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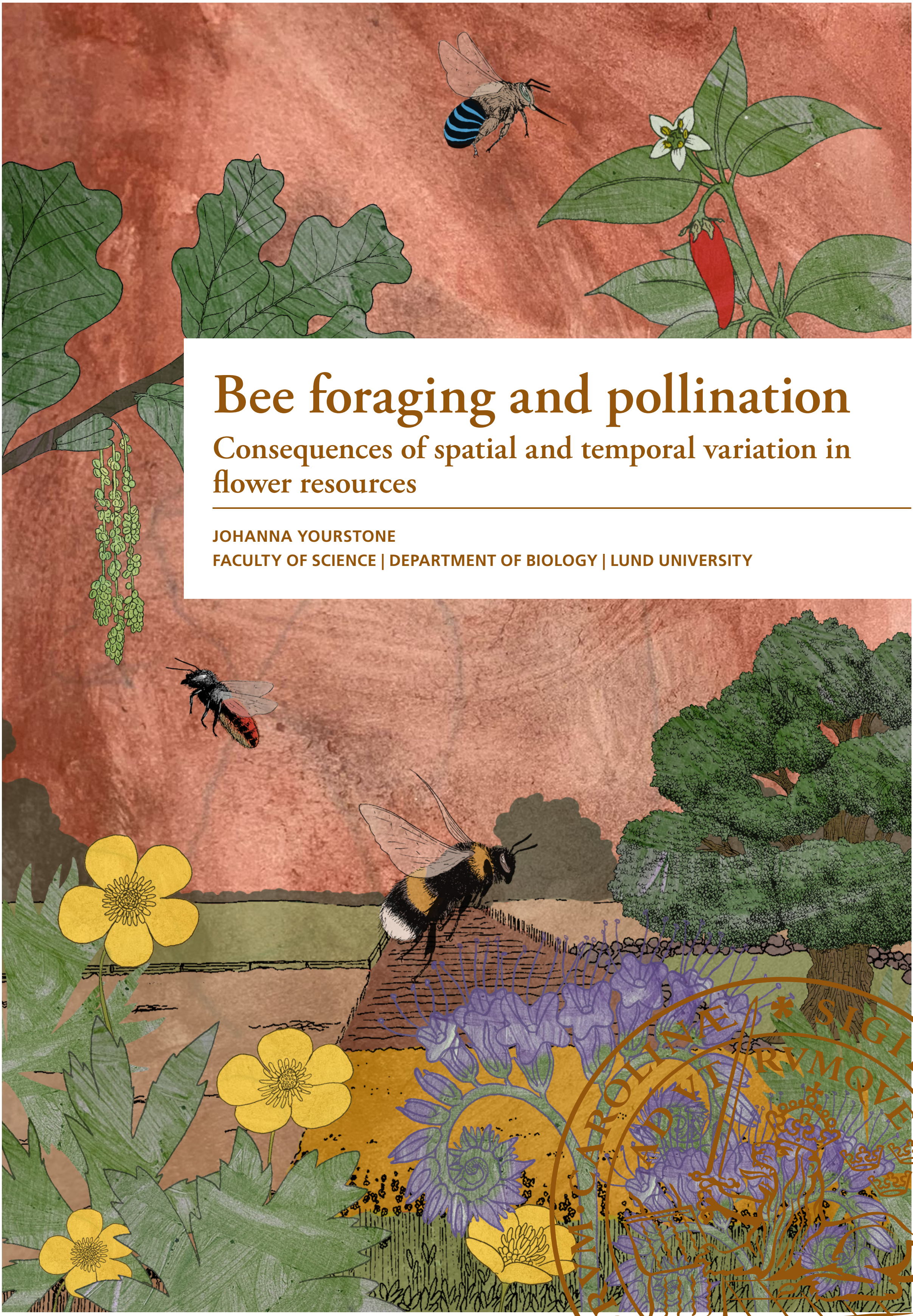

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Consequences of spatial and temporal variation in flower resources

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FACULTY OF SCIENCE | DEPARTMENT OF BIOLOGY | LUND UNIVERSITY

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Consequences of spatial and temporal variation in flower resources

Johanna Yourstone

LUND
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DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science, Lund University, to be publicly defended on 10 November at 09:00 in the Blue Hall, Department of Biology, Ecology building, Sölvegatan 37, Lund.

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Abstract:

Wild bees foraging in contemporary agricultural landscapes are, because of agricultural intensification, faced with the challenges of reduced flower-rich habitats, as well as a changed spatio-temporal distribution of flower resources. As a result of this and other stressors such as pesticide exposure, widespread declines of bees have been reported. However, all bees are not equally affected. To be able to mitigate bee declines and promote the important pollination services they provide to both crops and wild plants, it is crucial to understand why bees with different functional traits respond differently to varying resources in space and time, and how competitive interactions between bees modify these responses. Furthermore, it is important to study needs for crop pollination and pollinator deficiencies, especially in small-holder farming communities in the global south where the dependence on pollinated crops is great and the process of agricultural intensification often intense. In this thesis, I use replicated large scale landscape designs and experiments to investigate effects of varying flower resources and competition on bee foraging behaviour and fitness, and the effects of varying bee abundances on the pollination and pollen limitation of a crop. I found that multiple resources are important to bee fitness, not only forbs in seminatural habitats, but also crops and woody plant species, in particular highlighting the importance of trees as pollen resources for bees. The mentioned resources are both spatially and temporally spread-out, illustrating the importance of resource complementation in both space and time. I further found that bumblebees collected diversities of pollen during single foraging trips, and that although individual bumblebees show some degree of temporary preferences, these are temporary and change over time. This likely facilitates bee persistence in agricultural landscapes where resources may change swiftly. I found that it was possible to detect competition effects from honeybees by observing the foraging behaviour in bumblebees, which opens up new ways to study competition pressures on wild bees. Finally, I found that traits related to nesting rather than traits related to foraging determine bee communities in smallholder agricultural landscapes compared to adjacent forests, which suggests that bee communities in these agricultural landscapes may benefit from the enhancement of appropriate nesting habitats. This could benefit many crops, for example chili crops, which I show require pollinators for sufficient fruit set, although there was no evidence for pollinator deficiency in the area studied. Altogether, my thesis contributes increased knowledge on resource needs and behaviour in bees in contemporary agricultural temperate and tropical landscapes, which may inform more efficient policy actions for bee conservation.

Key words: Apoidea, bumblebees, foraging behavior, landscape ecology, land-use change, oilseed rape, trees, flower constancy, honeybee competition, functional traits, seminatural habitats, chili

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Till Malve och Lo

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Abstract

Wild bees foraging in contemporary agricultural landscapes are, because of agricultural intensification, faced with the challenges of reduced flower-rich habitats, as well as a changed spatio-temporal distribution of flower resources. As a result of this and other stressors such as pesticide exposure, widespread declines of bees have been reported. However, all bees are not equally affected. To be able to mitigate bee declines and promote the important pollination services they provide to both crops and wild plants, it is crucial to understand why bees with different functional traits respond differently to varying resources in space and time, and how competitive interactions between bees modify these responses. Furthermore, it is important to study needs for crop pollination and pollinator deficiencies, especially in small-holder farming communities in the global south where the dependence on pollinated crops is great and the process of agricultural intensification often intense. In this thesis, I use replicated large scale landscape designs and experiments to investigate effects of varying flower resources and competition on bee foraging behaviour and fitness, and the effects of varying bee abundances on the pollination and pollen limitation of a crop. I found that multiple resources are important to bee fitness, not only forbs in seminatural habitats, but also crops and woody plant species, in particular highlighting the importance of trees as pollen resources for bees. The mentioned resources are both spatially and temporally spread-out, illustrating the importance of resource complementation in both space and time. I further found that bumblebees collected diversities of pollen during single foraging trips, and that although individual bumblebees show some degree of temporary preferences, these are temporary and change over time. This likely facilitates bee persistence in agricultural landscapes where resources may change swiftly. I found that it was possible to detect competition effects from honeybees by observing the foraging behaviour in bumblebees, which opens up new ways to study competition pressures on wild bees. Finally, I found that traits related to nesting rather than traits related to foraging determine bee communities in smallholder agricultural landscapes compared to adjacent forests, which suggests that bee communities in these agricultural landscapes may benefit from the enhancement of appropriate nesting habitats. This could benefit many crops, for example chili crops, which I show require pollinators for sufficient fruit set, although there was no evidence for pollinator deficiency in the area studied. Altogether, my thesis contributes increased knowledge on resource needs and behaviour in bees in contemporary agricultural temperate and tropical landscapes, which may inform more efficient policy actions for bee conservation.

Populärvetenskaplig sammanfattning

Bin är en stor grupp insekter, kända för sin roll som pollinerare av både vilda växter och många jordbruksgrödor. Gemensamt för nästan alla bin är att de lever uteslutande på pollen och nektar från blommor som föda. Proteinrikt pollen ges framförallt till larverna, och energirik nektar äts framförallt av de vuxna bina. Trots det, så finns det en stor variation mellan olika arter av bin. Vissa bin söker sin föda bland flera olika typer av blommor, medan andra är mycket kräsna och håller sig till blommor av en viss art eller växtfamilj. Somliga bin kan flyga många kilometer för att leta mat, andra skulle aldrig flyga längre än hundra meter från sina bon, och storleksmässigt varierar de från två millimeter till mer än fyra centimeter i längd. Medan de stora kändisarna bland bina, honungsbina, lever sociala liv i stora kolonier, så lever majoriteten av världens cirka 20 000 arter bin solitära liv, eller som parasiter hos andra bin. Denna stora variation bland bina gör att de kan påverkas på många olika sätt när miljöer med blommor minskar i omfattning, och förändras i geografisk utbredning.

Processen att effektivisera jordbruket har lett till stora förändringar i jordbrukslandskapet, i hög grad i många tempererade områden, och i en varierande grad i tropiska områden. I Sverige har till exempel blomrika ängar och betesmarker försvunnit, fältkanter har blivit färre när fälten blivit större och kemisk gödning har gjort att exempelvis klövervallar ofta kan slås innan klövern blommat. Denna typ av förändringar i jordbrukslandskapet, ihop med till exempel en ökad exponering för bekämpningsmedel, är troliga huvudorsaker till de minskningar av bin som observerats på många platser i världen. För att kunna mildra pågående minskningar av bin så är det viktigt att förstå hur, och varför, bin med olika egenskaper reagerar på att utbudet av blommor varierar i rum och tid, och hur konkurrens mellan olika bin påverkar dem. Det är också viktigt att studera olika grödors behov av pollinering och om de lider brist på pollinerare, särskilt i tropiska områden med småskaligt jordbruk under förändring, där pollinerare är extra känsliga för brist på livsmiljöer.

Min avhandling kretsar kring hur vilda bins beteende när de söker föda, så kallat födosöksbeteende, och hur deras reproduktion påverkas av att mängden och utbudet av blommor varierar, samt när konkurrensen om blommorna ökar. Jag fokuserar också på hur viktiga bin och andra pollinerare är för en lokalt odlad gröda i södra Indien, och hur olika egenskaper hos bin påverkar deras utbredning i dessa varierande jordbrukslandskap och intilliggande skogar. Detta har jag undersökt genom storskaliga studier och experiment i jordbrukslandskap i både Skåne i södra Sverige, och Andhra Pradesh i södra Indien.

Mina studier visar att flera olika typer av blommor och miljöer, från blommande rapsfält, till träd och smörblommor, gynnade reproduktionen hos rödmurarbiet. Särskilt pollen från ek användes av biet, vilket är intressant eftersom ek är vindpollinerad och lätt förbises som en resurs för bin. Det visar också att ett och samma bi behöver resurser från flera olika miljöer, både vid en given tidpunkt och över tid, eftersom de flesta träd till stor del blommar före smörblommorna. Jag fann också att individer av mörk jordhumla visade vissa preferenser för vilka typer av pollen de samlade, även om de gärna samlade flera olika sorters pollen under en och samma runda, men dessa preferenser försvann och byttes ut över tid. Det här betyder att de förmodligen klarar av att byta preferenser relativt snabbt, vilket är viktigt i jordbrukslandskap där utbudet av blommor kan förändras mycket fort, som till exempel när ett rapsfält slutar blomma.

I en annan av mina studier var det möjligt att genom observationer av humlors födosöksbeteende se att de påverkades när mängden konkurrerande honungsbin ökade. När honungsbina var fler, så minskade förmodligen nektarnivåerna i blommorna i snabbare takt, vilket gjorde att humlorna minskade tiden de spenderade på blomställningarna. Det kan vara svårt att studera konkurrens mellan bin, så att observera födosöksbeteende skulle kunna utöka möjligheterna till forskning inom området. Detta är viktigt att göra när mängden honungsbikupor ökar, samtidigt som mängden blommor på många ställen minskar.

Slutligen, så visade mina studier i Indien att förekomsten av bin i jordbrukslandskap jämfört med närliggande halvöppna skogar förklarades av egenskaper som kan kopplas till var och hur de bygger sina bon. Detta resultat betyder att mängden miljöer som är lämpliga som boplatser är begränsande för olika arter i jordbrukslandskapet respektive skogen, och att åtgärder för att gynna bin i jordbrukslandskapet lämpligen bör inrikta sig på att identifiera och gynna boplatsmiljöer. Detta skulle kunna främja pollineringen av grödor, som till exempel chili som jag visar behöver pollinerare för bra fruktsättning. Även om jag också såg att just chili inte var begränsad av mängden pollinerare i studieområdet, så kan det vara viktigt ifall mängden pollinerare skulle minska, och det är möjligt att andra grödor har större eller mer specifika behov av pollinerare.

Sammantaget, så bidrar min avhandling med en ökad kunskap om behov av olika födoresurser för bin och om bins beteende i både tempererade och tropiska jordbrukslandskap. Detta kan bidra till utformandet av bättre åtgärder för att gynna bina och de viktiga ekosystemtjänster de utför som pollinerare.

List of Papers

Paper I

Yourstone, J., Karlsson, M., Klatt, B.K., Olsson, O., and Smith, H.G. (2021) Effects of crop and non-crop resources and competition: High importance of trees and oilseed rape for solitary bee reproduction. Biological Conservation 261, 109249.

Paper II

Yourstone, J., Varadarajan, V., and Olsson, O. (2023) Bumblebee flower constancy and pollen diversity over time. Behavioral Ecology 34, 602-612.

Paper III

Yourstone, J., Smith, H.G., Bommarco, R., Lindström, S., Lundin, O., Raderschall, C.A., and Olsson, O. Bumblebee foraging behaviour in response to varying resource levels and honeybee densities. *Manuscript.*

Paper IV

Yourstone, J., Erixon, F., Kelber, A., Somanathan, H., and Smith, H.G. IV. Trait-dependent responses of bees to local and landscape features in tropical agricultural drylands. *Manuscript.*

Paper V

Yourstone, J., Gunnarsson, J., Smith, H.G., and Somanathan, H. (2021) High dependency of chilli fruit set on wild pollinators in southern India. Journal of Pollination Ecology 28, 65-74.

Author's contribution to the papers

Paper I

All authors conceived the idea of the study; MK and JY collected the data; MK performed laboratory analyses; MK and JY analysed and visualised the data with help from BK; JY wrote the first draft with help from MK; all authors reviewed and contributed to the paper; OO and HGS acquired the funding.

Paper II

OO and JY conceived the idea of the study; JY collected the data with help from OO, OO and VV performed laboratory analyses with help from JY; OO and JY analysed and visualised the data; JY wrote the first draft; all authors reviewed and contributed to the paper; OO acquired the funding.

Paper III

OO and JY conceived the idea of the study; RB, SL, OL and CR designed the study system; JY collected the data; JY analysed and visualised the data with help from OO; JY wrote the first draft; all authors reviewed and contributed to the paper; all authors acquired the funding.

Paper IV

JY conceived the idea with help from FE, HGS and HS, FE and JY collected the data; JY analysed and visualised the data with help from FE; JY wrote the first draft; all authors reviewed and contributed to the paper; AK, HGS and HS acquired the funding.

Paper IV

JY conceived the idea with help from JG, HGS and HS; JG collected the data with help from JY; JY analysed and visualised the data with help from JG; JY wrote the first draft; all authors reviewed and contributed to the paper; HGS and HS acquired the funding.

Authors: Johanna Yourstone (JY), Melanie Karlsson (MK), Björn Klatt (BK), Ola Olsson (OO), Henrik G. Smith (HGS), Vidula Varadarajan (VV), Riccardo Bommarco (RB), Sandra Lindström (SL), Ola Lundin (OL), Chloé Raderschall (CR), Filippa Erixon (FE); Almut Kelber (AK); Hema Somanathan (HS); Josefin Gunnarsson (JG).

All authors in the list of papers have given their consent for the use of their work in the thesis.

Abbreviations

NDVI	Normalized Difference Vegetation Index
OSR	Oilseed rape
SNH	Seminatural habitats

Introduction

Bees are a diverse group of insects, famous for their role as pollinators of crops and wild plants as they forage. Some are picky in their food preferences and others are generalists. Some fly several kilometres away from their nests while others will not fly further than a hundred metres, and they vary in size from two millimetres to more than four centimetres long (Michener 2000, Greenleaf et al. 2007; Table 1). While some of the most well-known bees, the honeybees, live a social life in large colonies, most of the around 20,000 bee species found in the world live a solitary life or nest in aggregations, and yet others live their life parasitizing on other bee species (Michener 2000, Cardinal and Danforth 2011). Notwithstanding the diversity of traits exhibited by bees almost all share one: they are completely reliant on nectar and pollen from flowers for their diet, both as larvae and as adults (Michener 2000).

Flowers of different plants vary widely in shape, colour, and many other properties, which during 123 million years has given rise to the diversity of bees and their foraging strategies (Cardinal and Danforth 2013). Plants also vary naturally in prevalence in both space and time as environments and land-use types give prerequisites for different plant communities, and the timing of flowering varies with species specific phenology. Agriculture and animal husbandry has for thousands of years shaped landscapes in many parts of the world such as in the study regions of this thesis, Southern Sweden and Southern India (Emanuelsson 2002, Gupta 2004), and thus the plant and bee communities within them. However, a transformation of agriculture towards more intensive practices in the last centuries has dramatically reduced flower-rich habitats in many agricultural landscapes (Mueller et al. 2021), as well as altered the flowers' spatiotemporal occurrence. This, together with other side-effects of agriculture such as pesticide exposure (e.g. Rundlöf et al. 2015), is thought to be the main cause of declining bees (Brown and Paxton 2009, Goulson et al. 2015), which has been reported widely the last decades (e.g. Biesmeijer et al. 2006, Colla et al. 2012, Nieto et al. 2014, De Palma et al. 2017).

In this thesis, I use a mechanistic understanding of foraging behaviour to inform about bees' responses to human induced changes of flower distributions, and thus notify about problems and solutions to benefit bees in these landscapes. To this end I use landscape scale experiments and study fitness, foraging behaviour and trait-dependent effects in bees. Finally, I study the importance of pollination, the important side effect of bee foraging, for crop fruit set.

Bees in agricultural landscapes

Bees in temperate regions are mainly found in open areas, such as in agricultural landscapes that are kept open through grazing, mowing, and cultivation of crops. Agricultural landscapes can provide abundant flower resources in semi-natural grasslands, field borders, hedgerows, and inside fields in terms of flowering crops as well as weeds. In a mutualistic manner, bees and other pollinating insects play an important role in agriculture as they contribute to the pollination of about 75 % of the worlds' most common crops (Klein et al. 2007). However, in e.g. Sweden, more than 99% of the flower-rich unfertilized meadows and more than 70% of all types of managed grasslands have disappeared since the end of the 19th century (SwedishBoardofAgriculture 2011) and more efficient agricultural practices have reduced the amount of weeds as well as flower-rich field borders significantly in many regions (Robinson and Sutherland 2002, Mueller et al. 2021). As a result, flowers in these simplified landscapes are more sparsely and unevenly distributed (Baude et al. 2016) and nesting habitat for many bees is reduced and fragmented (cf. Everaars et al. 2018).

In modern, intensive agricultural landscapes, mass-flowering crops, such as oilseed rape and fruit trees, may constitute a large proportion of available flower recourses and could potentially compensate for the loss of wildflowers. Some bees are indeed benefitted by availability to oilseed rape (Westphal et al. 2003, Holzschuh et al. 2013, Diekötter et al. 2014), but e.g. social species with a long colony-cycle may not benefit as an initial flower boost does not compensate for a succeeding floral scarcity at the time of sexual reproduction (Westphal et al. 2009, cf. Schellhorn et al. 2015). Additionally, mass-flowering crops can attract bees and other pollinators away from other parts of the landscape (Holzschuh et al. 2016), reducing pollination of wildflowers (Holzschuh et al. 2011), which could reduce the occurrence of flower resources even more in the long run. Any potential benefit of mass-flowering crops is also affected by the spatial arrangement of crop fields. Because bees are central-place foragers and need to return to their nest after each foraging bout, they can only utilize resources within flight range from their nest (Olsson et al. 2008). To understand how bee communities are affected by mass-flowering crops, it is therefore important to investigate effects on bees with different foraging range, both before and after the crop's flowering period, as well as potential competitive interactions between bees that differ in mobility when one, but not the other, can reach the crop fields (see section on competition om page 23). This is something I undertake in **paper I**.

While landscape effects on bees have been widely studied in temperate agricultural landscapes (Senapathi et al. 2017), this has received less attention in tropical, especially dry, agricultural landscapes (Winfree et al. 2011), despite pollinators' comparably higher sensitivity to habitat loss in these areas (Ricketts et al. 2008). In many tropical agricultural areas small-holder farming is dominating (e.g. Samnegård et al. 2015, Basu et al. 2016, Sawe et al. 2020), which creates a landscape mosaic of different crop types bordered with seminatural vegetation, often interspersed with fallow and other seminatural habitats. This stands in stark contrast to the intensive agricultural landscapes in many temperate areas (Figure 1). However, e.g. in India, these diverse agricultural landscapes have also undergone changes both spatially and in intensity with mechanization, new high-yielding crops and chemical fertilizers (Tian et al. 2014). This has likely had negative effects on pollinators such as bees (cf. Basu et al. 2011). In particular, the usage of chemical pesticides has been shown to affect bees negatively (Basu et al. 2016, Steinhübel et al. 2022, Wenzel et al. 2022), and one study found negative effects of declining amount of fallow land (Basu et al. 2016), which can be seen as a measurement of landscape heterogeneity. However, improved knowledge about how bees are affected by landscape variation in tropical drylands is needed to accurately inform policy makers aiming to mitigate negative effects on bees of on-going agricultural intensification, as conclusions cannot be generalised from temperate ecosystems with different histories and ecologies (cf. Daam and Van den Brink 2010; Figure 1). To contribute to this knowledge was one of the goals of **paper IV**.

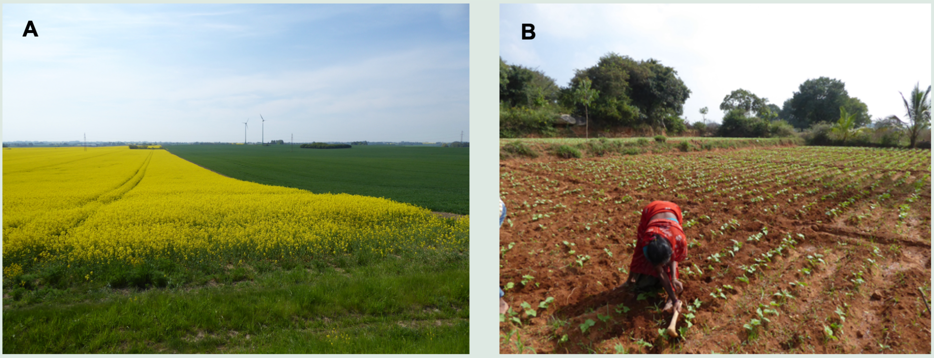


Figure 1. Photos of typical agricultural fields in temperate regions with high agricultural intensity (B; Sweden) and in tropical regions dominated by small-holder farming (B; India). In A) crop fields are large, there is very little or no seminatural vegetation between fields and the distance between different seminatural habitats is large, while in B) there is much seminatural vegetation between fields, and the small fields are interspersed with seminatural habitats.

Studying landscape effects

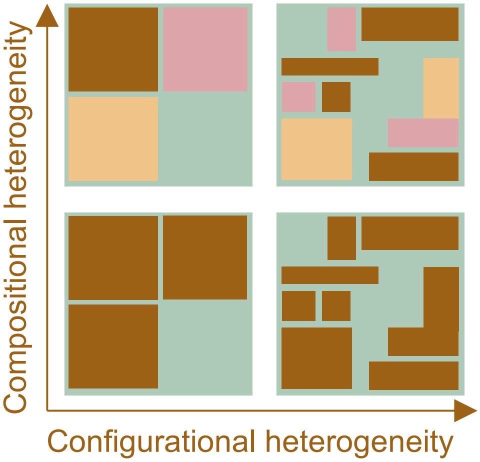


Figure 2. Landscape heterogeneity can be explained by both composition (Y-axis) and configuration (X-axis) of habitats. Adapted from Fahrig et al. (2011). The green areas represent seminatural habitats (SNH), that are particularly important to bees.

Agricultural change has resulted in loss of landscape heterogeneity (Benton et al. 2003). Such changes can be divided into changes in landscape *composition*, the amount and diversity of different habitat types, and *configuration*, the spatial arrangements of these habitats, such as connectivity between them (Fahrig et al. 2011, Jeanneret et al. 2021; Figure 1). These are two components of *landscape heterogeneity*, which can be measured as either, or both, of these components (depending on who defines it; Tonetti et al. 2023). While it is relatively straightforward to determine reductions in landscape heterogeneity over time by e.g. using historical maps and aerial photos (e.g. Skånes and Bunce 1997), only a few studies have been able to relate these to bee declines (e.g. Senapathi et al. 2015), as comparable historical bee data is largely lacking. Instead, the relation between bee performance and certain landscape characteristics can be studied spatially across replicated landscapes with different characteristics that are independent from each other. For example, this can be done by comparing bee data from "simple" landscapes (e.g. bottom left in Figure 2), with "complex" landscapes (e.g. top right in Figure 2), or using a gradient of landscape complexity. This approach, called space-for-time-distribution (Pickett 1989), relies on inferring causality based on correlative results with risks of an influence of confounding factors, which can be handled by careful design and analysis (Blüthgen et al. 2022). When investigating landscape effects on bees, seminatural habitats (SNH), including *e.g.* unfertilized old pastures and field borders, are often in focus and used as the measurement of either composition (SNH amount) or configuration (e.g. connectivity between SNH), as these are important to bees both in terms of flower and nesting resources. In **paper I**, **III**, and **IV**, we use SNH amount as the measurement of landscape heterogeneity. Additionally, we study the effect of landscape configuration, in terms of the distance to a mass-flowering crop, in **paper I**.

Trait-dependent bee responses to landscape change

While many bee species have declined in temperate homogenized landscapes, a few have expanded in range or increased their relative abundance over time (Bommarco et al. 2012, Powney et al. 2019, Herbertsson et al. 2021). Bees vary in an array of traits (Table 1), that may explain differing responses to changes in spatial and temporal distribution of resources. For example, long-tongued bumblebees in some areas have declined dramatically in relative abundance compared to short-tongued bumblebee species (Dupont et al. 2011, Bommarco et al. 2012). Long-tongued bees are specialised in foraging on flowers with long corolla tubes (Ranta and Lundberg 1980), i.e., the basal part of the flower where nectar is produced, while short-tongued bees are often foraging generalists. Many plants with long corolla tubes such as red clover and other legumes have declined in agricultural landscapes (Carvell et al. 2006, Scheper et al. 2014) as a result of grassland losses, higher fertilizer usage that makes it possible to mow clover leys before flowering and gives a benefit to fast-growing plants outcompeting more slow-growing plant species. Another example is that bumblebee species with long colony cycles and small colonies are more negatively affected by landscape simplification than their counterparts with short colony cycles and large colonies (Ekroos et al. 2013, Persson et al. 2015). A longer colony cycle or lifetime implies a higher sensitivity to temporal variations and shortages of resources and requires a higher degree of flexibility to cope with swift flower community turnovers (Schellhorn et al. 2015, Ogilvie and Forrest 2017). Among bumblebees, colony size is suggested to be correlated with foraging range (Goulson 2010), which means that species with smaller colonies might be more sensitive to spatial variations of flower resources. These examples have in common that they all relate to foraging, which is likely to be central in predicting bee responses to simplified landscapes because of the resulting spatiotemporal variations in flower resources (De Palma et al. 2015, Persson et al. 2015, Coutinho et al. 2018).

To be able to mitigate the negative effects of landscape change on bee populations it is important to understand the mechanism behind the different, often negative, responses to landscape changes. Even though numerous studies have investigated traits that link to functions, such as foraging distance or diet breadth, and how these modify the responses in bee communities (e.g. De Palma et al. 2015, Persson et al. 2015, Carrié et al. 2017, Öckinger et al. 2018), the generated results and conclusions are inconsistent (Bartomeus et al. 2017). This may be due to the fact that different mechanisms explain responses to different types of stressors, or because correlations between traits (see e.g. Williams et al. 2010, Carrié et al. 2017) may lead to inadequate conclusions on the mechanism of response. In **paper IV** I investigate trait-dependent effects on bees of varying amounts of seminatural vegetation in southern India, to contribute knowledge on the mechanisms that shape bee communities in tropical agricultural drylands under change.

Table 1. Bee traits and their explanations

Trait	Trait levels	Explanation
Size		Often measured as ITD, = Intertegular distance (distance between wing-nodes)
Foraging range		How far bees fly from their nest to forage, which may be estimated based on maxium homing distance, feeder training experiments, and colour marking experiments
Diet breadth	Polylectic	Wide diet, collect pollen from plant species from various families
	Oligolectic	Narrow diet, collect pollen from a single family/genus/species
Proboscis length		= Tongue length, often measured in mm, but in some literature divided categorically (*e.g.* short, medium, long)
Nesting elevation	Above-ground	*E.g.*in pre-existing cavities, excavated wood and carded grass
	Below-ground	*E.g.* soil tunnels, old rodent nests
Nesting substrate	Small cavitites	Nesting in pre-existing small cavities, e.g. in reeds, other hollow stems, and beetle exit holes in old wood
	Large cavities	Nesting in pre-existing cavities, *e.g.* old rodent nests, in hollow trees, or large cavitites in house walls etc.
	Ground	Species that excavate wood or ground
	Wood	Wood excavating species
Sociality	Social	Species that form colonies, with a queen that lays all eggs and normally sterile workers supporting the queen
	Facultatively social	Species that are sometimes solitary, and sometimes form small social colonies
	Solitary	Species where each female founds their own nest and care for the offspring them self
	Parasitic	*Social parasites:* Single females that invade colonies, kill or overrule the present queen, and use the worker force to bring up their own offspring *Cleptoparasites:* Species that lay their eggs in brood cells of host species, after which their offspring kills the host larvae and feed on its food
Flight season length		A measurement of how long period a year the species is on the wing, foraging
Season timing		Timing of active season on the wing, can be measured as activity start or median date of flight season

Bee foraging ecology

Bees forage on flowers to get carbohydrate-rich nectar for energy and some nutrients, and to get pollen essential for larval growth which contains protein, lipids, and various micronutrients (Vaudo et al. 2015). To be able to collect nectar and pollen from morphologically varying flowers, newly emerged bees that are naïve to their environment need to learn to manipulate and recognize rewarding flowers. While some specialised bees have innate abilities to recognize preferred flower species that they will stick to throughout their life (so called *oligolectic* bees), most species are more generalistic, with learned, shifting preferences (*polylectic* bees) (Cane and Sipes 2006). In order to recognize and remember good flower species, bees can use scent, colour and shape cues (Menzel and Erber 1978) and if more than one cue is available, decision making is aided (Gegear and Laverty 2005, Kulahci et al. 2008). The learning process of recognizing flowers based on the above-mentioned cues can happen as fast as after encountering one to five flowers of the same type (Dukas and Real 1991, Hammer and Menzel 1995) and learning to manipulate and forage efficiently on a new flower species takes about 30-100 flower visits depending on the flower's morphological complexity (Waser 1986).

The occurrence, identity and abundance of flowers vary over the year as the season and weather changes, and because different plants have different strategies of when to flower. Especially early in the spring, flowering trees and other woody plants may constitute a large proportion of many bees' diet (Bertrand et al. 2019, Brodschneider et al. 2019, Yourstone et al. 2021b), followed by a dietary domination of forbs (Bertrand et al. 2019).

When bees forage, they most often do so in a patchy environment because flower resources are in general unevenly distributed and often occur in more or less distinct patches of various size (Forman and Godron 1981). A patch can be defined at different scales, from very small to large: a single flower, an inflorescence, a flowering fruit tree or an entire field of e.g. oilseed rape are all examples of patches. Nesting bees are central-place foragers (Orians and Pearson 1979), which means that they have a fixed location (their nest) which they have to go back to after each foraging bout. How far they go from their nest to forage is species dependent, but is also dynamic and dependent on resource availability (Olsson et al. 2015).

Flower constancy

While foraging, a lot of information handling is taking place in short time; a bee flying over a pasture might process new information of observed flowers every tenth of a second, comparing it with its collected knowledge on known rewarding and unrewarding flowers, while making foraging decisions (Chittka et al. 1999b).

Foraging efficiency is generally higher when bees focus their foraging on a single common flower species, compared to when foraging on multiple equally rewarding species at the same time (Dukas and Real 1993a), in particular for social bees when resources are abundant (Gegear and Thomson 2004, Hayes and Grüter 2022). That individual bees focus their foraging on a single or few species at the time, even though they are generalists and other equally rewarding flowers are present, has intrigued researchers since Darwin's time (Darwin 1876, Grant 1950, Free 1963, 1970). The behaviour has been termed *foraging constancy* (Waser 1986). There is no consensus on the reasons behind flower constancy (Grüter and Ratnieks 2011), but it is likely linked to cognitive limitations and costs of sampling and learning alternative resources (Laverty 1994, Wilson and Stine 1996, Chittka et al. 1999a, Raine and Chittka 2007, Grüter and Ratnieks 2011).

Most studies on flower constancy have been done over short temporal scales, often in laboratory environments (e.g. Waser 1986, Dukas and Real 1993a, Austin et al. 2019, but see Martínez-Bauer et al. 2021). It is therefore not well-known if, and for how long, flower constancy lasts over time in nature. Life-long flower constancy in bumblebees has been observed in laboratory settings (Russell et al. 2017), and bumblebees as well as solitary bees have been shown to react with a delay of 0.5-1.5 days to declined resource levels in patches they returned to (Thomson 1981), indicating that flower constancy could hinder or delay the response of bees to changing flower resources. This could be especially suboptimal in intensive agricultural landscapes, where resource turnovers can be swift and dramatic, as in the case of ephemeral mass-flowering crops. The knowledge gap concerning whether flower constancy lasts over time and how it is affected by the presence of ephemeral mass-flowering crops is addressed in **paper II**.

Optimal foraging theory

Bees must constantly take decisions on when to leave a flower patch to move on to the next one, or to return to the nest. In order to maximize fitness these decisions should follow optimality models taking *e.g.* cost of transportation, search and lost opportunities elsewhere into account. *Optimal foraging theory* tries to explain patterns and mechanisms of foraging in mobile animals and is based on the assumption that animals, as a result of evolution, optimize their foraging behaviour to maximize fitness (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Brown 1988). Optimal foraging theory predicts that when food is scarce the animals will be less picky and consume more in each patch, while plentiful resources leads to a picky behaviour and a faster change between patches (Emlen 1966, MacArthur and Pianka 1966). As one of the pioneers within optimal foraging theory, Charnov (1976) focused on the missed opportunity cost, i.e. the value of all available alternatives (without considering costs of e.g. predation and metabolism). He defined the *Marginal value theorem*, predicting that when the intake rate in a patch has declined to the average intake rate for the overall habitat, an optimal forager should move on to another patch (Figure 3). The marginal value theorem assumes that the intake rate within patches decreases as a function of time spent in the patch, and it predicts that on an average intake rate curve the quitting harvest rate is found at the tangent of the average transfer time between patches (Figure 3). When the marginal value of the patch, i.e., the instantaneous intake rate, equals the opportunity cost, i.e., the net long-term intake rate in the environment, it is more beneficial for a mobile forager to move on to the next patch than to stay in the current one. The marginal intake rate at that point is called the quitting harvest rate. After Charnov (1976), Brown (1988) emphasised the metabolic and predation cost of foraging and formulated the point of optimal departure as the point in time when the “patch harvest rate is no longer greater than the sum of the metabolic, predation, and missed opportunity costs of foraging”, and modern versions of optimal foraging models describing central-place

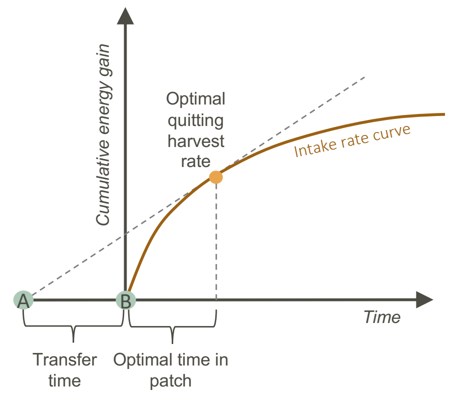


Figure 3. The marginal value theorem explained graphically. The optimal quitting harvest rate in a given enrvironment is found on the tangent of the intake rate curve when a straight line is drawn from the average transfer time between patches (A and B representing patches). The optimal time in an averge patch is marked out. However, the optimal time in a patch of higher or lower than average quality will be longer and shorter respectively, as the optimal quitting harvest rate in an environment is predicted to be constant and is reached later in a high-quality patch and sooner in a low-quality patch.

foragers also incorporate costs related to the homing distance, such as increased predation and foraging load costs (Olsson et al. 2008).

The question of how foraging bees know when they have reached the point of quitting harvest rate was early addressed by Hodges (1985) who investigated the *Threshold departure rule* in bumblebees (coined by Pyke 1978a). Low rewards trigger both departure from inflorescences and patches (Hodges 1985, Cresswell 1990), longer flight distances (Pyke 1978b, Dukas and Real 1993b), and change of plant species (Greggers and Menzel 1993, Chittka et al. 1997). Experimental evidence suggest that departure from a patch is based on integrated information assembled over the course of the foraging bout, and is thus not limited to a cue from a single flower (Kadmon and Shmida 1992, Lefebvre et al. 2007, Biernaskie et al. 2009). Both Kadmon and Shmida (1992) and Goulson (2010) saw that the departure from a patch of both solitary bees and a bumblebee could be well predicted by two succeeding low-rewarding flowers, and in one study integrated information from up to three succeeding flower visits contributed to the subsequent flight distance of a bumblebee (Dukas and Real 1993b).

In **paper III**, I use predictions from optimal foraging theory to investigate effects on bumblebees of nectar depletion and increased density of, and thus potential competition with, honeybees.

Competition for flower resources

Competition for resources is a key driver of organism community configuration and evolutionary processes, and is likely to play a role in certain bee declines and how bees respond to different environmental changes (Thomson and Page 2020). With diametrically altered agricultural landscapes leading to a changed spatiotemporal distribution of flower resources, it is important to understand how bee species with e.g. different dietary preferences and mobilities are affected by competition for resources. Not only by the competition for flowers occurring in lower amounts and with changed composition, but also how they are affected by competition for resources widely scattered in space, that might be reached by more mobile, but not by less mobile, species. As mentioned earlier, this is something that is tested in **paper I**.

Furthermore, competition from introduced or managed species such as honeybees may pose a contrived threat to wild bees with overlapping foraging preferences (Wojcik et al. 2018, Thomson and Page 2020, Iwasaki and Hogendoorn 2022), especially in ecosystems already degraded because of intensive agriculture (Herbertsson et al. 2016). Managed honeybee hives have increased significantly during the last half-century (Casanelles-Abella and Moretti 2022, Phiri et al. 2022), and several observational studies suggest that increases of honeybees affect bumblebees negatively (Forup and Memmott 2005, Sun et al. 2013, Thomson 2016, Nielsen et al. 2017). Additionally, there is some experimental evidence that experimentally increased honeybee density negatively affects local bumblebee abundance (Herbertsson et al. 2016, Wignall et al. 2020), as well as fitness (Thomson 2004, Bommarco et al. 2021). However, studies on the effect of honeybee competition on bees are not consistent (Mallinger et al. 2017, Iwasaki and Hogendoorn 2022), and one likely reason for discrepancies is that competition effects on fitness and populations may be hard to capture when doing observational studies in flower rich environments because of floral attraction effects, niche changes, or changes in temporal foraging patterns (Inouye 1978, Thomson 2006, Wcislo and Tierney 2009). Further, existing limited evidence for interference competition is conflicting, with some studies even showing bumblebees displacing honeybees when feeding rather than the opposite (Balfour et al. 2015, Iwasaki et al. 2020). Previous reviews call for more experimental studies on the competition impact of honeybees (Mallinger et al. 2017, Iwasaki and Hogendoorn 2022), which I contribute with in **paper III**, where effects of increased honeybee densities are investigated by focusing on foraging behaviour in bumblebees.

Pollination

While foraging, bees may unintentionally (from the bee perspective) bring pollen from one flower to another of the same species, where the pollen can land on the stigma leading to fertilization and seed set in the plant. This relationship that has been shaped by millions of years of coevolution, has created a multitude of adaptations in plants, including nectar, to attract flower visitors suitable as pollen vectors (Hu et al. 2008). Bees are generally seen as some of the most important pollinators, but other taxa such as butterflies, hoverflies and beetles are also important (Rader et al. 2016). As many as 87.5 % of the worlds flowering plants benefit from animal pollination (Ollerton et al. 2011), making the pollinators crucial for sustaining most terrestrial ecosystems. Pollinators are also important for crop production as they contribute to the pollination of three quarters of the 115 most common crops world-wide (Klein et al. 2007). They are particularly sensitive to fragmentation in tropical areas (Ricketts et al. 2008), which together with a reduced productivity of pollinator-dependent crops compared to other crops in India (Basu et al. 2011), raise concerns about future food security in these areas. It is important to expand the knowledge on pollen limitation and pollinator importance for local crops varieties in the tropics, as existing data from temperate systems may not be transferable. I contribute to this in **paper V**.

Thesis aims

The overall aim with this thesis is to improve the understanding of how, and why, bees are affected by varying flower resources in space and time in different agricultural landscapes, as well as how varying abundances of bees affect crop pollination. I revolve around foraging behaviour, which I believe is a key for this understanding. Specifically, I aim to answer the following questions:

- What flower resources are important for bee reproduction in agricultural landscapes with spatiotemporally distinctly varying resources? (**Paper I**)
- Does spatial configuration of mass-flowering crops modify competitive effects between bee species that vary in mobility? (**Paper I)**
- How does flower constancy behaviour and pollen diet in bumblebees vary over time and with varying resources in intensive agricultural landscapes? (**Paper II**)
- How is foraging behaviour, in terms of time expenditure and daily activity, affected by competition from increased honeybee densities? (**Paper III**)
- How are bees with different functional traits affected by landscape composition in a tropical small-holder agricultural landscape? (**Paper IV**)
- Are tropical crops benefitted and limited by abundances of wild pollinators? **(Paper V**)

Methods

Study design and data collection

This thesis is based on data from three different study systems (Figure 4). All study systems had in common that focal sites were situated in landscapes that differed in the amount of SNH.

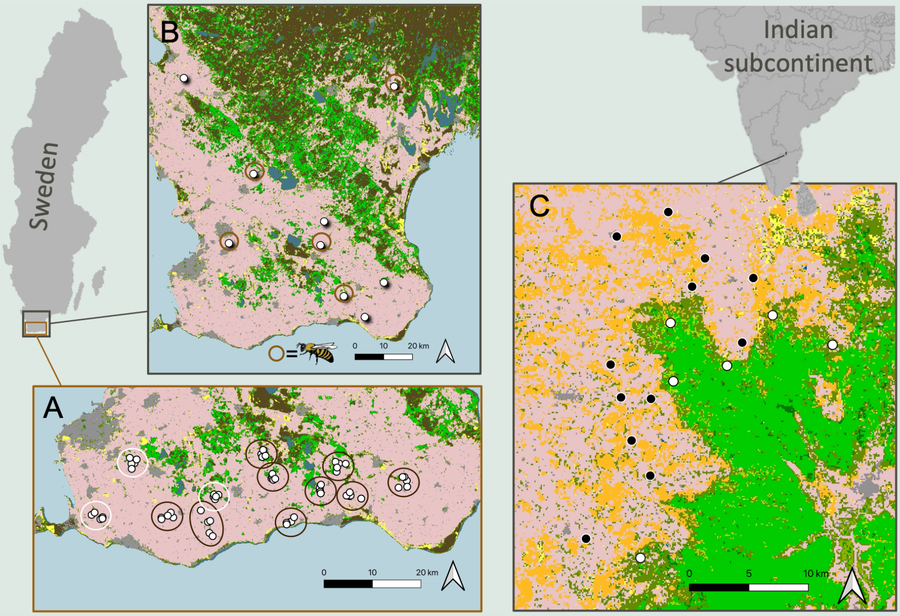


Figure 4. The three study systems used in this thesis. Data were collected from all sites in studysystem A for **paper I**, and data from the three sites with bumblebees within each of the white circles were used for **paper II**. The circles in A show the twelve geopgraphically separated areas. Study system B, used in **paper III** is a subset of a larger study system described in detail in Raderschall et al. (2022). In B, sites with a brown circle had added honeybee hives, and sites without brown circles were control sites. Data from all sites of study system C were used for **paper IV**, and data from the sites marked with black points located in agricultural landscapes were used in **paper V**. Sites maked with white points in C were located in forests. *Pink = cropland, green/brown hues = forest, grey = urban areas, orange = shrubland, yellow = herbaceous vegetation. Land use classes and map raster from Copernicus Global Land Service, 100 m resolution, 2018 (Buchhorn et al. 2020). Much of the land classified as shrubland in C is likely to be cropland (personal observation).*

Landscape design

In study system A we wanted to investigate if less mobile species are affected by competition from more mobile species, when it is easier for the mobile one to reach OSR. The study system, located in southernmost Sweden in 2017, is based on twelve different areas, with five sites in each. Three of the five sites had both commercial bumblebee (*Bombus terrestris*) and trap nests containing commercial solitary bee (*Osmia bicornis*) cocoons, and were located adjacent to, approximately 300 m from, and 1000 m from nearest oilseed rape (OSR) field, respectively. The two remaining sites only had trap nests with *O. bicornis* cocoons, and they were located adjacent to and 300 m from nearest OSR (Figure 5). There was a minimum of 300 m between all sites within an area. This design was repeated in all twelve areas (Figure 4A). The expectation was that at 0 m both species would have equal access and be equally benefitted by OSR, that at 300 m the bumblebees would easily access the OSR while it would be more costly for the solitary bees to reach the OSR, and that at 1000 m none of the bee species would easily reach and benefit from the OSR. The hypotheses are summarized in Figure 5, and were tested in **paper I**. A subset of this study system including the three areas marked with white circles in Figure 4A, including only sites with bumblebees (nine in total), were used to study the pollen diet of bumblebees in **paper II**.

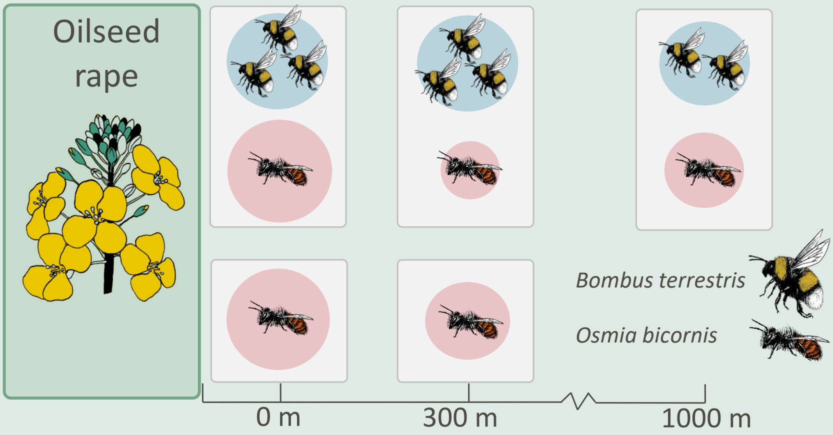


Figure 5. A schematic representation of the study setup in each of the 12 areas of study system A, with bees placed 0, 300 and 1000 m from oilseed rape (OSR), with (upper row) or without (lower row) bumblebees. The relative size of the circles corresponds to predicted reproductive output. The competition for local resources was excpected to result in a generally lower reproduction by *Osmia bicornis*, but that the effect would be modified by the access to OSR. At 0 m, the competition effect would be relaxed, at 300 m it would be strong because the bumblebees presumably reach the OSR without problem while it may be costly for *O. bicornis* to reach it, and at 1000 m the competition would be relaxed because neither bee species would be expected to benefit from the OSR. Figure modified from Yourstone et al. (2021b).

In study system B we wanted to investigate the effect of honeybee competition on bumblebee foraging behaviour (**paper III**). Therefore, we used an experimental study design consisting of five sites with added honeybee hives, and four sites with no added honeybees (Figure 4B). The control sites without honeybees were ensured to largely lack honeybee hives within 2 km from the site centres, The study system was located in southern Sweden in 2018, and consisted of faba bean *Vicia faba* fields with a flower strip sown next to each field. The flower strips were dominated by Phacelia (*Phacelia tanacetifolia*), which is attractive for both bumblebees and honeybees (Williams and Christian 1991). In the flower strips there was an additional experimental treatment – a net quadrat temporarily placed over a small area of the flower strip – creating a patch of nectar replenished flowers. The study system is a subset of a larger one described more in detail in Bommarco et al. (2021) and Raderschall et al. (2022).

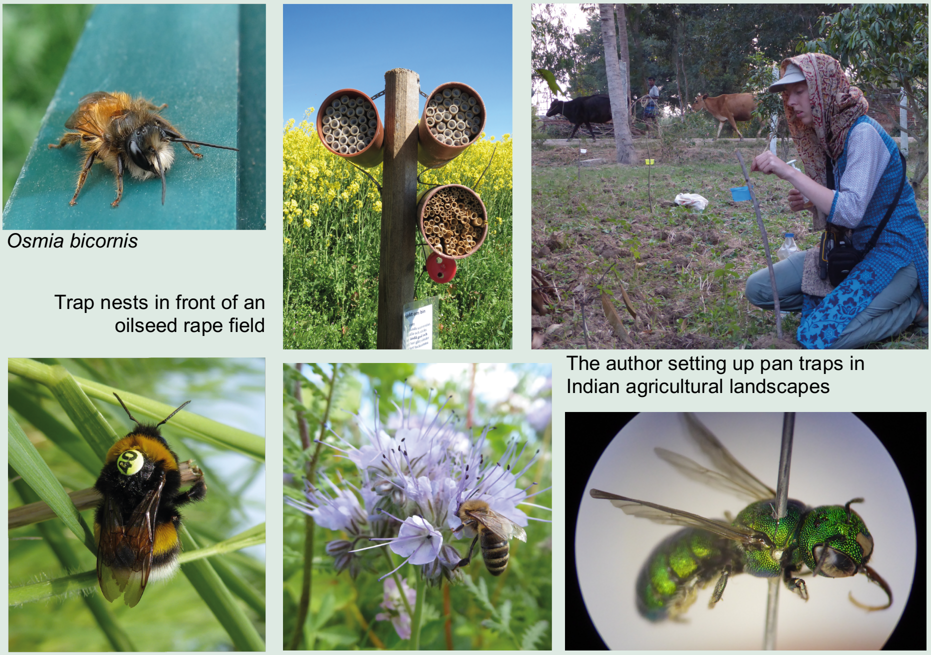
In study system C we wanted to investigate how bees with different functional traits were affected by landscape composition, and how to what degree chili crops were benefitted and limited by insect pollinators. It was located in India in 2018, and was made up of twelve sites in agricultural landscapes with a chilli field in the centre, and six sites in the forest (Figure 4C). Data from all sites were used in **paper IV**, and data only from the chilli fields were used in **paper V**.

Bee and pollen data

Several different methods to quantify bee abundance, diversity and foraging behaviour were used in this thesis. To get data on *O. bicornis* fitness for **paper I**, the reproductive output was measured by counting nest cells and cocoons in solitary bee trap nests, capitalizing on the fact that they readily breed in artificial nest sites. To determine the bee abundance and community composition of bees (**paper III-V**), transect walks in predetermined areas (normally 100 m^2) or random walks in crop fields during a predetermined time (15 or 20 minutes in my studies) were done. During the bee surveys bees were visually species and sex determined, and if a closer inspection was needed, bee individuals were caught with a butterfly net. In India, many individuals needed to be identified under a stereomicroscope and were therefore euthanised and brought back to a laboratory for identification (see Supplementary materials attached to **paper IV** for identification literature). In **paper IV** bees were also surveyed with pan traps, consisting of small white, inflorescent yellow, and blue cups that were filled with soap water and placed in the field for about 24 hours.

To assess the pollen diet of *O. bicornis* (**paper I**) and *B. terrestris* individuals (**paper II**), pollen collected by them were sampled from the solitary bee trap nests and the pollen baskets on the hind legs of the bumblebees, respectively. The solitary bee pollen were sampled from brood cells that were not yet sealed by the bees (i.e. ones the bee mothers were currently providing pollen to), in trap nests. This was done twice during the nesting period. To be able to track the diet of bumblebee individuals over time, individuals from commercial *B. terrestris* nests were marked with coloured number plates on top of their thorax. As many individuals as possible from each nest (one nest per site) were then sampled for pollen when returning to the nests, for one hour once a week if the weather allowed it, during the active period of the nests. Each collected pollen sample was homogenized, and a sub-sample was mounted on a microscopic slide. The pollen sub-sample was submerged in melted fuchsin-stained gelatine gel with a cover slide on top. Each sample was scanned using Leica Aperio CS2 Digital Pathology Slide Scanner, and pollen were identified to lowest possible taxa (species, genus or group) visually using the Aperio ImageScope software (version 12.3.2, Leica 2003) in **paper I**, and with an automated method using a convolutional neural network trained on pollen from over 200 locally occurring bee attractive plant species in **paper II** (Olsson et al. 2021).

In **paper III**, we estimated bumblebee performance by studying the foraging behaviour of bumblebees in a segment of a flower strip, using an event recorder software to record data of the time spent foraging per flower and inflorescence.



Osmia bicornis

Trap nests in front of an oilseed rape field

The author setting up pan traps in Indian agricultural landscapes

Bombus terrestris with a number plate

Apis mellifera (honeybee) foraging on phacelia

Ceratina binghami is identified through a stereo microscope

Figure 6. Photographs of study organisms and methods used in the thesis. Photo credits pan trap mounting: Michael Simmonds, trap nests: Melanie Karlsson.

Flower and habitat data

Wherever bees were surveyed for abundance and community composition, estimates of flower density were taken. The identity and approximate size of flowers present in each survey area were noted, and their numbers per square metre was estimated in classes (e.g. $<1/m^2$, $1\text{-}10/m^2$, $>10/m^2$). Additionally, comprehensive surveys of habitats, flowers and trees were done in **paper I** to estimate the availability to specific resources. The area within 500 m from each site was mapped visually in the field to determine habitat types and divide the area into habitat polygons. Within 300 m from each site centre, flowering potentially bee-attractive plants were surveyed in each of the mapped habitat polygons, according to the flower survey method described above. All trees were also surveyed within 500 m, determining species and coverage area of each species.

In **paper III**, SNH within 500 m from each site centre was extracted from the National land cover database of Sweden (Nationella marktäckedata [NMD], available at https://www.naturvardsverket.se/), using the landcover type ‘vegetated other open land’, including field verges, road verges, semi-natural grasslands, gardens etc as a measurement for SNH. Because no detailed land-use data were readily accessible for the study area in India, a remote sensing method was used to estimate the amount of SNH. This was based on Normalized Difference Vegetation Index (NDVI) values created from Sentinel-2 satellite imagery, and the standard deviation (SD) of NDVI values across a year. Certain combinations of values that matched well with known SNH areas on the map were selected to represent SNH across the whole study area (cf. Alcaraz-Segura et al. 2009).

Pollination

In **paper V**, the effect of bee abundance on pollination of chili crops was investigated, using a replicated landscape design. This was based on the contention that using a gradient in landscape structure should result in varying bee abundances, that then could serve as a gradient in treatment. To control for variation between landscape in non-pollination related factors affecting crop yield, we used bagged flowers to create a base-line pollination level without insect pollinators. To investigate if there was any pollen limitation caused by a lack of pollinators, the fruit set from open control flowers was compared with that from extra hand pollinated flowers. Each treatment was replicated on six different chilli plants per field, including five flowers per plant.

Statistical analyses

All statistical analyses in this thesis were made in R (RCoreTeam 2023).

In **paper I**, generalized linear mixed models were used to investigate the relation between reproduction in *O. bicornis* and the predictor variables bumblebee presence, SNH and tree availability and distance to OSR, and the relation between the presence of certain pollen species in the bee food with availabilities of these resources in the landscape.

In **paper II**, three different types of response variables reflecting different aspects of pollen foraging consistency were used: *foraging constancy* during single foraging trips, defined as >95% of a single pollen type in the sample collected by an individual, *pollen sample similarity* calculated as inverted quantitative Jaccard distances between all the pollen samples, both within and between individuals, and *pollen diversity* per pollen sample calculated as Shannon diversity (Hill 1973). The relation between the response variables foraging constancy and pollen diversity and the predictors time of season and distance from OSR were investigated with generalised linear and linear mixed models. Pollen sample similarity was analysed as a function of logical variables describing whether the compared samples were from the same individual and nest, as well as the number of days between samples, with a linear mixed model. Additionally, the relation between individual and nest pollen diversity was investigated with linear models.

In **paper III**, linear mixed and generalized linear mixed models were used to investigate the relation between the response variables *time spent per flower* or *inflorescence*, *bumblebee abundance* and *nectar levels* and the predictors honeybee treatment, time of the day, SNH, local flower resources, and weather covariates. Additionally, similar models, including the effect of the net treatment that generated nectar replenished flowers, were used to investigate the effect of replenished resources on foraging behaviour, and how this interacted with the honeybee treatment.

In **paper IV**, generalised linear mixed models and linear models were used to assess the relation between bee abundance and richness on one hand, and local flowers SNH, and landscape type on the other. The modulating effect of different bee traits on bee communities along a SNH gradient and in agricultural landscapes compared to natural forests, was investigated with fourth-corner analyses (Brown et al. 2014).

In **paper V**, chilli fruit set was analysed as a function of experimental treatment and pest load with a binomial generalised linear mixed model. The impact of bee abundance on chilli fruit set was analysed with a similar model without the pest variable, and with bee abundance in interaction with experimental treatment.

Result and discussion

Flower resource use in agricultural landscapes

In **paper I** and **II**, we found that the pollen diet of one solitary bee and one bumblebee species shifted over time and was dominated by tree pollen in the earlier half of the active season, and forb pollen in the later half (Figure 7). The fitness of *O.bicornis* increased with access to trees, oilseed rape and buttercups, which are resources providing pollen at partly separate points in time. This underlines the importance of temporal resource complementation in time, as well as in space (cf. Dunning et al. 1992).

Even though the early dominance of trees in both of the investigated species' and honeybees' diets is known (e.g. Requier et al. 2015, Persson et al. 2018, Bertrand et al. 2019), there is a strong focus on herbaceous plants as resources for bees in agricultural landscapes (e.g. Sutter et al. 2017, Dainese et al. 2018, Klatt et al. 2020). For efficient conservation of bees in agricultural landscapes it is important to consider the value of trees, especially as we found that the reproduction of *O. bicornis* was positively related to tree availability. Also, wind-pollinated trees, such as oak which we found to be the preferred resource of *O. bicornis* during the first half of their active period, and that speeds up their nest building (Persson et al. 2018), need to be considered (cf. Saunders 2018). Additionally, recent studies showing large bee communities in the canopies of trees in temperate regions underlines the importance of trees for bees (Urban-Mead et al. 2021, Allen and Davies 2023).

The positive OSR effect on bee fitness is in line with earlier studies (Jauker et al. 2012, Holzschuh et al. 2013) and is likely explained by the nectar OSR provide, as the OSR pollen use was relatively low (Figure 7B). Buttercups are often used by *O. bicornis* (Persson et al. 2018, Bertrand et al. 2019), even though their pollen is toxic to other, even closely related, bee species (Praz et al. 2008, Sedivy et al. 2011). It is therefore likely that *O. bicornis* has adapted a tolerance to buttercup pollen, which underlines the existence of important resource preferences also in polylectic bees, which calls for an increased knowledge on flower preferences in different polylectic bee species.

Flower constancy and pollen diversity

In **paper II**, we found the bumblebee *B. terrestris* to show a relatively low level of strict flower constancy during single trips (23%) throughout the active season, and that individuals collect a diversity of around 2.5 pollen types on average per trip. The flower constancy is much lower than previously reported for the same species under natural settings (Leonhardt and Blüthgen 2012, Somme et al. 2015), which could be explained by the comparably flower resource poor agricultural landscapes in our study (cf. Persson and Smith 2013). With fewer resources in the landscape, theory predicts a generally lower flower constancy as the costs of moving between and finding preferred flowers exceed the cost of changing flower species (Hayes

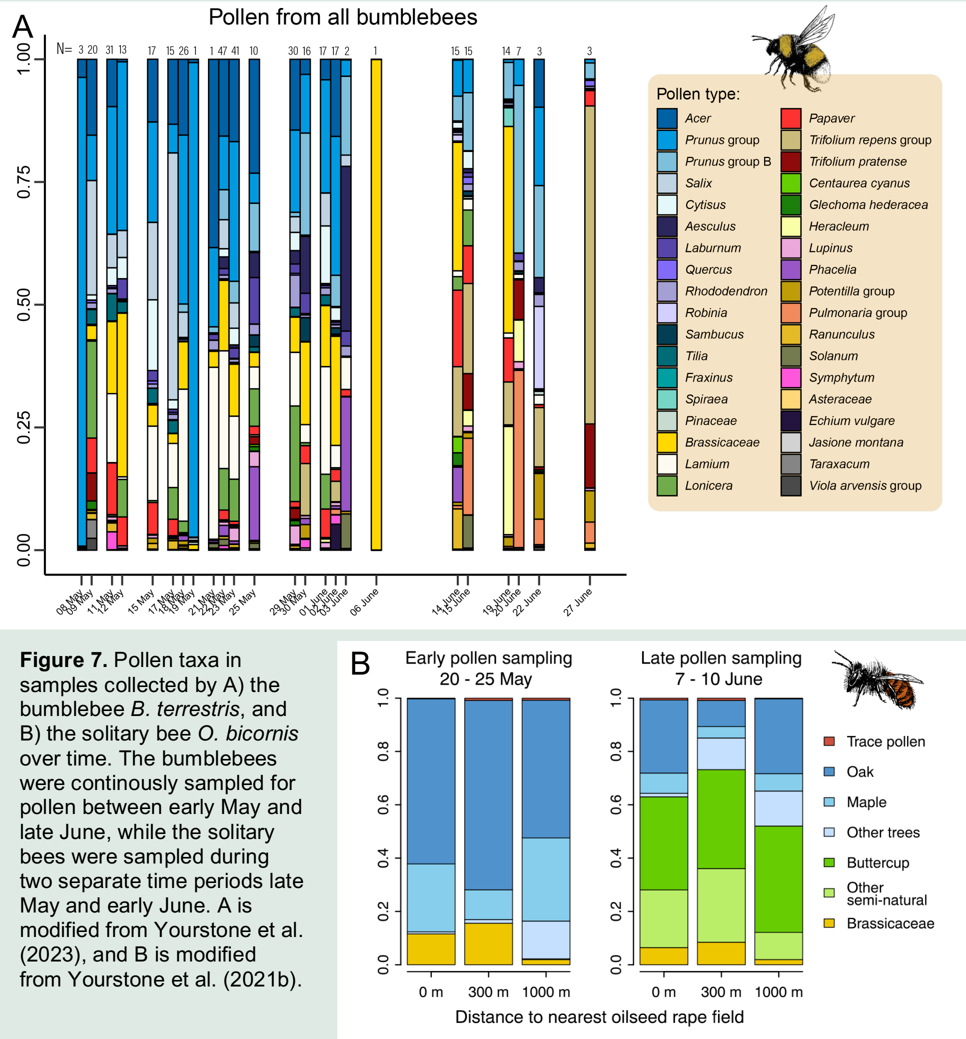


Figure 7. Pollen taxa in samples collected by A) the bumblebee *B. terrestris*, and B) the solitary bee *O. bicornis* over time. The bumblebees were continously sampled for pollen between early May and late June, while the solitary bees were sampled during two separate time periods late May and early June. A is modified from Yourstone et al. (2023), and B is modified from Yourstone et al. (2021b).

and Grüter 2022). This may have implications for the pollination of especially spatially scattered wildflowers (Goulson 1994, Dorin et al. 2022), as the pollination may be impeded in case interspecific pollen transfer increases (Morales and Traveset 2008).

Although the propensity to be flower constant was the same over time, the similarity between pollen samples collected by the bumblebees was higher if the samples were from the same individuals, and if there was little time between the samples. This means that individuals to some degree keep flower preferences over time, but that they also likely follow changes in plant phenology. However, with the resolution of our data it is not possible to conclude whether there is a delay in the response to changing resources (cf. Thomson 1981), caused by flower constancy.

Flower constancy was also highest furthest away from OSR (1000m), but only significantly higher than on the intermediate (300m) distance. As OSR is an immense resource while flowering and is likely to be the species contributing to most of the flower constant foraging trips, we would have expected the opposite direction of variation in flower constancy. However, because the replication per OSR distance was low in this study, any conclusions based on this somewhat puzzling result might be misleading.

Resource competition

In **paper I**, we investigated the potential presence of scale-dependent competition, by studying if the reproduction of a less mobile species was affected by the nearby presence of a more mobile species when only the mobile species could easily reach OSR, but found no such effects. It is possible that the results reflect a true lack of competition between the species, due to the absence of, or only a small, resource overlap. Pollen from maple and OSR are used by both species (Kämper et al. 2016, Bertrand et al. 2019), but to my knowledge pollen from buttercups and oaks, which were widely used by the less mobile *O. bicornis*, are not used by the more mobile *B. terrestrsis*. It could also be that competition effects are not detected because at the distance where the mobile species was expected to be able to reach the OSR easier than the less mobile species, the less mobile species collected almost as much OSR pollen as the individuals placed just next to the OSR field. Alternatively, the addition of bumblebee colonies (two per site) was not enough to stand out from the background competition with wild bee populations.

In **paper III**, we did not find any effect of increased honeybee densities on either the time bumblebees spent per flowers or inflorescences, or on nectar levels in otherwise unmanipulated flower strips. However, when experimentally increasing the nectar levels in a small subset of the flower strip, the time bumblebees spent per nectar replenished inflorescence was generally lower in sites with increased honeybee densities compared to in control sites. This indicates that the bumblebees are affected by competition from honeybees, even though this is not apparent when focusing on effects on bumblebee abundance (cf. Bommarco et al. 2021). The time spent per patch (in this case inflorescence) within an environment is expected to increase with the amount of resources available within the patch (Hodges 1981, Ohashi and Thomson 2005), hence, the result is likely caused by a much more efficient harvest of the nectar replenished flowers in honeybee sites. The reason to why this was not clear when studying the foraging behaviour or nectar levels in open unmanipulated inflorescences in the flower strip could be that the general degree of nectar depletion was very high regardless of honeybee density, making it difficult to detect the marginal effect of increased honeybee densities.

Landscape effects on bees

Seminatural habitats in the landscape are important for bees in terms of both flower and nesting resources (Williams and Kremen 2007, Kennedy et al. 2013), and still, we found no relation between SNH and bee fitness or abundance in any of the papers it was investigated (**paper I, III** and **IV**). It is possible that the used spatial scale of the SNH effect was inappropriate for the species in focus (cf. Miguet et al. 2016), but at least in **paper I** several other landscape-scale predictors, such as the tree and buttercup availability, were related to bee fitness. This illustrates the importance of knowing what resources are important to the bees in focus, both when designing landscape studies, and when implementing actions to support bees.

Trait-dependent landscape effects

In **paper IV** we found that trait-environment interactions were generally stronger when comparing natural forest with agricultural landscapes in tropical drylands, than when investigating the effect of SNH variation in agricultural landscapes. This is expected, as natural forests and agricultural landscapes are different habitat types providing different resources, which presumably can support bee communities characterized by different functional traits. In particular, we found that species excavating their nests in wood were more common in forests, that parasitic species and species nesting in small pre-existing cavities were more common in agricultural landscapes, and that wood nesters declined with increased proportion of SNH at a 500 m scale in agricultural landscapes. There is naturally more wood in forests, explaining the high presence of wood-nesters, and even though the forest also might contain natural pre-existing cavities, there are likely plenty of these in built-up areas, such as in straw roofs. The reason parasitic species are favoured in agricultural landscapes could be explained by the fact that there were generally more species in the agricultural landscapes, which presumably increase the amount of host species. The results indicate that nesting resources may be more important than flower resources for determining the bee community in these landscapes.

Crop pollination

In **paper V**, we found that the fruit set of chilli crops was more than twice as high in the control and pollen supplementation treatments, compared to the pollinator exclusion treatment (Figure 8). This means that chili fruit set depends on animal pollination to a high degree, and the important pollinators are likely to be wild bees as these represented 98% of the flower visitors. Previous data on pollinator importance for chilli pollination comes mainly from greenhouse studies (Jarlan et al. 1997, Ercan and Onus 2003, Azmi et al. 2016), and it has been assumed that under natural conditions where wind occurs the contribution of animal pollination to chilli fruit set and quality is as low as 0-10% (Klein et al. 2007). Our study is the first well-replicated field study on the impact of open pollination on chili fruit set, and we show that pollinators are indeed more important than previously assumed for chili pollination. This raises questions on whether the importance of pollinators also for other rather poorly studied crops has been underestimated (cf. Klein et al. 2007).

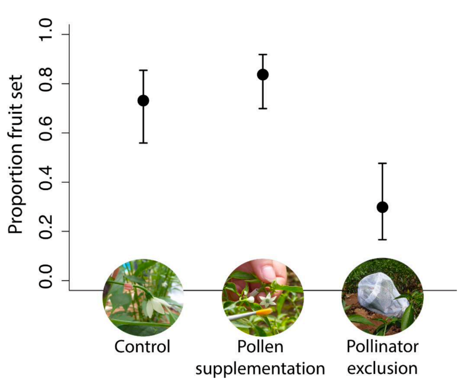


Figure 8. Fitted means ± 95% confidence interval of fruit set in the three treatments control, pollen supplementation by hand pollinaition, and pollinator exclusion with a mesh bag. Figure from Yourstone et al. (2021a).

There was no difference between fruit set in the pollen supplemented treatment compared to the control treatment, which suggests that there were sufficient pollinators to satisfy the pollination needs for chilli in the area. Still, we found a positive relation between flower visitor abundance and fruit set, but it was only significant in the pollen supplemented treatment. It is possible that the pollen supplemented flowers were not perfectly hand pollinated and could still benefit from more flower visitors, but nevertheless we would have expected the fruit set in the control treatment to increase significantly as well. A likely explanation is that there is one or several unknown factors correlated with flower visitor abundance influencing all treatments, but that this by chance was significant only for the supplemented treatment. However, the seemingly satisfactory pollination of chili crops should not be generalised to other crop species grown in the area that might have higher requirements on their pollinators, such as eggplants with poricidal anthers that require buzz-pollination (i.e., a certain type of vibration to release the pollen; De Luca and Vallejo-Marín 2013), or monoecious cucurbits that require transfer of pollen between male and female flowers (Bomfim et al. 2016).

Conclusion and future perspectives

In this thesis, I show the importance of resource complementation in both space and time. Initiatives to mitigate bee declines in agricultural landscapes should carefully consider the scale of their actions to match them with both the foraging ranges of declining bees, and their temporal usage of resources. Knowledge on preferred diets of different polylectic bee species needs to be expanded to be able to benefit a diversity of bees, and it is important to also understand how alternative diets that may be presented in agricultural landscapes compare in terms of fitness effects. Given that trees such as oaks are shown to be important for bee fitness, more research is needed to elucidate the importance of trees to a diversity of bees. Oak, which is famous for having thousands of species associated with it (without bees being mentioned, cf. Mitchell et al. 2019), should be considered as important parts of field borders and forest patches in the agricultural landscape. More research is needed to clarify how trees in terms of species identity and spatial arrangement could be used to benefit bees (cf. Ulyshen et al. 2023).

I show that flower constancy may be lower than previously thought for bumblebees foraging in intensive agricultural landscapes. How well this reflects their fitness, as well as if this behavioural property has a negative effect on the pollination of plants through interspecific pollen transfer (cf. Morales and Traveset 2008) should be subject to future research. Also, the link between landscape complexity and flower constancy as well as individual and colony pollen diversity should be established with replicated landscape studies (cf. Martínez-Bauer et al. 2021). Flower constancy is especially common in social species and is assumed to be beneficial only to such species (Hayes and Grüter 2022). However, it remains to be investigated whether it also occurs among solitary bee species. Also, it should be investigated if flower constancy is more strongly exhibited in other bumblebee species than the investigated one, which may be suboptimal in contemporary agricultural landscapes with their swiftly changing resources.

I show that it is possible to use predictions from optimal foraging theory to detect competition effects from honeybees on bumblebees, at least when flowers were experimentally replenished (in contrast to naturally almost completely depleted flowers). This opens possibilities for future studies on competitive interactions between bees, which otherwise can be difficult because of confounding effects of the attractiveness of the habitat where bee data are collected. For example, predictions based on flower constancy levels in response to competition could be used in future research. Future research should also establish the strength of the link between altered foraging behaviour and fitness.

I show that some functional traits in bees linked to nesting behaviour explain their distribution when comparing forests and small holder dominated agricultural landscapes, while traits did not do well to explain bees' distribution across the agricultural landscapes varying in heterogeneity. The results suggest that nesting substrates rather than foraging resources are limiting bees, and research is needed to identify what type of substrate that is missing in agricultural landscapes and how to implement it to best benefit a diversity of bees. There are indications of pollination service loss in India (Basu et al. 2011), and tropical pollinators are generally more sensitive to fragmentation (Ricketts et al. 2008). For future food security, it is therefore important to do more research to support bees for increased crop pollination, as well as to identify pollination needs in a variety of local crops. Even though the chili crops in our study system did not seem limited by the pollinator abundance, other crops might be. The fact that previous conclusions on pollinator dependency in chili, based on mainly greenhouse studies, are not in line with our results raise questions on whether previous conclusions on pollinator dependencies in other crop varieties also may be under-estimated.

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Bee foraging and pollination

Paper I

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Paper II

Yourstone, J., Varadarajan, V., and Olsson, O. (2023) Bumblebee flower constancy and pollen diversity over time. Behavioral Ecology 34, 602-612.

Paper III

Yourstone, J., Smith, H.G., Bommarco, R., Lindström, S., Lundin, O., Raderschall, C.A., and Olsson, O. Bumblebee foraging behaviour in response to varying resource levels and honeybee densities. *Manuscript.*

Paper IV

Yourstone, J., Erixon, F., Kelber, A., Somanathan, H., and Smith, H.G. IV. Trait-dependent responses of bees to local and landscape features in tropical agricultural drylands. M*anuscript.*

Paper V

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