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Interaction between *Bombus terrestris* and honeybees in red clover fields reduces abundance of other bumblebees and red clover yield

Interaksjon mellom *Bombus terrestris* og honningbier i rødkløveråkre reduserer tettheten av andre humler og fører til redusert rødkløveravling

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Preface

This thesis marks the end of my Master's degree in Ecology at the Norwegian University of Life Sciences at Ås. The process has given me valuable experience and insight into the field of ecological research. I am grateful to the resarchers at the Norwegian Institute for Nature Research (NINA), especially Jens Åström and Graciela Rusch, for the opportunity to be a part of the 'PolliClover' project.

There are several people I would like to thank for helping me complete this thesis. First of all, my supervisors Jens Åström, Anne Sverdrup-Thygeson and Tone Birkemoe for constructive feedback, patience and support, which made it possible for me to finish what I started. Jens, thank you for letting me work with a topic of my own choosing, and for invaluable help with statistical analysis. Anne and Tone, thank you for your genuine interest and compassion. I have learned a lot about entomology, research and critical thinking from the booth of you, both as lecturers and supervisors.

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Abstract

Pollinator dependent crops have increased by 300% the last 50 years. At the same time many pollinator species are declining, including honeybees and bumblebees. Red clover is one of the crops dependent on bees for seed set. It is the single most important leguminous crop for milk and meat production in Norway, but over the last years crops have declined, and insufficient pollination is a likely hypothesis to explain this. Long tongued bumblebees are the most efficient pollinators of this crop, and are simultaneously the bumblebee species declining the most. To improve yields, honeybees and another bumblebee, *B. terrestris*, is added to fields. Evidence on how this affects the other bumblebee species, especially long tongued species, and yield is conflicting. However, honeybees are considered poorer pollinators of red clover than bumblebees, and *B. terrestris* is a known nectar robber. The aim of this study was to identify whether competition occurs between honeybees, *B. terrestris* and other bumblebee species in red clover fields, and how these interactions may affect red clover yield.

To that objective the composition of pollinator communities in 40 red clover fields over two years were examined, and estimates for red clover yield were obtained. *B. terrestris* abundance was manipulated in five fields. The results suggest that *B. terrestris* act as nectar robbers, facilitating honeybees and other short tongued bumblebees acting as secondary robbers. Honeybees negatively affects abundance of both long and short tongued bumblebees, indicating that competition occurs. Interaction between increased abundance of honeybees and *B. terrestris* seems to reduces long tongued bumblebee abundance and red clover yield.

Sammendrag

Avlinger avhengige av pollinatorer har økt med 300% de siste 50 årene. Samtidig er mange av pollinatorene i tilbakegang, blant annet honningbier og humler. Rødkløver er en av avlingene som er avhengig av insektpollinering for å sette frø, og er den viktigste belgveksten for melk- og kjøttproduksjon i Norge. De siste 10-15 årene har det vært nedgang i frøproduksjonen, og mangelfull pollinering er en av de mest sannsynlige årsakene til dette. Langtungede humler er de mest effektive pollinatorene av rødkløver, men er også den humlegruppen i sterkest tilbakegang. For å øke avlingene settes det tidvis ut bikuber og kolonier av *B. terrestris.* Det Hvordan dette påvirker andre humlearter og avling er noe usikkert, men honningbier antas å være dårligere pollinatorer enn humler generelt, og *B. terrestris* opptrer ofte som nektarrobber. Målet med denne studien var å finne ut om det finnes et konkurranseforhold mellom honningbier og humler og *B. terrestris* og andre humlearter, og hvorvidt dette påvirker rødkløveravlingene. Sammensetningen av pollinatorer og rødkløveravling ble derfor undersøkt i 40 rødkløveråkre i to år. Tettheten av *B. terrestris* ble manipulert ved å sette ut bol i fem åkre. Resultatene antyder at *B. terrestris* fungerer som primære nektarrobbere i rødkløver åkrene, og at honningbier og andre korttungede humler fasiliteres av denne adferden ved å benytte seg av hullene allerede laget av *B. terrestris.* Honningbier påvirker tettheten av både langtungede- og korttungede humler negativt, noe som indikerer er konkurranseforhold. Samtidig økt tetthet av honningbier og *B. terrestris* ser ut til å ha negativ effekt på antall langtungede humler og rødkløveravling.

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1. Introduction

Worldwide, the diversity of pollinators is in decline (Biesmeijer et al. 2006; IPBES 2016; Totland et al. 2013), and the loss of pollinators may have dramatic effect on the global food security (Gallai et al. 2009; IPBES 2016; Potts et al. 2010; Totland et al. 2013)). It is estimated that 75% of all crops used for direct human consumption depends at least in part on insect pollination (IPBES 2016), and has an annual monetary value between US$235 and US$577 billion (2016). At the same time as the pollinators are in decline, the pollinator dependent crops have increased by 300% the past 50 years (IPBES 2016).

The primary pollinators of both crops and many wild flowers are insects, and in particular bees (Potts et al. 2010). In Europe alone it is estimated that 12% of croplands require pollination by wild and managed bees for optimal production, and that it is essential for fruit or seed set in 3% (Schulp et al. 2014). The most common pollinating bee species in commercial agriculture is the honeybee, *Apis mellifera* (Potts et al. 2010). Honeybees belong to the large and exceedingly successful order Hymenoptera, and are eusocial insects living in perennial colonies with up to 80 000 workers in a good year. Wild honeybees have become rare, and the majority are kept in hives. They are considered as livestock as they will often not survive without human interference, especially in the northern hemisphere, and are mostly kept for their honey but also as commercial pollinators of crops. Since 2006 extensive losses of honeybee hives have been reported in the US, a phenomenon called colony collapse disorder (CCD). The reasons are hotly debated, but most scientists now agree that a combination of stressors such as mite, viruses, migratory beekeeping and pesticides is the most likely cause (Johnson 2015; Le Conte et al. 2010; Potts et al. 2010). The honeybee losses has led to increased interest in wild bees as well, such as the bumblebees. Evidence suggests that several bumblebee species have declined in Europe over the past 60 years (Goulson et al. 2008; Williams & Osborne 2009), and the trend is similar in the US (Cameron et al. 2011; Goulson et al. 2008). Bumblebees are specially adapted to the cold climate in the temperate regions, and are therefore often more efficient pollinators in countries such as Norway than honeybees. Whilst honeybees forage in fair weather (Willmer et al. 1994), bumblebees will forage in cold and even rainy conditions (Corbet et al. 1993).

1.1 Bumblebees

Like the honeybees, the bumblebees belong to the Hymenoptera and are eusocial, but build annual colonies of up to 350 workers in some species (Goulson et al. 2001). During autumn all workers and males die off, and only the young queens lives through the winter to start a new colony when spring arrives (Goulson 2010; Ødegaard et al. 2015). Globally, there are just over 250 bumblebee species, and 35 of them are naturally occurring in Norway, which is almost 14% of the worlds bumblebee species. Six of these species are on the national red list: *Bombus subterraneus* (critically endangered), *Bombus distinguendus* (endangered), *Bombus quadricolor* (vulnerable), *Bombus muscorum* (near threatened) and *Bombus ruderarius* (near threatened) (Henriksen & Hilmo 2015).

The decline of bumblebees is mainly caused by land use change and habitat fragmentation, but pesticide use, invasive species, pathogens, and altered plant-pollinator relationships due to climate change are likely contributors as well (Goulson et al. 2008; IPBES 2016; Kjøhl et al. 2011; Rundlöf et al. 2008; Whitehorn et al. 2012). Although many species are declining, some are increasingly successfull, such as *Bombus terrestris*. It was observed for the first time in Norway by Astrid Løken in 1958, and is thus a relatively new species in the country (Gjershaug & Ødegaard 2012). *B. terrestris* is a generalist of large body size, and it emerges early in spring, all of which gives it a competitive advantage (Gjershaug & Ødegaard 2012). The species is also reared by professional breeders for use as pollinators of e.g. tomatoes, strawberries and sweet peppers in green houses, from where the bumblebees occasionally escape, and also establish outside (Dafni et al. 2010; Ings et al. 2006). Evidence suggests that *B. terrestris* is able to outperform native bees, and it is reason to believe that interspecific competition could be part of the reason some bumblebee species are declining (Gjershaug & Ødegaard 2012; Ings et al. 2006).

All the red listed bumblebee species in Norway except *B. quadricolor* have long proboscis, or tongue, in contrast to *B. terrestris*, and it is indeed the long tongued species that are declining the most (Gjershaug & Ødegaard 2012) both in Norway, Sweden (Bommarco et al. 2012) and Europe in general (Goulson 2010). Bumblebees are morphologically very similar, but in addition to body size, tongue length is one of the few varying traits (Goulson 2010). Goulson and Darvill (2004) found that the rare bumblebee species have narrower diet breadth than the common species, and that narrow diet breadth is often associated with the long tongued species (Williams 2005) which are more specialized. The long tongue is an adaptation to reach the nectar at the bottom of flowers with deep corollas. One such flower is the red clover (*Trifolium pratense),* an herbaceous perennial plant belonging to the Fabaceae family, and a favourite amongst many bumblebees.

1.2 Red clover pollination

Red clover is a self-incompatible plant and therefore completely dependent on pollination for fertilization and seed set (Goulson 2010). In Norway commercially grown red clover is the single most important leguminous crop in grassland based milk- and meat production (Norsk Landbruksrådgivning 2016). It is nitrogen fixating which improves the soil quality, and is a common component in organic crop rotation. It also improves the forage value because of its high content of proteins and minerals. Red clover is used in seed mixes for both silage and pastures at a proportion of 10-15%. Studies have shown that cows that are fed silage based on mixed leys with grass and red or white clover (*Trifolium repens L*.) produce milk with a more favourable milk-fat ratio for human consumption than cows fed on exclusively grass based silages (Adler et al. 2013).

During the past 10-15 years, the red clover yields have decreased (Havstad et al. 2015), and the Norwegian seed production covered less than 50% of the demand in 2009-2011 (Landbruksdirektoratet). There is an increasing shortage of seeds, and pollination deficiency is a likely hypothesis to explain at least a part of this (Åström et al. 2014; Totland et al. 2013). As the red clover flowers have deep corollas the specially adapted long tongued bumblebees are thought to be the most efficient pollinators of the plant (Fussell et al. 1991; Goulson 2010; Palmer-Jones et al. 1966). As mentioned, these are among the species in strongest decline, which could support the pollination deficiency hypothesis. Bommarco et al. (2012) found that over the last 70 years the species composition in Swedish red clover fields had changed dramatically. Two short tongued species, *B. terrestris* and *B. lapidarius,* went from 40% to near complete dominance at 89%, and at the same time mean red clover yields decreased.

The deep corollas of the red clover is thought to make the plant less interesting to species with short tongues, such as short tongued bumblebees and honeybees (Goulson 2010), as the nectar is either unavailable or the handling time is prolonged. Nevertheless, the red clover pollen is rich in protein and contains vital amino acids which makes it attractive to species with short tongues as well. A study by Goulson and Darvill (2004) found that collectively, 76% of pollen collected by the 13 bumblebee species recorded was from Fabacea, and some species such as *Bombus humilis* collected exclusively from red clover. There is reason to believe that the short tongued species mainly collects pollen from the flowers as the pollen grains are easily accessed. The quantity of pollen attached to the bee is probably lower when merely collecting the pollen, than if the bee passes the anthers to access the nectar at the bottom of the corolla. This may lead to poorer pollination.

Although short tongued species have difficulties reaching the red clover nectar legitimately, some species are known to steal nectar, so called primary or secondary nectar robbers (Maloof & Inouye 2000). The primary nectar robbers, such as *B. terrestris* and other bumblebees belonging to the subgenus *Bombus* s. str., bite holes at the bottom of the corolla, accessing the nectar. Secondary nectar robbers, which honeybees and some short tongued bumblebee species often are (Free 1962; Maloof & Inouye 2000; Rust 1979; Stout et al. 2000), utilize the holes made by primary robbers. This behaviour is unlikely to enhance pollination as the bees will not come into contact with the pollen grains. More likely, this activity will decrease pollination and pose a competitive disadvantage to the long tongued bumblebee species as the nectar derived and damaged flowers becomes less interesting (Goulson 2010). However, in a review of existing literature on nectar robbing Maloof and Inouye (2000) concludes that nectar robbing can have both negative, neutral and positive effects on yield.

1.3 Study aim and predictions

Even though the long tongued bumblebees presumably are the most efficient red clover pollinators, honeybee hives and *B. terrestris* colonies are being added to some red clover fields to improve yield (Totland et al. 2013). Honeybees are generally thought to pollinate less efficiently than bumblebees, including *B. terrestris* (Fuchs & Muller 2004; Willmer et al. 1994), even though several studies have also found that honeybees pollinate red clover efficiently (Brødsgaard & Hansen 2002; Palmer-Jones et al. 1966; Stephen 2015), and Brødsgaard and Hansen (2002) recommends adding *B. terrestris* and honeybee hives to improve yield.

Little research has been done on how adding honeybees and *B. terrestris* colonies affects bumblebee species and red clover yield, but the existing results are contradictory. Wermuth and Dupont (2010) found that honeybees negatively affects abundance of long tongued bees in red clover fields, and Bommarco et al. (2012) found that honeybees has a negative effect on both long tongued bumblebees and red clover yield. Brødsgaard and Hansen (2002) on the other hand found that both honeybees and *B. terrestris* are efficient pollinators of red clover. Other studies investigating the potential competition by honeybees (Herbertsson et al. 2016) have found that honeybees can have a negative effect on bumblebee densities in homogenous landscapes such as crops, indicating interspecific competition, and that the presence of honeybee colonies reduced the size of bumblebee workers of four different species in Scotland (Goulson & Sparrow 2009). Steffan-Dewenter and Tscharntke (2000) on the other hand, found that honeybees did not significantly affect wild bee populations, including six species of bumblebees, in central Europe. Observational studies are often misinterpreted and struggling with confounding effects, and there are few experimental studies (Paini 2004). Trying to assess the impact of honeybee competition is clearly challenging, and more studies are required.

Because it is evident that both honeybees and *B. terrestris* forage on red clover, I hypothesize that they do compete with other bumblebee species, both long and short tongued, in the red clover fields due to resource limitation. We do know that the long tongued bumblebees forage on red clover, and the other short tongued bumblebee species do collect pollen and sometimes nectar from the red clover (Goulson & Darvill 2004). Niche overlap is therefore sufficient to expect resource competition with honeybees and *B. terrestris* for both groups. I also hypothesize that such competition will have a negative impact on red clover yield as the long tongued bumblebees are thought to be the most efficient pollinators of the crop.

B. terrestris colonies were therefore added to five fields to evaluate the effect they have on both bumblebees and yield. According to the assumption of resource limitation, *Phacelia tenacetifolia* (Phacelia) was planted along five fields to act as an early resource and attract more pollinators in order to increase yield. This has been shown to have a positive effect on yield in another study adding strips of wild flowers adjacent to strawberry fields (Feltham et al. 2015).

Finding ways to increase the yields of red clover is not only important for the economy of the farmers producing the crops, but also for the Norwegian milk- and meat production as a whole, and thereby the Norwegian self-sufficiency. Albeit small, it will also be a contribution to the global food security. The governmental aim is 15% organic farming in 2020 (Landbruks-og Matdepartementet 2009), and to reach this goal it will be essential to produce more nitrogen fixing crops like red clover. Additionally, the red clover crops are an essential foraging plant for long tongued bumblebee species (Gjershaug & Ødegaard 2012; Goulson & Darvill 2004) which quite clearly are declining. Conserving a species rich bumblebee fauna is not only important for crop yields (Brittain et al. 2013a; Garibaldi et al. 2016), but also in order to maintain the integrity of many wild plant communities (Totland et al. 2013). Additionally, as much as 14% of the worlds bumblebee species occur in Norway, and we have a special responsibility to conserve them regardless of human needs.

The aim of this study is to identify whether competition occurs between honeybees and bumblebees, and between *B.terrestris* and other bumblebee species in red clover fields. In addition I will investigate how such competition may affect the red clover yield. In order to achieve this goal, I will test the following predictions:

P1: Bumblebee abundance is reduced at high abundances of honeybees
P2: Abundance of long tongued bumblebee species is reduced by increasing abundance of honeybees and *B. terrestris*
P3: Abundance of short tongued bumblebee species is reduced by increasing abundance of honeybees and *B. terrestris*
P4: Bumblebee species richness is reduced by increasing abundance of honeybees and *B. terrestris*
P5: High abundance of honeybees and *B. terrestris* combined with low abundance of long tongued bumblebees will reduce red clover yield

2. Method

This thesis-project was carried out as part of the project ‘PolliClover’ lead by NIBIO (Norwegian Institute of Bioeconomy Research). More specifically, the work is part of the work package lead by NINA (Norwegian Institute for Nature Research), which also contributes data to a large international project assessing pollinators’ status world wide organized by FAO (the Food and Agriculture Organization of the United Nations). The field work was therefore carried out according to the relevant parts of the protocol provided by FAO (Vaissière et al. 2011).

2.1 Study area

The study was conducted in the rural areas of Akershus, Vestfold, Østfold and Buskerud counties in South-Eastern Norway. They are all dispersed around the Oslo fjord (figure 1), and the landscape is characterized by intensified agriculture interspersed by small urban areas and Norway spruce (*Picea abies L.)* forest. Cereals are the dominating crops within the area. The field work was carried out during July and August of 2014-2015. The mean July temperature in the area was 19.8°C in 2014 and 15.5°C in 2015. Mean precipitation in July for the same period was 55.3 mm and 127.75mm, respectively (Meterologisk Institutt 2016).

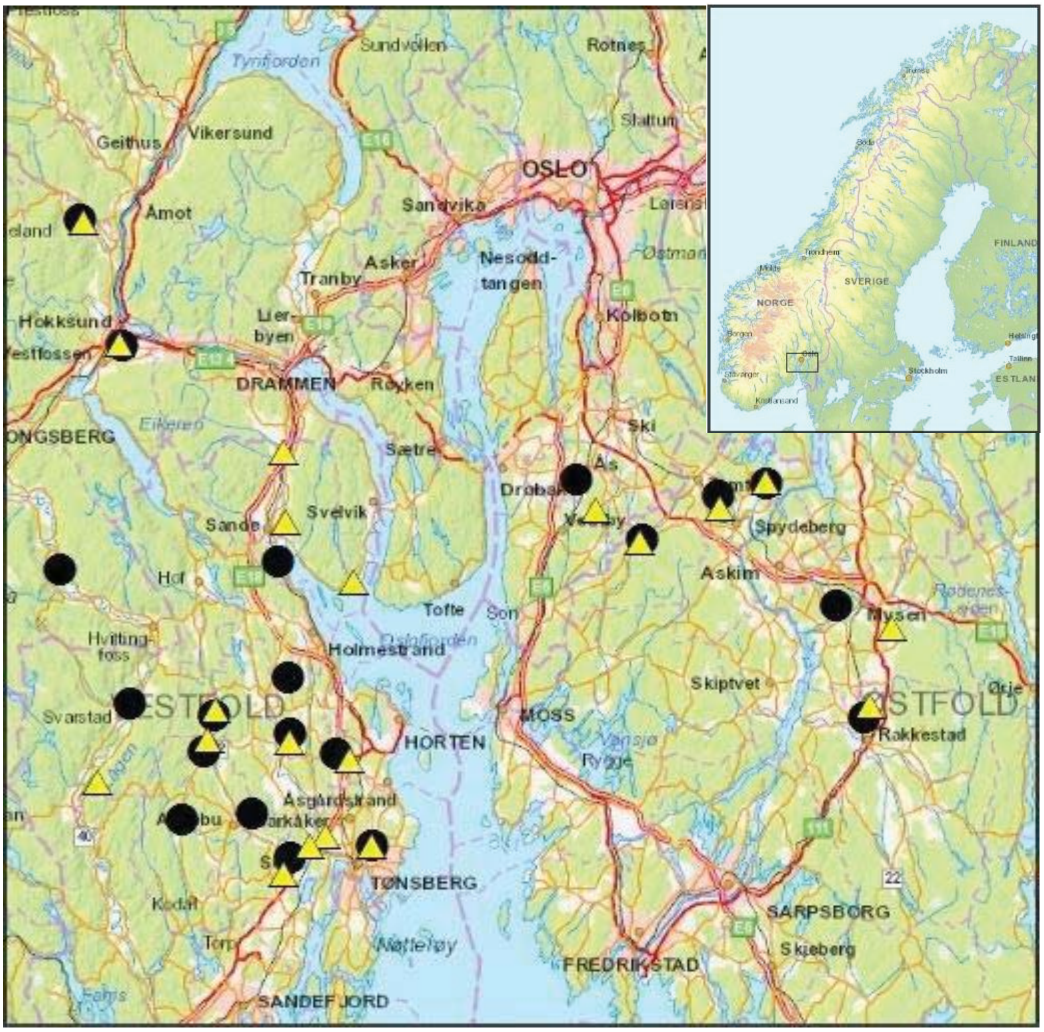

Figure 1. Digital map of the study area in south-eastern Norway. Study fields are marked with circles (2014) and triangles (2015) 1:800,000 (ArcGIS Pro 2016).

2.2 Study design

40 red clover fields in total (figure 1) were included as study sites during 2014 and 2015 (n=20 in 2014, n=20 in 2015). An overview of the size, year included and location of the fields is included in Appendix 1. Only one field was replanted with red clover and reused as study site the second year. In each clover field, one experimental plot of 50m x25m was established in a representative area(figure 2). The sides of the experimental plots constituted six numbered transects à 25m x 2m. To estimate yield and for flower density counts, four subplots of 1m x1m were established in the corners of the main plot. The experimental plots were set up in the beginning of each flowering season (early July), and remained in the same place for the duration of each growing season. The pollinator

recordings was carried out under preferable weather conditions for pollinator foraging, which is low wind, no rain, dry vegetation, and above 15°C.

All fields were planted with the diploid red clover variety 'Lea'. Pesticides were not used on any fields, and herbicides were added early in the season, well before flowering.

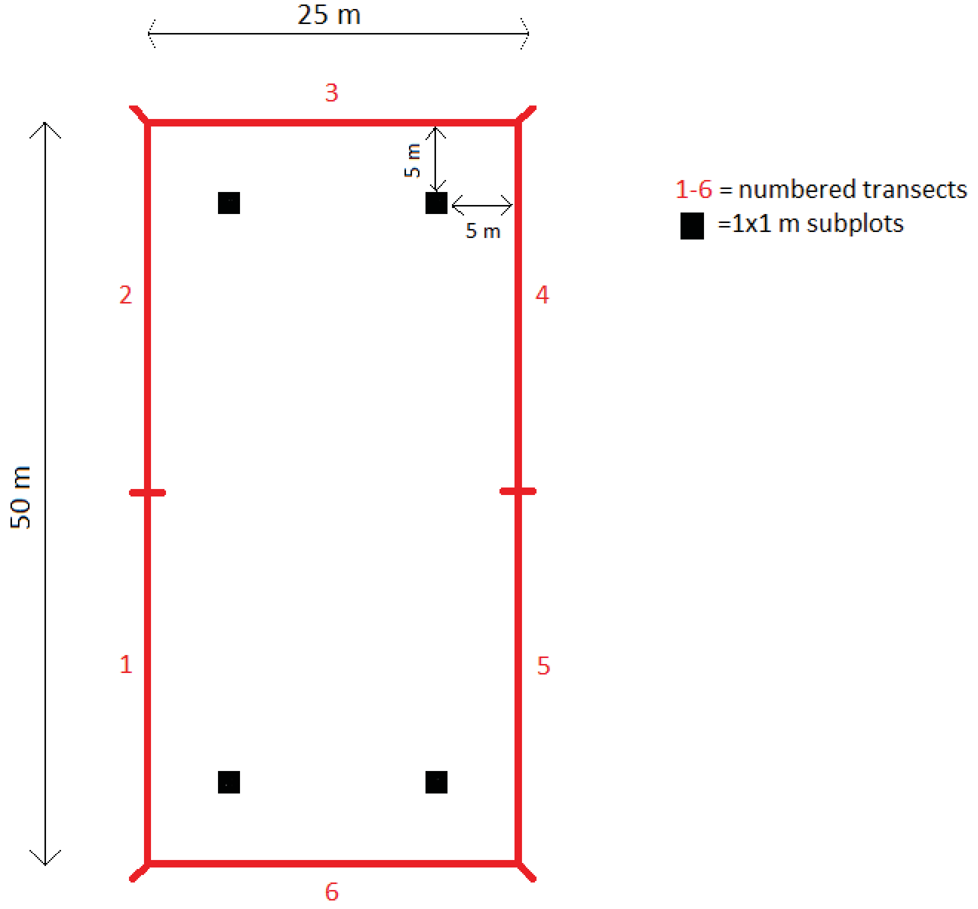

Figure 2. Schematic representation of the experimental plot design. From FAO protocol (Vaissière et al. 2011), customized by the author.

2.2.1 Experimental treatments

In the PolliClover project some fields were manipulated by adding bumblebee colonies and planting Phacelia as an early resource.

Treatment 1 (T1): *B. terrestris* colonies added

To assess the effect of *B. terrestris* on other bumblebees and on red clover yield, *B. terrestris* colonies were added to five fields in mid July 2015, at a density of five colonies/daa, a total of 152 colonies. All colonies were acquired through professional bumblebee breeders using Norwegian bumblebees.

Treatment 2 (T2): Phacelia added

Phacelia was sown as an early resource and attractant for pollinators in a narrow strip along one field edge of five study fields each year. The Phacelia designated fields were allocated at random.

T1 and T2 were never applied simultaneously.

2.3 Data collection

2.3.1 Pollinator recordings

The first pollinator recording event was carried out when about 5% of the red clover was in bloom, which was 9.7.14 and 20.7.15. Four recording events took place throughout July and August each year, spread out to reflect the entire flowering period. The last recordings took place 17.8.14 and 8.8.15. Seven different fieldworkers paired in varying teams of two carried out each recording. Species identification was based on morphology.

Stage 1

Recording of pollinators was performed in two stages. The first was by means of transect walks. The observer walked slowly forward spending five minutes per transect (25m x2m, see figure 2) netting all insects within the transect, a total of 30x4 minutes of netting per field/year.

Stage 2

In the second stage the density of pollinators sitting on open flowers was estimated. This was done by counting 400-1200 inflorescences (depending on how many open flowers there were in the transect at time of recording) within transects 1,2,4 and 5 (figure 2) at random. Honeybees and bumblebees sitting on the counted inflorescences were recorded. For data analysis the pollinator density was scaled to number of pollinators per 100 inflorescences.

All bumblebees and honeybees were identified to species level and released in the field when possible, and only brought back to the lab for identification under stereomicroscope when necessary.

2.3.2 Yield

To get an estimate of yield the four subplots in each experimental field were harvested at the end of each season. This was done by cutting all the clover in each $1m^2$ plot, storing and drying them in jute bags, before being sent off to NIBIO Landvik for threshing and weighing. The yield is expressed as g (of seed)/inflorescence.

2.3.3 Environmental variables

Flower density and temperature were included as environmental variables in the statistical analyses. The flower density was estimated by counting all the inflorescences within the $1m^2$ subplots at each pollinator recording event. Temperature was measured at the beginning of each recording.

2.4 Data Analysis

2.4.1 Bumlebee functional groups

The bumblebee species were pooled in appropriate functional groups for the statistical analyses (table 1). The group '*B. terrestris*-complex', here after called *B. terrestris* –c, takes into account the difficulty in separating the four closely related *Bombus* species *B.terrestris, B.lucorum, B.cryptarum*, and *B. magnus* (all belonging to the subgenus *Bombus s. str*.) based solely on morphology (Carolan et al. 2012; Ødegaard et al. 2015; Williams et al. 2012). All individuals fitting the morphology of either of the four species were therefore recorded as belonging to the *B. terrestris*- c.

Species were assigned to the functional groups 'long tongue' and 'short tongue' according to the widely agreed upon classifications in which the subgenera *Thoracobombus, Megabombus* and *Subterraneobombus* are long tongued species, *and Kallobombus, Melanobombus, Alpigenobombus, Callumanobombus, Alpinobombus, Bombus s. str*. and *Pyrobombus* are short tongued species (Goulson 2010; Ødegaard et al.

2015). *B. terrestris*-c were not included in the short tongued group to be able to separate the effect on other short tongued species, as *B. terrestris*-c dominates bumblebee abundance in this study.

Table 1. The bumblebee species recorded assigned to appropriate functional groups.

FUNCTIONAL GROUP	SPECIES	SUBGENERA	NORWEGIAN NAME
Bumblebees	All bumblebees pooled		
***B. Terrestris*-c**	*B. terrestris*	*Bombus* s. str	Mørk jordhumle
	B. lucorum	*Bombus* s. str	Lys jordhumle
	B. cryptarum	*Bombus* s. str	Kilejordhumle
	B. magnus	*Bombus* s. str	Kragejordhumle
Long tongue	*B. distinguendus*	*Subterraneobombus*	Kløverhumler
	B. hortorum	*Megabombus*	Hagehumle
	B. humilis	*Thoracobombus*	Bakkehumle
	B. pascuorum	*Thoracobombus*	Åkerhumle
	B. ruderarius	*Thoracobombus*	Gresshumle
	B. subterraneus	*Subterraneobombus*	Slåttehumle
	B. sylvarum	*Thoracobombus*	Enghumle
Short tongue	*B. hypnorum*	*Pyrobombus*	Trehumle
	B. lapidarius	*Melanobombus*	Steinhumle
	B. pratorum	*Pyrobombus*	Markhumle
	B. sporadicus	*Bombus* s. str.	Taigahumle
	B. wurflenii	*Alpigenobombus*	Tyvhumle

2.4.2 Statistical analysis

Statistical analyses were conducted in R (R Development Core Team 2015).

All variables were checked for co-linearity performing a correlation test using the cor-function (R Development Core Team 2015) and were found to be below the rule-of-thumb threshold of 0.5 (Zuur et al. 2009)(appendix 2).

Competition models

Data derived from stage 1 of the pollinator recordings (subchapter *2.3.1 Pollinator recordings*) were used for these models. All variables were tested for normal distribution fitting a simple linear regression, where the residuals were found not to be normally distributed. Mixed-effects logistic regression model (GLMM) with poisson distribution was therefore chosen to explore the relationships between the abundance of the various bumblebee functional groups and honeybees, treatments and environmental variables using the package ‘lme4’ (Bates et al. 2015). GLMM does not assume normal distribution and permits fitting models without transforming the variables, and allows including both fixed explanatory variables and random effects adjusting for repeated samples within year and field.

The fitted models consist of a response variable, fixed explanatory variables and random effects. The response variables are the abundance of the different bumblebee functional groups, abundance of honeybees and bumblebee species richness. The variables specified as fixed explanatory variables are *B. terrestris* colonies added (T1), Phacelia added (T2), temperature, flower density, number of individuals of the four different bumblebee functional groups (table 1), number of honeybees and interactions between *B. terrestris* and honeybees. T1 and T2 are categorical variables: added (Y) and not added (N). All other fixed explanatory variables were scaled to improve model estimates and to ease interpretation and comparison. Scaled variables are interpreted as the effect of the increase of one SD of the scaled fixed effect on the response variable (table 2). Random effects were added as control for repeated measurements within each year, registration and field. In addition, an individual random effect (id) was added to control for possible overdispersion.

Table 2. The standard deviations (SD) with associated units for all scaled variables used in the models in tables 5 and 6. The effect on the response variable is estimated as the effect of the increase of one SD of the fixed variable.

SCALED VARIABLE	SD	UNIT
Temperature	3.96	°C
Flower density	96.07	Nr. inflorescences/m^2
Honeybees	17.00	Nr. of individuals
***B. Terrestris*- c**	18.65	Nr. of individuals
Long tongue	4.32	Nr. of individuals
Short tongue	3.60	Nr. of individuals

Yield models

To investigate the effect of pollinators on red clover yield, data from stage 2 of the pollinator recordings (subchapter *2.3.1 Pollinator recordings*) were applied. Yield was only recorded once per field/year, therefore the calculated mean value per field/year of all other variables were used in the models. Yield was found to be normally distributed, and consequently maximum likelihood (LMER) models with gaussian distribution were fitted, applying the lmer-function in the package ‘lme4’ (Bates et al. 2015). These models consist of a response variable, fixed explanatory variables and random effects, where the specified response variable is yield/inflorescence. The fixed explanatory effects are honeybees, long tongued bumblebees, *B. terrestris*- c, and bumblebee species richness combined in various interactions. Bumblebee species richness was not included in order to simplify the models as the effect was shown not to be significant. Year and field were included as random effects. Estimate significance was tested by comparing models with and without each interaction using the anova-function in R (R Development Core Team 2015). Estimates are significant at p values <0.05.

Each model, both competition and yield, was fitted with various combinations of fixed effects variables, and assessed according to Akaike information criterion, AIC. AIC is a model selection tool finding the best trade-off between how well the model fits the data and the complexity of the model (Akaike 1974; Cavanaugh & Neath 2011). Models with the lowest AIC relative to other models with different combinations of variables are considered best fit (Akaike 1974). Conditional R^2 was calculated for all chosen models, and presents the proportion of the variance explained by both fixed explanatory and random effects (see appendix 3 and 4 for overview of all models with AIC values and conditional R^2).

Level of heteroscedasticity was visually investigated by plotting the fitted residuals, and found acceptable for all fitted models.

3. Results

A total of 17 249 individual honeybees (12 816 in 2014, 4 433 in 2015), and 35 990 individual bumblebees (23 161 in 2014, 12 829 in 2015) were registered in the red clover fields in July and August of 2014 and 2015.

The bumblebees belong to 12-16 different species (table 1). The *B. terrestris*-c was the most common bumblebee functional group and was found in all fields. They represent 58.8% of all observed honeybee and bumblebee individuals across both years, followed by the honeybees at 31.4%, long tongued bumblebees at 6.1 % and short tongued bumblebees at 3.8%. The most common bumblebee species following the *B. terrestris*-c both years was *B. lapidarius*, *B. pascuorum* and *B. hortorum*. They comprised 5%, 4.3% and 2.7% of all observed individuals, respectively. All other bumblebee species represent less than 1% of all observed individuals each, both years. An overview of mean, minimum and maximum number of individuals per functional group at different spatial scales is given in table 3.

Table 3. Mean, minimum and maximaum abundance of the various functional groups recorded in red clover fields in July-August 2014 and 2015.

FUNCTIONAL GROUP	**NUMBER OF INDIVDUALS/FIELD/ REGISTRATION**			**NUMBER OF INDIVDUALS/TRANSECT**			**NUMBER OF SITTING INDIVDUALS/100 INFLORESCENCES**		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
***B. Terrestris*-c**	185.5	64.25	315.25	25	0	105	0.6	0	3.5
Long tongue	21.5	1.5	85.8	2.6	0	27	0.1	0	1.75
Short tongue	14.5	1.3	90.3	1.6	0	36	0.1	0	2
Honeybees	115.3	6.5	263.5	13.3	0	87	0.5	0	4.5
Bumblebee species richness	2.4	1.4	3.6	2.5	0	7	0.3	0	4

Recorded values for the environmental variables; temperature and flower density, ranged between 15-32° C, and 19-524 flowering inflorescences per m^2 at time of recording (table 4).

Table 4. Mean, minimum and maximum values in 2014 and 2015 for the environmental fixed response variables fitted in the models.

	YEAR	MEAN	MIN.	MAX.
Temperature (°c)	2014	25	18	32
	2015	19	15	23
Inflorescences/m^2	2014	207	19	524
	2015	186	24	358

3.1 The effect of honeybees on bumblebee abundance and species richness, and bumblebees on honeybee abundance

Table 5. Generalized linear mixed models with poisson distribution explaining how bumblebee functional groups and honeybees are affected by abundance of other bumblebee functional groups and honeybees, environmental variables and experimental treatments included in PolliClover. Intercept presents a reference variable as the mean value of the response variable when all fixed effects are set to zero. Exp. (Est.) is calculated to rescale the varibles back to the same scale as the original data and ease interpretation. The bold numbers indicate significant variables (p<0.05).

RESPONSE VARIABLE	FIXED EFFECTS	ESTIMATE	EXP. (EST.)	SE	Z	PR(>|Z|)
All bumblebees	Intercept	3.03293	20.7	0.40750	7.443	**<0.0001**
	B. terrestris added (T1)	0.37286	1.45	0.05491	6.791	**<0.0001**
	Phacelia added (T2)	0.17657	1.19	0.02871	6.15	**<0.0001**
	Temperature	-0.03749	0.96	0.01456	-2.575	**0.01**
	Flower density	0.18429	1.20	0.01027	17.937	**<0.0001**
	Honeybees	0.15757	1.17	0.01147	13.735	**<0.0001**
***B.terrestris*-c**	Intercept	2.80682	16.6	0.35816	7.837	**<0.0001**
	B. terrestris added (T1)	0.44315	1.56	0.0581	7.627	**<0.0001**
	Phacelia added (T2)	0.24661	1.27	0.03053	8.079	**<0.0001**
	Temperature	-0.04470	0.96	0.01539	-2.905	**0.00367**
	Flower density	0.24215	1.27	0.01095	22.12	**<0.0001**
	Honeybees	0.17444	1.19	0.01213	14.383	**<0.0001**

RESPONSE VARIABLE	FIXED EFFECTS	ESTIMATE	EXP. (EST.)	SE	Z	PR(>|Z|)
Long tongue	Intercept	0.46177	1.59	0.73624	0.627	0.530528
	B. terrestris added (T1)	-0.29745	0.74	0.13001	-2.950	**0.022147**
	Phacelia added (T2)	-0.32937	0.72	0.05442	-6.053	**<0.0001**
	Temperature	0.06453	1.07	0.02727	2.367	**0.017957**
	Flower density	-0.08139	0.92	0.02094	-3.887	**0.000101**
	Honeybees	-0.00940	0.92	0.02437	-0.386	0.069955
	B. terrestris-c	0.18292	1.20	0.02027	9.024	**<0.0001**
	Honeybees**B.terrestris*-c.	-0.08778	0.99	0.01374	-6.391	**<0.0001**
	Honeybees* *B.terrestris*	-0.31129	0.73	0.18626	-1.671	0.09467
Short tongue	Intercept	-0.460358	0.63	0.57123	-0.806	0.42
	B. terrestris added *(T1)*	0.090981	0.09	0.15064	0.586	0.558
	Phacelia added *(T2)*	0.084608	1.09	0.08386	1.009	0.313
	Temperature	0.004363	1.00	0.03712	0.118	0.906
	Flower density	-0.128463	0.88	0.02520	-5.096	<**0.0001**
	Honeybees	-0.190083	0.83	0.03433	-5.536	**<0.0001**
	B. terrestris-c	0.244291	1.28	0.02592	9.423	**<0.0001**
	Honeybees* *B.terrestris*-c.	-0.035863	0.96	0.02148	-1.670	0.09501
	Honeybees* *B.terrestris* added	0.378594	1.46	0.12701	2.981	**0.00288**
Bumblebee species richness	Intercept	0.8725	2.39	0.21794	4.003	**<0.0001**
	B. terrestris added (T1)	0.09842	1.10	0.07352	1.339	0.18067
	Phacelia added (T2)	-0.04826	0.95	0.03663	-1.318	0.18766
	Temperature	0.03946	1.04	0.02032	1.942	0.05216
	Flower density	0.03255	1.03	0.01434	2.269	**0.02326**
	Honeybees	-0.06382	0.94	0.01649	-3.869	**0.00010**
	B. terrestris –c	0.05784	1.06	0.01539	3.758	**0.00017**
	Honeybees* *B.terrestris*-c.	-0.02223	0.98	0.01043	-2.130	**0.0332**
Honeybees	Intercept	1.47961	4.39	0.27752	5.332	**< 0.0001**
	B. terrestris added (T1)	1.10799	3.03	0.10766	10.2924	**< 0.0001**
	Phacelia (T2)	0.21853	1.24	0.05289	4.132	**< 0.0001**
	Temperature	0.33748	1.40	0.02864	11.7852	**< 0.0001**
	Flower density	0.54587	1.73	0.01961	7.83812	**< 0.0001**
	Long tongue	-0.27483	0.82	0.02194	-12.528	**< 0.0001**
	Short tongue	-0.19365	0.82	0.02786	-6.952	**< 0.0001**
	B. terrestris-c	-0.20273	1.32	0.02178	-9.308	**< 0.0001**

3.1.1 Honeybees

The results from the models (table 5) shows that an increase of 17 honeybees (SD 'Honeybees', table 2) significantly affects the number of bumblebees positively by an increase of 17%, or 3.5 individuals per transect. The *B. terrestris*-c is similarly affected and increase by 19% (3.9 individuals). A similar response in these two groups is not surprising, as the *B. terrestris*- c comprise 86% of all bumblebee individuals. The effect of the same increase in honeybee abundance on short tongued bumblebees on the other hand is slightly negative, as is the effect on bumblebee species richness. The short tongued bumblebees is reduced by 17% (0.11 individuals), and bumblebee species richness by 6% (0.14 species). The long tongued bumblebees are also reduced by 8% (0.13 individuals), but note that this effect is not significant.

To investigate the effects and relationships from a different angle a model with honeybees as response variable was produced (table 5). The results corresponds with the models above, and show that the honeybees are positively affected by most variables, except increased abundance of long and short tongued bumblebees. The relationship between the honeybees and added *B. terrestris* colonies is very strongly positive; the honeybees increase by 203% (8.91 individuals) when colonies are added. The effect of increased abundance of the *B. terrestris* –c by 18.65 individuals (1 SD '*B. terrestris*- c' table 2) is also positive with an increase of 32% (1.40 individuals). The effect of increased abundances of long (4.32 individuals, SD 'Long tongue' table 2) and short tongued (3.60 individuals, SD 'Short tongue' table 2) bumblebees is a decrease of 18% (0.79 individuals) for the honeybees.

3.1.2 *B. terrestris*

Increased abundance of the *B. terrestris*-c (1 SD '*B. terrestris*- c', 18.65 individuals, table 2) has a positive effect on all investigated groups. The long tongued bumblebees increase by 20% (0.32 individuals), short tongued by 28% (0.18 individuals) and bumblebee species richness by 6% (0.14 species). When adding *B. terrestris* colonies, the trend differs slightly. The *B. terrestris*-c is positively affected while the long tongued bumblebees decrease by 26% (0.41 individuals). The short tongued bumblebees and bumblebee species richness is not significantly affected by the added colonies. The positive effect on the *B. terrestris*-c, an increase of 56% (9.30 individuals), clearly indicates that the added colonies were successful and actually contributed to an increased abundance of *B. terrestris*.

3.1.3 Interactions between honeybees and *B. terrestris*

The effect of interactions between honeybees and *B. terrestris* both as functional group and as added colonies, was investigated for long and short tongued bumblebees, and bumblebee species richness. Note that plots are shown for interactions with both significant and not significant effects (figures 3-4).

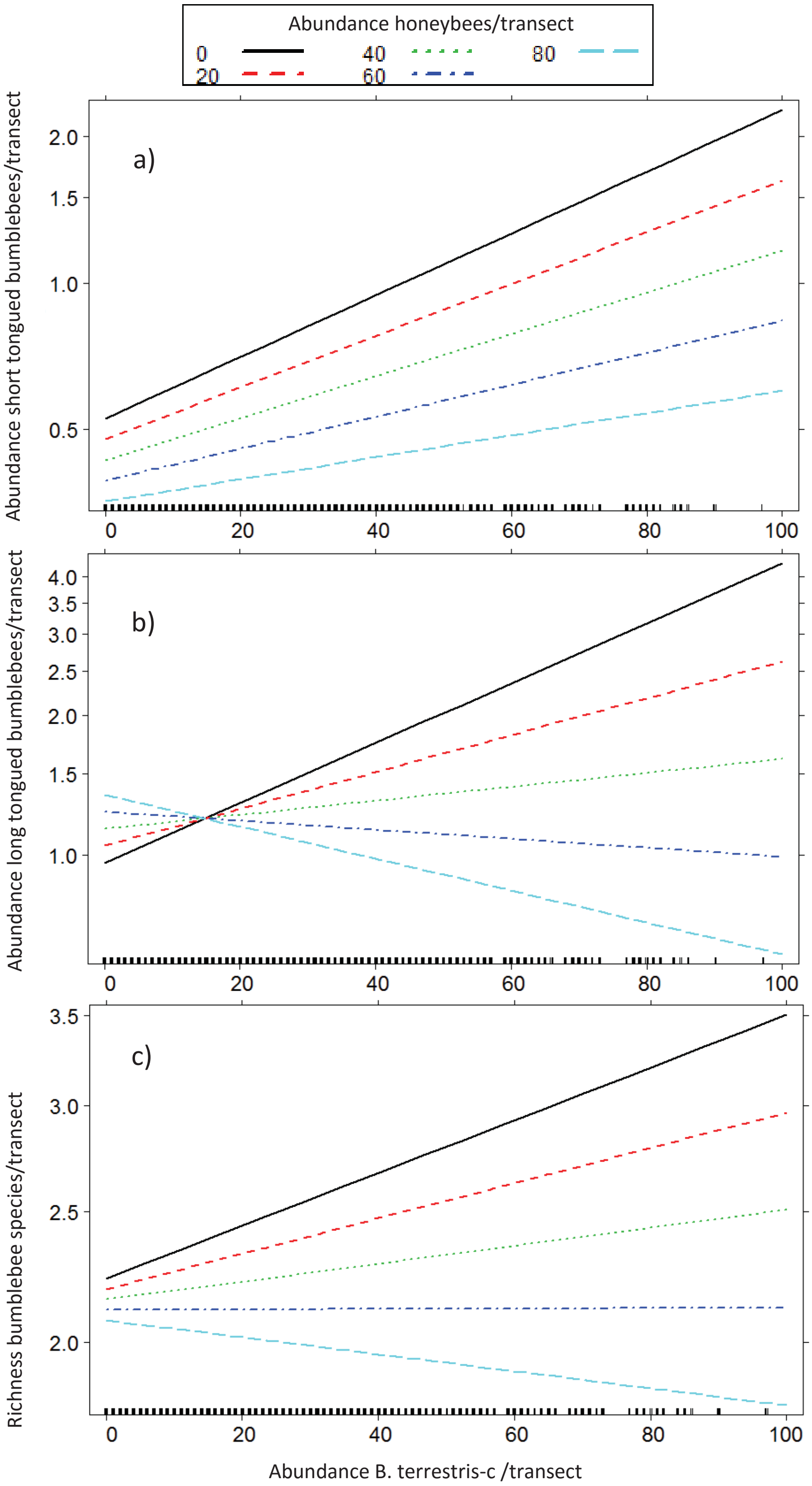

Figure 3. The effect of the interaction between honeybee and the *B. terrestris*-c abundance on a) short tongued bumblebee abundance, b) long tongued bumblebee abundance and c) bumblebee species richness. All other model variables are at their mean values.

As shown in figure 3 b and c, the effect of the interaction between honeybees and the *B. terrestris*-c on the abundance of long tongued bumblebees and bumblebee species diveristy seems to be synergistic and clearly negative. Increasing numbers of honeybees neagatively affects the bumblebees even at low abundance (20 individuals). When the abundance of honeybees is beyond a certain threshold, which in this case seems to be between 40-50 individuals per transect, increasing abundance of the *B. terrestris*–c no longer affects the long tongued bumblebees and species richness positively (figure 3b). The same interaction affects the short tongued bumblebees differently (note that the effect is not significant) , as the *B. terrestris*-c still affects them positively while increasing numbers of honeybees diminish that positive effect (figure 3a).

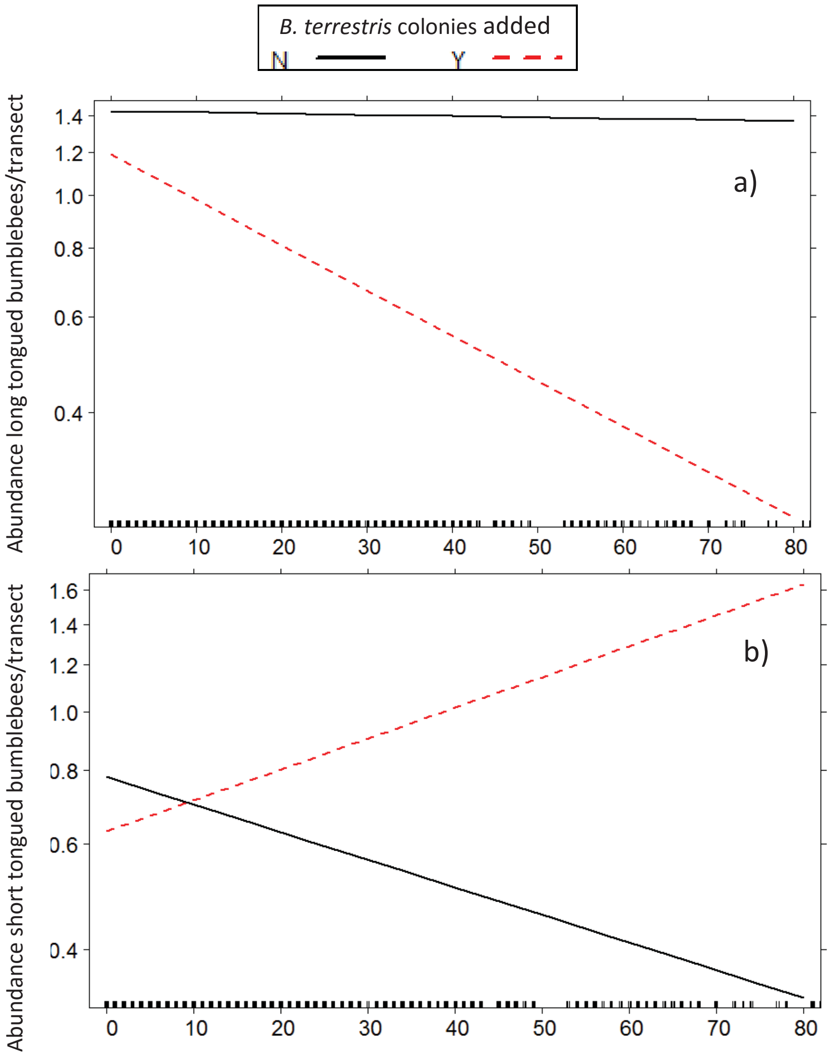

Figure 4. The effect of the interaction between honeybee abundance and added *B. terrestris* colonies on a) long and b) short tongued bumblebees. N= *B. terrestris* colonies added, N= *B. terrestris* colonies not added. All other model variables are at their mean values.

When *B. terrestris* colonies are added to the fields, the effect of increased abundance of honeybees on the abundance of long tongued bumblebees is negative, whilst in the fields without added *B. terrestris* colonies the honeybees exert little impact (figure 4a, note that the effect is not significant). The short tongued bumblebees seems to be positively affected by the interaction between increased abundance of honeybees and added *B. terrestris* colonies, and negatively affected by the honeybees when the colonies are not added (figure 4b). The effect of the above mentioned interaction was not included in the bumblebee species richness model as evaluated by AIC (appendix 3).

3.1.4 Flower density and Phacelia

The effect of increased flower density is estimated as the effect of the increase of 96.07 inflorescences/m^2 (SD 'Flower density' table 2). The *B. terrestris*-c and honeybees are positively affected by an increase of 27% (4.48 individuals) and 73% (3.20 individuals), respectively. Long and short tongued bumblebees are slightly negatively affected by a decrease of 8% (0.13 individuals) and 12% (0.08 individuals) respectively.

Adding Phacelia to the red clover fields again has a positive effect on the *B. terrestris*-c (27%, 4.48 individuals) and honeybees (24%, 1.05 individuals). Phacelia negatively affects the long tongued bumblebees (28%, 0.45 individuals).

3.2 The effect of honeybee and bumblebee abundance on red clover yield

The mean yield/inflorescence was 0.54g (min. 0.09g, max. 4.19g) in 2014 and 0.16g (min. 0.03g, max. 0.99g) in 2015.

Table 6. Generalized linear mixed model with gaussian distribution explaining how the abundance of honeybees an bumblebees affect the red clover yield/inflorescence. Bold numbers indicate significant variables (p<0.05). Intercept presents a reference variable as the mean value of the response variable when all fixed effects are set to zero.

RESPONSE VARIABLE	FIXED EFFECTS	ESTIMATE	SE	T	PR(>|Z|)
[1]**yield/inflorescence 1**	Intercept	0.41876	0.24362	1.719	0.1197
	B. terrestris –c	0.15482	0.02872	5.391	**<0.0001**
	Honeybees	-0.59090	0.04151	-14.236	**<0.0001**
	B. terrestris –c*honeybees	-0.50678	0.08586	-5.902	**0.0006**
Yield/inflorescence 2	Intercept	0.28529	0.18595	1.534	0.1604
	Long tongue	-0.09580	0.06072	-1.578	0.1490
	Honeybees	0.06443	0.06724	0.958	0.3631
	B. terrestris- c	-0.16990	0.06861	-2.476	0.0352
	Long tongue*honeybees	-0.22070	0.06462	-3.415	**0.0019**
	Long tongue**B. terrestris*-c	0.52985	0.04400	12.042	**<0.0001**

[1] Two different models were used to investigate effects on yield to avoid inncluding too many fixed variables in a single model as this could have confounding effects on the results. This warrants caution when interpreting the results.

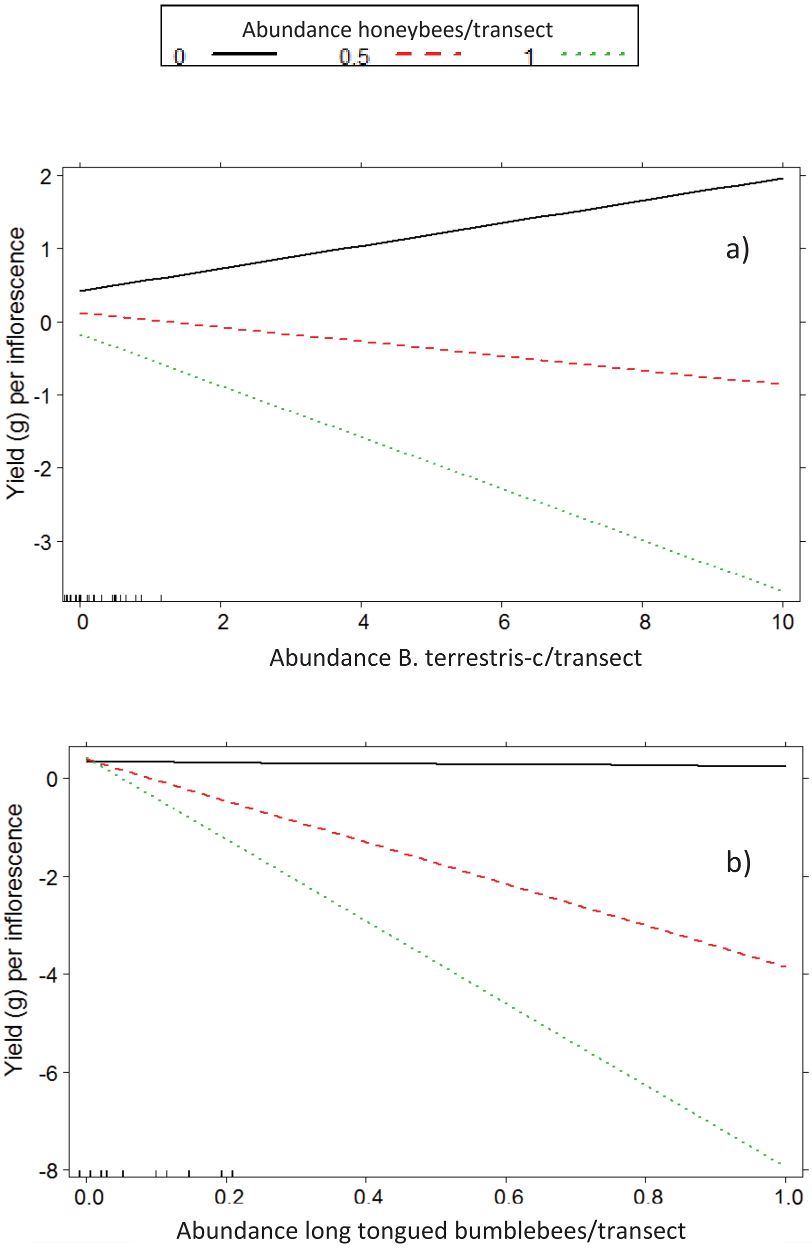

Figure 5. The effect on yield of the interaction between a)honeybee and *B. terrestris* –c abundance, b)honeybee and long tongued bumblebee abundance. All other model variables are at their mean values. Note that the figures derive from separate models.

As indicated by table 6 and figure 5a, increased abundance of the *B. terrestris* –c predicts increased red clover yield when honeybees are absent, but the interaction between honeybees and *B. terrestris*-c is clearly negative. The long tongued bumblebees does not seem to affect the yield in absence of honeybee, but the interaction between honeybees and long tongued bumblebees also negatively affects yield (figure 5b).

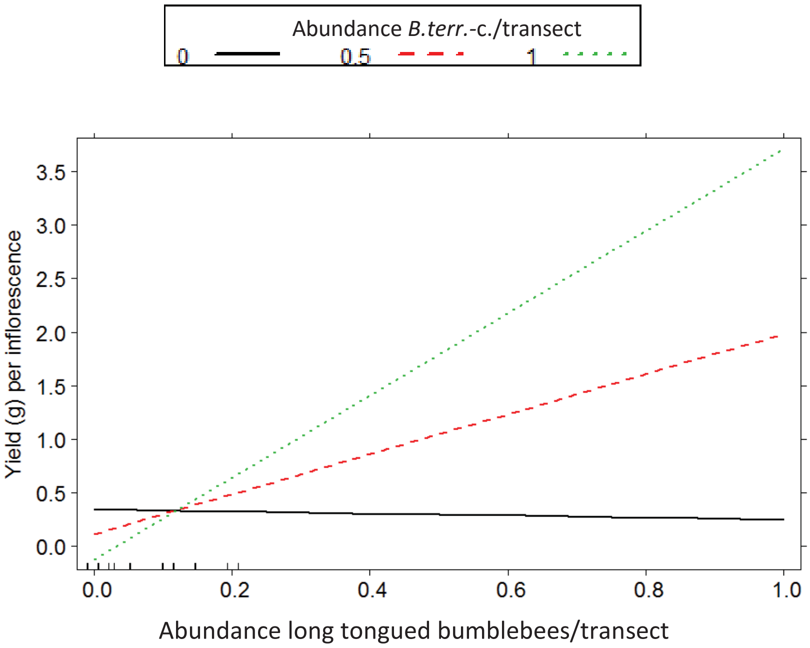

Figure 6. The effect on yield of the interaction between *B. terrestris* –c abundance and long tongued bumblebee abundance. All other model variables are at their mean values.

Interaction between *B. terrestris*-c and long tongued bumblebees shows a positive synergistic effect; the higher abundance of *B. terrestris*-c – the larger effect of long tongued bumblebees on yield. Without the presence of *B. terrestris*-c however, long tongued bumblebees does not show any effect on crop yield (figure 6).

3.3 Comment to between year variations

The results shows a considerable variation between the two years as regards both pollinator abundance and yield. As noted in subchapter 2.1 ‘Study area’, 2015 was substantially colder and wetter than 2014. The mean July temperature was 4.3°C lower (19.8°C vs. 15.5°C) in 2015 than 2014, and the mean July precipitation was 72.45 mm higher (127.75mm vs. 55.3mm), more than double the amount compared to the previous year. The temperatures measured during pollinator recordings shows the same trends (table 4). This difference in weather condition is likely the main cause of the large between year variation in both pollinator abundance and yield.

4. Discussion

The aim of this study was to identify whether competition occurs between honeybees, *B. terrestris* and other bumblebee species in red clover fields, and how these interactions may affect red clover yield.

4.1 Competition

Although we did only manipulate densities of *B. terrestris* and our data is primarily based on correlations, the results suggests resource competition between honeybees and some bumblebees, and *B. terrestris* and long tongued bumblebee species.

Looking at the effect on all bumblebees, honeybees does not seem to out-compete them, contradicting my first prediction (P1). Dividing the bumblebees into separate groups reveals another pattern. This highlights the importance of studying bumblebees in appropriate functional groups according to biology and ecology, or at species level, rather than the genus as a whole. High abundance of honeybees seems to reduce the abundance of short tongued bumblebees and bumblebee species richness. Similarly, the long tongued bumblebees was also reduced at high densities of honeybees, although this effect is only close to significant. These results supports my predictions (first part of P2, P3 and P4) that short and long tounged bumblebees, and hence bumblebee species richness, are negatively affected by honeybees, and may suggest competition between honeybees and some bumblebee species in accordance with the findings of Wermuth and Dupont (2010) and Herbertsson et al. (2016). In contrast and unexpectedly, the abundance of the *B. terrestris*-c and is positively associated with increasing abundance of honeybees. This positive association can be caused by confounding factors such as similar foraging behaviour and preferences connected to parameters not controlled in this study. The positive association between increasing flower densities and both honeybees and *B. terrestris*-c supports this assumption. Nevertheless, the positive effect between the honeybees and *B. terrestris*-c/colonies may also be caused by *B. terrestris* facilitating the honeybees by acting as nectar robbers, behaviour that we did observe frequently during field work (pers. obs.) and which corroborates findings of Palmer-Jones et al. (1966). This allows the honeybees to act as secondary nectar robbers.

B. terrestris-c affects all bumblebee groups positively, and only the long tongued bumblebees are negatively affected by added *B. terrestris* colonies. Again, the positive correlations between the other bumblebees and B. *terrestris*-c may be caused by covariation by factors not included in the models. However, the effects of the experimentally added colonies of *B. terrestris* are more robust to such covariates and clearly indicate that long tounged bumblebees are indeed negatively affected by *B. terrestris,* as predicted (P2). The lack of a direct negative effect of *B. terrestris*-c individuals might also be caused by the fact that *B. terrestis*-c may consist of as many as four different species which might have different effects on long tongued bumblebees despite the fact that they are biologically and ecologically similar. This further emphasize the importance of using experiments when studying interactions between taxonomically difficult species. Regarding the short tongued bumblebees, it is surprising that they are not negatively affected by *B. terrestris*, especially by the added colonies, as they are morphologically similar and utilize resources similarly. The explanation could be that short tongued bumblebee species act as secondary robbers like the honeybees, and so are facilitated by *B. terrestris* in the same way.

The interactions between honeybees and *B. terrestris*-c/colonies further supports the assumption that competition does occur. The honeybees are very strongly and positively affected (203% increase) by added *B. terrestris* colonies. These results substantiates the idea that honeybees could be facilitated by *B. terrestris.* The combination of increasing honeybee and *B. terrestris*-c abundance negatively affects long tongued bumblebee abundance and bumblebee species richness, indicating that increasing *B. terrestris*-c abundance leads to higher abundance of honeybees and thereby increased competition by resource limitation. Honeybees are known to effectively communicate the location of resources worth exploiting to hive members, and have large colonies of up to 80 000 workers. This makes them able to drain large patches of flowers over a short period (Dupont et al. 2015) and efficiently locate favourable sites, such as sites with high densities of nectar robbing *B. terrestries*-c.

The planting of Phacelia may also enhance this effect as it has a positive effect on honeybee and *B. terrestris*-c abundance, and also on other short tongued bumblebees, but negative effect on long tongued bumblebees. Phacelia has shallow flowers which is preferred by short tongued bees such as *B. terrestris* and honeybees. Long tongued bumblebees are able to forage on the short corollas, but often choose not to (Heinrich 1976) as the long tongue is a hindrance increasing handling time (Plowright & Plowright 1997; Pyke 1982b). Planting Phacelia may therefore give the honeybees and *B. terrestris*-c an advantage, and thereby disadvantage the long tongued bumblebees further. How the other short tongued bumblebees are affected by the honeybee/*B. terrestris*-c interaction is not entirely clear. They seem to be facilitated by *B. terrestris*-c and compete with honeybees, maybe because they both act as secondary robbers. Phacelia attracts the short tongued bumblebees, as expected, but increased flower densities reduces their abundance. This further suggests that they do suffer from competition as increased flower densities increases abundance of honeybees and *B. terrestris*-c. But simultaneously, when *B. terrestris* colonies are added to the fields, and thereby boost *B. terrestris* abundance, the honeybees seem to positively affect the short tongued bumblebees. I assume that some of these contrasting results stems from confounding effects.

To conclude, it appears that honeybees are facilited by *B. terrestris*-c as may also be the case for short tonged bumblebees. This facilitative interaction seems to out-compete other bumblebee species, in particular the long tongued ones, and thereby also reduces bumblebee species richness. One Swedish study found that *B. terrestris* and *B. lapidarius* have gone from constituting 40% of the bumblebee community in red clover fields, to near dominance at 89 % over the last 70 years (Bommarco et al. 2012). If this is applicable to Norway as well, it may also be that the exclusion of species has already happened. This is not unlikely as the abundance of both long tongued (6.1% of all recorded pollinators) and short tongued bumblebees (3.8%) is extremely low compared to both *B. terrestris*-c (58.8%) and honeybees (31.4%).

4.2 Yield

Contradictory to my predictions (P5) and the widely supported theory that long tongued bumblebees are the most efficient red clover pollinators (Bommarco et al. 2012; Fussell et al. 1991; Goulson 2010; Palmer-Jones et al. 1966), the long tongued bumblebees actually seems to have none or even a slight negative effect on yield, but show a positive effect of interaction with *B. terrestris-c*. Increasing abundance of long tongued bumblebees positively affects the yield when abundance of *B. terrestris*-c also increase. That they have insignificant effect on yield may arise from the fact that the proportion of long tongued bumblebees in the field is already very low compared to both honeybees and *B. terrestris*-c, and so their contribution to the pollination success may be negligible. As the interaction between long tongued bumblebees and *B. terrestris*-c indicate, competition is not necessarily negative for crop yields. Synergistic effects may arise through species interactions altering the various pollinator species behaviour and thereby boost pollination efficiency (Brittain et al. 2013b). Maloof and Inouye (2000) found that nectar robbing can benefit plant fitness by altering the behaviour of other pollinators. Nectar robbing does reduce the level of nectar available in the flower, but at least one study found that some nectar is often left behind by bumblebees (*B. occidentalis*) (Maloof 1999). When visiting flowers with low level of nectar, bumblebees often change foraging behaviour. They are known to fly longer distances between each inflorescence and visit fewer flowers per inflorescence (Kadmon & Shmida 1992; Pyke 1982a). This may result in increased pollen flow and outcrossing for the plants (Zimmerman & Cook 1985). Low levels of nectar is also connected to less time spent on each flower (Thomson & Plowright 1980). This may reduce the amount of pollen deposited (Thomson & Plowright 1980), but could potentially increase pollination success if less time per flower translates to more flowers visited per time unit (Maloof & Inouye 2000). If these results are applicable to red clover and *B. terrestris* as well, it may explain the positive effect of the interaction between *B. terrestris* –c and long tongued bumblebees on yield, especially as red clover is a self-incompatible plant for which cross pollination is essential for seed set.

The positive effects of nectar robbing may depend on sufficient abundance of efficient pollinators. As indicated by the competition models, the long tongued bumblebees are likely out-competed by *B. terrestris*-c and honeybees. This interaction also reduces red clover yield, and based on other studies (Fussell et al. 1991; Goulson 2010; Palmer-Jones et al. 1966) it is reason to believe that long tongued bumblebees in sufficient abundance are important for red clover seed set. Combined, *B. terrestris*-c and honeybees constitutes 90.2% of the individuals recorded in this study, indicating that not many other bumblebees were present in the fields to significantly affect yield. The negative effect on yield of the interaction between the *B. terrestris*-c and honeybees can be caused by several mechanisms, first of all the nectar robbing. Robbed flowers are not necessarily positively affected as discussed above. Robbing can have detrimental effects through decreased visitation rates (McDade & Kinsman 1980) and reduced seed set (Irwin & Brody 1999). It is evident from both the results in this and other studies that *B. terrestris*-c do pollinate red clover to some extent even when robbing (Brødsgaard & Hansen 2002; Palmer-Jones et al. 1966). The honeybees on the other hand seems to be poorer pollinators of red clover, especially when facilitated by primary nectar robbers. When acting as secondary robbers, as Eaton and Stewart (1969) found that they prefer, the honeybees avoid contact with the pollen grains at all. Some contact is made when they collect pollen, but as they do not pass the anthers and stigma less pollen get attached to the bee. They also have less fur than bumblebees, possibly also resulting in less pollen attaching (Goulson 2010). Willmer et al. (1994) found that at least in raspberries, bumblebees deposited substantially more pollen on the stigmas than the honeybees.

5. Conclusion

This study indicates that competition occurs between honeybees and both long and short tongued bumblebee species. The honeybees may be facilitated by the primary nectar robbing *B. terrestris*-c, an interaction which is likely to out-compete other bumblebee species due to resource limitation, and reduce red clover yields. Positive effect of interaction between *B. terrestris*-c and long tongued bumblebees on yield may suggest that nectar robbing can increase plant fitness by altering the behaviour of other efficient pollinators such as the long tongued bumblebees. This effect likely depends on sufficient abundance of efficient pollinators. High abundance of honeybees and *B. terrestris*-c out-competes the long tongued bumblebees, suggesting that it could be advantageous not to place honeybee hives close to red clover fields, especially if *B. terrestris*-c is already dominant in the fields, in order to conserve the most efficient pollinators.

Conserving the long tongued bumblebees, and indeed other bumblebee species, is not only important for red clover yields, but also to maintain the integrity of many wild flower communities and the intrinsic value of the species.

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7. Appendixes

Appendix 1

Overview of size, location and year of the fields included in the study.

YEAR	FIELD	SIZE DAA	GPS COORDINATES	
			LATITUDE	LONGITUDE
2014	Green1	90	59.55726	10.231962
2014	Green2	100	59.30486	10.087168
2014	Green4	70	59.66027	11.132369
2014	Green5	70	59.40530	10.134177
2014	Green6	40	59.31689	10.217646
2014	Red1	58	59.39395	10.276437
2014	Red2	39	59.29428	10.441363
2014	Red3	100	59.37823	10.362741
2014	Red4	100	59.37179	10.117546
2014	Red5	125	59.65261	10.776839
2014	Black1	150	59.41223	9.974578
2014	Black2	70	59.44698	10.266656
2014	Black3	75	59.74906	9.910340
2014	Black4	50	59.44473	11.342907
2014	Black5	80	59.86528	9.810982
2014	Blue1	60	59.60051	10.908689
2014	Blue2	80	59.64555	11.047432
2014	Blue3	95	59.53348	9.824106
2014	Blue4	61	59.54925	11.277310
2014	Blue5	70	59.27661	10.291268
2015	GREEN1	50	59.59511	10.235869
2015	GREEN4	70	59.66220	11.131706

2015	GREEN5	45	59.41256	10.133231
2015	GREEN7	50	59.54147	10.371637
2015	BLACK1	150	59.33592	9.921260
2015	BLACK4	50	59.45558	11.346309
2015	BLACK5	80	59.86397	9.816785
2015	BLACK6	50	59.75100	9.901869
2015	BLACK7	70	59.62577	10.816133
2015	BLACK8	35	59.29983	10.351585
2015	BLUE1	60	59.59725	10.900977
2015	BLUE2	100	59.63492	11.045129
2015	BLUE4	52	59.52965	11.382311
2015	BLUE6	75	59.66051	10.223597
2015	BLUE7	60	59.26062	10.281580
2015	RED1	60	59.38650	10.272299
2015	RED2	39	59.29389	10.440571
2015	RED3	80	59.37429	10.388665
2015	RED4	100	59.38282	10.122885
2015	RED6	50	59.28989	10.324332

Appendix 2

Correlation matrix for the fitted variables in the GLMM and LMER models. The data derive from stage 1 and 2 of the pollinator recordings, where the *B. terrestris*-c sitting, Long sitting and Honeybees sitting belongs to stage 2. Correlations between the two different stages have not been calculated as they are not fitted to the same models. Bold, italic numbers indicate variables fitted in the same models.

	All bumblebees	*B. terrestris*-c	Long tongue	Short tongue	Species richness	Honeybees	Temperature	Mean flower density	*B. terrestris*-c sitting	Long sitting	Honeybees sitting
All bumblebees	1	0.97	0.42	0.42	0.5	***0.37***	***0.34***	***0.36***	-	-	-
B. terrestris-c		1	***0.18***	***0.21***	***0.32***	***0.36***	***0.30***	***0.44***	-	-	-
Long tongue			1	***0.21***	0.66	***0.02***	***0.24***	***0.00***	-	-	-
Short tongue				1	0.40	***-0.08***	***0.14***	***-0.15***	-	-	-
Species richness					1	***0.03***	***0.31***	***0.14***	-	-	-
Honeybees						1	***0.38***	***0.48***	-	-	-
Temperature							1	***0.20***	-	-	-
Mean flower density								1	-	-	-
B. terrestris-c sitting									1	***0.16***	***0.06***
Long sitting										1	***-0.05***
Honeybees sitting											1

Appendix 3

Overview of the fitted models investigating the relationship between bumblebee functional groups, bumblebee species richness and honeybees presented with AIC value and degrees of freedom. The models chosen for further analysis are written in bold. R^2 is presented for chosen models.

RESPONSE VARIABLE	FIXED EXPLANATORY VARIABLES	RANDOM EFFECTS	DF	AIC	R^2
Bumble-bees ~	**bombus_colony + p.tenacetifolia + scale(temperature) + scale(mean_flow)+ scale(honeybees)**	**+(1 | year)+(1 | field) + (1 | recording)+(1 | id)**	**10**	**28734.10**	**0.79**
	bombus_colony + p.tenacetifolia + scale(temperature) + scale(mean_flow)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	9	28915.68	
	bombus_colony + p.tenacetifolia + scale(temperature)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	8	29647.49	
	bombus_colony+p.tenacetifolia	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	7	30116.99	
	bombus_colony	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	6	30179.07	
		+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	5	30204.85	
***B. terrestris-c* ~**	**bombus_colony + p.tenacetifolia + scale(temperature) + scale(mean_flow)+ scale(honeybees)**	**+(1 | year)+(1 | field) + (1 | recording)+(1 | id)**	**10**	**28026.68**	**0.77**

RESPONSE VARIABLE	FIXED EXPLANATORY VARIABLES	RANDOM EFFECTS	DF	AIC	R^2
	bombus_colony + p.tenacetifolia + scale(temperature) + scale(mean_flow)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	9	28225.03	
	bombus_colony + p.tenacetifolia + scale(temperature)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	8	29203.33	
	bombus_colony+p.tenacetifolia	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	7	29657.17	
	bombus_colony	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	6	29746.22	
		+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	5	29769.60	
Long tongue ~	**p.tenacetifolia + scale(temperature) + scale(mean_flow) + scale(honeybees)*scale(b.terrestris) +scale(honeybees)* bombus_colony**	**+(1 | year)+(1 | field) + (1 | recording)+(1 | id)**	**13**	**11775.27**	**0.76**
	p.tenacetifolia + scale(temperature) + scale(mean_flow+ scale(honeybees)* scale(b.terrestris)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	11	11887.87	
	p.tenacetifolia + scale(temperature) + scale(mean_flow)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	8	11889.67	

RESPONSE VARIABLE	FIXED EXPLANATORY VARIABLES	RANDOM EFFECTS	DF	AIC	R^2
	p.tenacetifolia + scale(temperature)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	7	11904.77	
	p.tenacetifolia	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	6	12029.41	
		+(1 | year)+(1 | field) + (1 | recording)+(1 |id)	5	12055.88	
Short tongue ~	**p.tenacetifolia + scale(temperature) + scale(mean_flow)+ scale(honeybees)*scale(b.terrestris)+ scale(honeybees)*bombus_colony**	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	**13**	**9430.67**	**0.63**
	p.tenacetifolia + scale(temperature) + scale(mean_flow) +scale(honeybees)* scale(b.terrestris	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	11	9507.80	
	p.tenacetifolia + scale(temperature) + scale(mean_flow)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	9	9529.70	
	p.tenacetifolia + scale(temperature)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	8	9559.90	

RESPONSE VARIABLE	FIXED EXPLANATORY VARIABLES	RANDOM EFFECTS	DF	AIC	R^2
	p.tenacetifolia	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	7	9722.60	
		+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	6	9720.62	
Species richness ~	p.tenacetifolia + scale(temperature) + scale(mean_flow)+ scale(honeybees)*scale(b. terrestris) + scale(honeybees)*bombus_colony	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	13	11341.39	
	p. tenacetifolia + scale(temperature) + scale(mean_flow) + scale(honeybees)*scale(b.terrestris)	**+(1 | year)+(1 | field) + (1 | recording)+(1 | id)**	**11**	**11339.01**	**0.34**
	p.tenacetifolia + scale(temperature) + scale(mean_flow)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	8	11362.55	
	p.tenacetifolia + scale(temperature)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	7	11365.58	
	p.tenacetifolia	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	6	11503.46	
		+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	5	11507.05	
Honey-bees ~	**bombus_colony + p.tenacetifolia + scale(temperature) + scale(mean_flow)+ scale(b. terrestris) + scale(short)+ scale(long)**	**+(1 | year)+(1 | field) + (1 | recording)+(1 | id)**	**12**	**23935.50**	**0.72**
	bombus_colony + p.tenacetifolia + scale(temperature) + scale(mean_flow)+ scale(b.terrestris)+scale(short)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	11	24018.17	

RESPONSE VARIABLE	FIXED EXPLANATORY VARIABLES	RANDOM EFFECTS	DF	AIC	R^2
	bombus_colony + p.tenacetifolia + scale(temperature) + scale(mean_flow)+ scale(b.terrestris)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	10	24072.83	
	bombus_colony + p.tenacetifolia + scale(temperature) +scale(mean_flow)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	9	24182.14	
	bombus_colony+p.tenacetifolia+scale(temperature)	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	8	25506.98	
	bombus_colony+p.tenacetifolia	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	7	26073.29	
	bombus_colony	+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	6	26085.65	
		+(1 | year)+(1 | field) + (1 | recording)+(1 | id)	5	26118.69	

Appendix 4

Overview of the fitted models investigating the relationship between pollinator densities, species richness and yield presented with AIC value and degrees of freedom. The models chosen for further analysis are written in bold.

RESPONSE VARIABLE	FIXED EXPLANATORY VARIABLES	RANDOM EFFECTS	DF	AIC	R^2
Yield ~	**Long_tongued*honeybees+ long_tongued*B.terrestris**	**+(1 | year)+(1 | field)**	**9**	**3271.66**	**0.64**
	Long_tongued*honeybees	+(1 | year)+(1 | field)	7	3347.42	
		+(1 | year)+(1 | field)	4	3860.63	
Yield ~	**B.terrestris*honeybees**	**+(1 | year)+(1 | field)**	**7**	**3495.68**	**0.69**
		+(1 | year)+(1 | field)	4	3860.63	

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