may be the first step towards finding management strategies to increase pollination services in the landscape.

The forests contribute with many other services, and possible disservices, to local people than the ones I have addressed in this thesis. To address the whole impact of forest on local people all ecosystem services must be identified and evaluated (including supporting, provisioning, regulating and cultural services, Box 1). Identified key ecosystem services may be an argument for conserving the remaining forests. However, even without identified ecosystem services, the intrinsic value of primary forest should be a conservation argument on its own. The forest cover in southwestern Ethiopia has continuously been reduced and simplified during the last 40 year (Hylander *et al.* 2013). With an increasing human population in the area, the need to increase agricultural yields is obvious. An increases in production requires either more

land, i.e. further forest conversion, or higher yield per land unit. There is an urgent need for studies on how production can be increased without degrading the environment in Afro-tropical landscapes. In this thesis I have optimistic results which suggest that increased yields per land unit for pollinator-dependent crops is possible through increased pollination services. If applicable, this is an ecological intensification of crop production, which may increase yields without bringing negative environmental impacts (Bommarco *et al.* 2013).

Acknowledgement
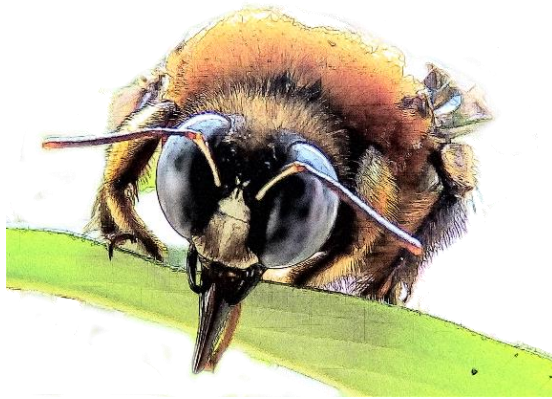
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Populärvetenskaplig sammanfattning

De senaste tre hundra åren har vår natur förändrats markant. År 1700 var mer än halva jordens isfria mark vild eller nästintill vild. I dag domineras den av jordbruksmark, betesmarker och städer. De stora omställningarna i markanvändning har påverkat växt- och djurlivet. Medan en del arter har anpassat sig till de nya markanvändningarna, så finns andra endast kvar i kvarlevor av tidigare livsmiljöer. Även hur vi brukar marken och vad vi odlar har inverkan på växer och djurs förekomst. Intensiteten i jordbruket har ökat avsevärt sedan 1950-talet. Större fält, monokulturer (fält med endast en växtart), konstgödsel, insekts- och växtgifter samt minskning och borttagande av icke-odlade områden (diken, vägrenar, stenmurar, alléer och åkerholmar) har lett till en tydlig minskning av växter och djur i dagens jordbruk. Studier har visat att mångfalden av olika djurgrupper påverkas av en kombinerad effekt av brukningssätt och mängden högkvalitativa livsmiljöer i jordbruksmark. Högkvalitativa livsmiljöer är kvarlevor av vild eller nästintill vild natur, eller andra livsmiljöer som innehåller mycket födoresurser och boplatser. Om det finns gott om högkvalitativa livsmiljöer i ett område kan arterna i detta område spridas till intilliggande miljöer, såsom jordbruksmark, och öka mångfalden – trots intensivt jordbruk. Där det saknas eller finns få högkvalitativa livsmiljöer är brukningssättet desto viktigare. Lågintensivt jordbruk, som vid ekologisk odling, har till exempel större positiv inverkan på lokal mångfald av växter och djur där det finns liten mängd högkvalitativa livsmiljöer. Hur långt från högkvalitativa livsmiljöer djur kan sprida sig beror på art och spridningsförmåga. En del arter drar även fördelar av närheten till olika typer av livsmiljöer. Exempelvis behöver vissa fladdermössarter träddungar att vila och sova i men söker gärna föda i öppna jordbruksmiljöer. Även vissa bi-arter behöver träd att bygga bo i medan de besöker öppna blomrika områden för att hitta mat i form av nektar och pollen.

Arters utbredningar påverkar människan på olika sätt; bland annat påverkar de vår matproduktion. I jordbruket finns djurarter som bidrar till ökade skördar och djurarter som bidrar till minskade skördar. Grödor kan exempelvis angripas av skadedjur, vilket kan leda till minskade skördar. Skadedjuren kan i sin tur bli angripna av andra djur. De djur som angriper skadedjur kallas naturliga fiender och kan vara fåglar, fladdermöss, insekter och spindlar eller parasitoider (insekter som lägger ägg i andra djur). De naturliga fienderna är nyttodjur som håller nere skadeangrepp på grödor. Andra viktiga nyttodjur i jordbruket är pollinatörer. Pollinatörer är djur, till exempel bin och

blomflugor, som sprider pollen mellan blomindivider och därmed bidrar till att växtens gener sprids. Spridningen av pollen bidrar även till högre fruktsättning hos pollinationskrävande grödor som tomat, gurka, äpple, hallon, kiwi, kakao, mandel och många fler. Studier har visat att en högre mångfald av pollinatörer leder till bättre pollination, eftersom olika arter då kompletterar varandra. Pollinatörer kan även störa varandra så de oftare byter blomma, vilket leder till effektivare pollinering. Dålig pollination leder inte bara till lägre skördar utan kan även leda till sämre kvalité på frukten eller fröerna. Det är alltså viktigt att det finns tillräckligt med pollinatörer då grödor blommar.

Både pollinatörer och naturliga fiender är nyttodjur som ofta gynnas av lågintensiv brukning och högkvalitativa livsmiljöer i jordbrukslandskapet. Intensifieringen av jordbruket har lett till utarmning av nyttodjuren på många håll i världen. Minskningen av pollinatörer har lett till oro över minskade och instabila skördar av pollinationskrävande grödor. Eftersom det är vi människor som brukar och påverkar markanvändningen har vi stor möjlighet att påverka vilka nytto- och skadedjur som finns – bara vi är medvetna om vilka faktorer som påverkar deras utbredning. Vad som påverkar utbredningen av en art beror delvis på vilken art den tillhör, hur landskapet sett ut tidigare och var i världen vi befinner oss. Högkvalitativa livsmiljöer i Europa förknippas ofta med naturbetesmarker medan högkvalitativa livsmiljöer i tropikerna ofta förknippas med skog. I den tempererade delen av världen, särskilt i Västeuropa och Nordamerika, har många utförliga studier lett till att vi i dag vet en hel del om vad som påverkar utbredningen av jordbruks-relaterade djur. I tropikerna däremot, och särskilt i tropiska Afrika, vet vi betydligt mindre. I den här avhandlingen har jag undersökt hur skog och andra landskapselement påverkar utbredningen av skadedjur och pollinatörer på kaffe (kapitel **I** och **II**) och utbredningen av bin (kapitel **III**) samt pollinatörstjänster (kapitel **IV**) i ett jordbrukslandskap i Etiopien.

Kaffe, *Coffea arabica*, kommer ursprungligen från Etiopien och förekommer vilt i de större skogarna i det landskap jag har studerat. I min första studie besökte jag kaffeodlingar i sammanhängande, större skogar samt odlingar i mindre isolerade dungar. Min hypotes var att skadenivåerna generellt skulle vara lägre i sammanhängande skog. Eftersom skogen är kaffets naturliga livsmiljö bör här finnas flest naturliga fiender som skyddar det. Jag fann att de flesta kaffeskadedjur fanns spridda i hela landskapet och påträffades i majoriteten av de 31 besökta kaffeodlingarna. De fanns både i sammanhängande skog och i skogsdungar av olika storlekar och avstånd från sammanhängande skog. Skadedjuren verkade alltså inte vara spridnings-begränsade i landskapet. Variationen i skadeangrepp var större mellan kaffeplantor inom en kaffeodling än mellan olika odlingar, vilket tyder på att lokala faktorer har större inverkan på skadenivåer än landskapsfaktorer. Jag hittade inget entydigt belägg för min hypotes. Istället fann jag att de olika skadedjursarterna påverkades av olika faktorer. Det gick inte att hitta en

generell förklarande variabel som förklarade skadenivåerna på kaffe för alla skadedjur. Vissa skadedjur, såsom babianer och fruktflugor, var i motsats till min hypotes knutna till sammanhängande skog. Medan svampen kafferost visade indikation på lägre nivåer inne i sammanhängande skog.

Kaffe odlas i olika system som skiljer sig åt i brukning. Kaffeplantorna odlas under skuggträd och i en del system är det endast en trädart som skuggar kaffet, medan i andra system är det lika stor mångfald av träd som i vild skog. Mängden skuggträd och antalet arter av träd indikerar hur intensivt kaffet är brukat. Färre träd tyder på en mer intensiv odling. I min andra studie undersökte jag hur pollinatörssamhället, bestående av bin och blomflugor, påverkades av odlingsintensitet, det vill säga mängden träd. Jag fann att honungsbiet var den absolut främsta pollinatören av kaffe och att den var opåverkad av skuggträden. Mängden honungsbin påverkades däremot av mängden kaffeblommor i odlingen. Tvärtemot honungsbiet så påverkades de övriga pollinatörerna, det vill säga blomflugor och alla bin förutom honungsbin, av skuggträden och ökade i antal med fler träd. Lågintensiva system med många skuggträd leder alltså till en högre mångfald av pollinatörer på kaffe men inte nödvändigtvis till ett ökat antal pollinatörer.

I min tredje och fjärde studie undersökte jag utbredningen av bin och pollinationstjänster i jordbrukslandskapet i förhållande till omgivande mängd skog eller trädtäckta ytor. Bin är kända för att vara väldigt effektiva pollinatörer av vilda växter och grödor och är därför en intressant och viktig grupp att studera. I tropiska studier har ofta närhet till skog positiv inverkan på mängden och mångfalden av bin. Tropisk skog erbjuder föda, boplatser och bomaterial. Floran i landskapet påverkas tydligt av nederbörden. Under torrperioden är landskapet dammigt och överbetat medan det under och efter regnperioden är grönskande och lummigt. Under torrperioden blommar många skogsträd och även fruktträd och kaffe, medan ettåriga grödor och många örter blommar under och efter regnperioden. Blommande träd har väldigt mycket blomresurser för bin men är spridda i landskapet, medan blommande örter har mindre resurser per växt men är mer jämnt fördelade över landskapet. Jag ville undersöka dels hur mängden trädtäckta ytor i omgivningen påverkade binas antal och mångfald samt undersöka om denna påverkan förändrades mellan säsonger i och med att födoresurserna förändras.

Jag fann att sammansättningen av biarter var olika under torr- och regnperioden. Fler små biarter var aktiva under regnperioden medan fler stora biarter var aktiva under torrperioden. Då stora bin är mer rörliga än små tyder detta på att fler långflygande arter var aktiva under torrperioden. En större andel av de aktiva bina under regnperioden var marklevande i jämförelse med de aktiva bina under torrperioden. Bin, både till antal och mångfald, påverkades positivt av mer trädtäckta ytor i omgivningen under både torr- och regnperioden. Således förändrades inte bins påverkan av trädtäcket mellan säsonger. Däremot tyder resultaten på att biarterna under torrperioden var rörligare (större) och därför också mer anpassade till spridda resurser.

När det kommer till pollinationstjänster kunde jag konstatera att de var otillräckliga i landskapet. Jag odlade rapsplantor som utsattes för olika pollinationsbehandlingar, där några plantor fick extra pollen på sina blommor, vissa blev täckta med nät för att utesluta pollinatörer och andra lämnades som kontroller. Plantor som fått extra pollen representerar plantor med optimal pollination. De visar hur mycket frukt optimalt pollinerade plantor producerar. Plantor täckta med nät visar hur mycket frukt en planta som ej blivit pollinerad producerar medan kontrollplantor visar hur mycket frukt en planta normalt producerar (under rådande omständigheter). Jag ville se om pollinationstjänsterna, i form av frö- och fruktsättningen, var relaterad till mängden bin och trädtäckta ytor i omgivningen. Jag såg generellt ingen skillnad i skörden mellan plantor där jag uteslutit pollinatörer och kontrollerna, vilket tyder på att pollinatörerna inte nämnvärt påverkarde skörden. Däremot dubblerades nästan skörden om jag hade tillsatt extra pollen för hand. Detta visar att skörden går att öka om mer pollen når blommorna, det vill säga om det finns fler insekter som pollinerar. Pollinationstjänsterna påverkades, till skillnad från binas antal och artrikedom, inte av omkringliggande mängd trädtäckta ytor. Jag fann att mängden bin i landskapet var generellt låg vilket kan förklara de otillräckliga pollinationtjänsterna. Detta var något förvånande då landskapet verkar vara rikt på högkvalitativa livsmiljöer med mycket födoresurser och boplatser för bin. I landskapet används inte heller gifter som dödar insekter i någon större utsträckning och jordbruket är både lågintensivt och småskaligt. Däremot är det möjligt att det finns många djur som äter bin och på så sätt håller nere binas antal. Bönderna och deras familjer skulle dra stora fördelar av ökade skördar, både hälsomässigt och ekonomiskt, därför är det viktigt att vi fortsätter att undersöka hur pollinationen i landskapet kan förbättras.

Sammantaget i denna avhandling har jag funnit att mängden, sammansättningen och den rumsliga fördelningen av skog eller trädtäckta ytor har påverkan på många jordbruksrelaterade organismer. Påverkan skiljer sig dock för olika arter och sambanden är inte alltid så starka. Naturen är komplex och komplexiteten är speciellt hög i tropikerna och därmed är tydliga, enkla samband sällsynta. Många arter påverkar varandra både direkt och indirekt via flertalet länkar. För att i framtiden kunna utveckla strategier och brukningssätt för att minska skadeangrepp och öka pollinationen av grödor, måste vi lära oss mer om enskilda arters ekologi och förhållande till andra arter.

Tack! Thank you! Galatooma! አመሰግናለሁ!

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