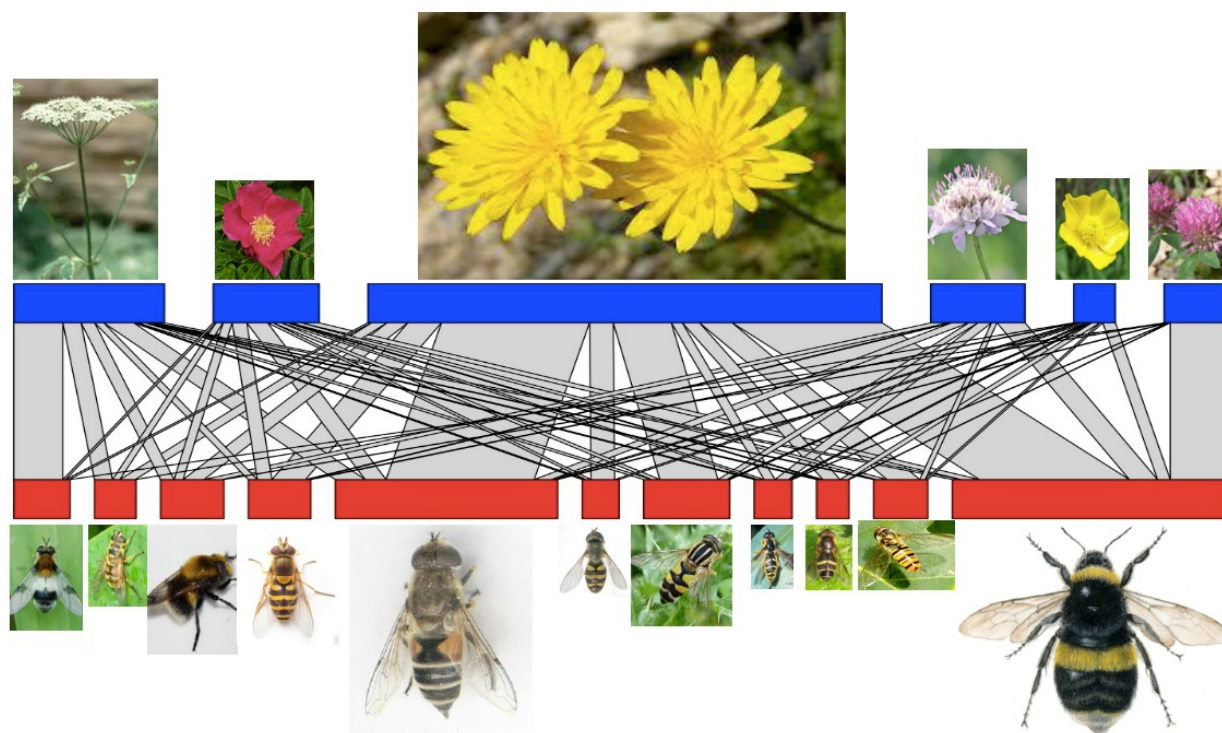


INTERACTION PATTERNS AND SPECIALIZATION IN A LOCAL AND NATIONAL NORWEGIAN POLLINATION NETWORK



Master of Science Thesis
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Abstract

Pollination is an important ecosystem service that is threatened and not very well studied in Norway. Interaction patterns and specialization is one important aspect of pollination that needs to be studied to better understand pollination networks. This study tries to map pollination interactions and the degree of specialization in a local and a national Norwegian pollination network. In addition, bumblebee tongue length, hoverfly flight length and species abundance, are investigated as possible factors correlated with specialization. The local network was from a hayfield and was sampled with transect walks. The national network was sampled from the user based public internet portal artsobsevasjoner.no and a part goal of this study is to evaluate the usability of this portal. Interactions in the networks were not randomly allocated and species had preferences for interaction partners. For instance bumblebees and Fabaceae plants did as expected interact much. Most species had many interactions, classically seen as generalist, but many species had non opportunistic interaction patterns, seen as specialization. Species varied in how specialized their interaction pattern were. For hoverflies from the national network specialization did as expected significantly increase with shorter flight period. Abundance of plants and pollinators showed a varying relationship with the specialization degree of plants and pollinators. Long tongued bumblebees were the most specialized, but this relationship was not significant. The data from the public internet portal was useful, although there are many problematic biases that one needs to be aware of when using such data. That species have preferences for interaction partners and often were specialised should be taken into consideration when evaluating redundancy in pollination networks.

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Introduction

Background

Pollination is the process in seed plants (Spermatophyta) whereby pollen (plant male gametophytes) is transferred from male flower parts to the female flower parts, thus enabling fertilization of seeds. Transfer of pollen can happen between different individual plants, between different flowers within one individual plant and within a single flower (Abrol, 2012). A pollinator is the agent that transports the pollen and if the plant is not self-pollinating this agent is deemed “external”. External pollinator agents can be either biotic or abiotic. Wind is the dominant abiotic pollinator agent, but also water can function as a pollinator agent for aquatic plants (Abrol, 2012). Biotic pollinators are animals, and since this thesis focuses on animal pollinators the term pollinator will only include animals from this point. Many plants need pollinators visiting their flowers to become pollinated, and since animals do not directly gain anything from visiting flowers rewards are often offered to attract the pollinators. Food resources in the form of pollen and nectar are the most prevalent type of reward exist, but also other rewards exist such as a site for protection or oviposition. Some plants do not offer rewards at all and simply trick pollinators into visiting them (called deceptive pollination) for instance through chemical or visual mimicry of food rewards, oviposition sites or potential mates.

Importance of pollination

Animal pollination plays a key role in most terrestrial ecosystems since many plants depend on this type of ecosystem service for reproduction (Potts *et al.*, 2010). It is estimated that 87.5% of the world's flowering plant species are pollinated by animals, with the highest proportion in the tropics (94%) and a bit lower in temperate regions (78%) (Ollerton *et al.*, 2011). Not only is pollination very important for plant reproduction but the pollinators get vital food resources from the process through protein-rich pollen and carbohydrate-rich nectar produced by the flowers as a reward for the pollinators. Therefore animal pollination is usually a mutually beneficial process, crucial for both pollinators and plants.

The world faces formidable challenges in the future concerning global food security (Godfray *et al.*, 2010), and in light of this animal pollination is crucial. Of 115 leading crops 87 are fully or partially dependent on animal pollination, making pollination very important for securing a diverse crop production (Klein *et al.*, 2007). In Norway pollination by animals is important for agricultural

production of fruits and berries, oil seed crops and seeds of legumes (Fabaceae) such as clover (Totland *et al.*, 2013). In terms of crop volume animal pollination-dependent crops comprise 35% of world production (Klein *et al.*, 2007). Pollination is also important for good crop quality and production of seeds (Bommarco *et al.*, 2012b; Klatt *et al.*, 2014). Economically, pollination of crops is estimated to have had a value of €153 billion in 2005, representing 9.5% of the total world crop value in that year (Gallai *et al.*, 2009). In particular, wild pollinators seem to be very efficient crop pollinators; enhancing fruit set by twice as much as honeybees (Garibaldi *et al.*, 2013). In summary, a healthy animal pollination service by both wild and domestic pollinators is important for global food security, and is of large economic value.

The Pollinators

The dominating pollinators are insects, but other animals such as bats, lemurs and birds can also pollinate (Abrol, 2012). Many insect taxa may function as pollinators, but bees (Apiformes) are widely considered as the most important pollinator taxa (Winfree *et al.*, 2011). Other insect taxa that may serve as pollinators are flies (Diptera), butterflies and moths (Lepidoptera), beetles (Coleoptera), thrips (Thysanoptera), and non-bee hymenopterans such as ants (Formicidae) and sawflies (Symphyta) (Abrol, 2012; Winfree *et al.*, 2011; Kevan and Baker, 1983).

Bees are commonly considered the most important pollinators for various reasons for instance including them often being the most frequent flowers visitors worldwide (Neff and Simpson, 1993). All the approximately 20 000 known bee species are obligate florivores (Winfree *et al.*, 2011) and are highly adapted for feeding on flowers and transporting pollen (Kevan and Baker, 1983). The domesticated honeybee (*Apis mellifera*) is the most economically valuable pollinator, since it pollinates monoculture crops worldwide (Klein *et al.*, 2007). Wild bees, on the other hand, are very important for pollination of wild plants. Bumblebees (*Bombus* spp) are one group of wild bees whose distribution is primarily throughout the northern hemisphere (although domesticated/commercialized bumblebees also exist) (Abrol, 2012), and are especially important pollinators of wild plants, as well as of many crops (Goulson *et al.*, 2008).

Flies are frequent visitors of flowers, but in generally they are considered inefficient pollinators since they often have less hair to which pollen can be attached (Totland *et al.*, 2013). They can, however, still be classed as important pollinators since they are often present in high numbers (Totland *et al.*, 2013). Some fly taxa are considered to be more efficient and important pollinators

than others, including Bombyliidae (beeflies), Muscidae (houseflies) and Syrphidae (hoverflies), but in fact the importance of other fly taxa may be overlooked (Larson *et al.*, 2001). Like bees, adult hoverflies are exclusive flower feeders and are often considered to be the most important fly taxa for pollination, but since fly pollinators in general are not very well studied, the importance of hoverflies as pollinators is difficult to judge (Larson *et al.*, 2001).

Pollinator decline

There is evidence indicating a global decline in pollinators (Kearns *et al.*, 1998; Potts *et al.*, 2010), with most evidence coming from Europe and North-America (Potts *et al.*, 2010). The precise extent of the decline is difficult to assess because of scarce information regarding pollinator population trends (Lebuhn *et al.*, 2013; Winfree, 2010). Plants that rely on pollinators will, ipso facto, also therefore be negatively affected by this decline and some evidence suggests that this in fact is already happening. A parallel decline in pollinators (notably bees and hoverflies) and pollinator-reliant plants has been found in Britain and the Netherlands (Biesmeijer *et al.*, 2006). This decline in pollinators emphasizes the need to study plant pollinator interactions (Elle *et al.*, 2012).

In recent years many studies have tried to explain possible reasons for the pollinator decline (Winfree *et al.*, 2009; Osborne, 2012; Fürst *et al.*, 2014). Pests and pathogens may threaten wild pollinators through spillover of diseases from domestic pollinators (mainly honeybees) in which diseases are more frequent (Meeus *et al.*, 2011; Fürst *et al.*, 2014). An alien pollinator species (often *A. mellifera* or sometimes the bumblebee *Bombus terrestris*) may compete with the native pollinators for floral resources, and decrease native pollinator populations (Traveset and Richardson, 2006), but whether this actually happens is debated (Stout and Morales, 2009). Pesticides have been shown to be damaging for honeybees (Cresswell & Thompson, 2012; Henry *et al.*, 2012) and recent studies have also shown this for bumblebees (Gill *et al.*, 2012; Laycock *et al.*, 2012; Whitehorn *et al.*, 2012). The actual level of pesticides to which pollinators are exposed to in nature is more or less unknown (Osborne, 2012), though this is critical since it is the key to determining the actual effect pesticides have on pollinator decline.

Land use changes resulting in habitat loss and degradation is often considered the most important factor in pollinator decline (Potts *et al.*, 2010; Goulson *et al.*, 2008). From the middle of the last century massive agricultural intensification in the western world has occurred (Goulson *et al.*, 2008). One of the consequences of this intensification has been the reduction of favourable feeding grounds

for pollinators, such as hay meadows, hedgerows and field margins (Goulson *et al.*, 2008; Kearns *et al.*, 1998). Agricultural intensification has also led to an increase in crop monoculture, a factor recognized in contributing to lower pollinator diversity (Kearns *et al.*, 1998).

Pollination networks

Studying plant-pollinator interactions at the community level is a new trend in ecology which has already yielded important insights into many aspects of these interactions (Bascompte and Jordano, 2007). Understanding the pollination interaction at a community level (rather than at the species level) is important since most pollinators and plants tend to be generalists (Waser *et al.*, 1996). One approach to studying plant/pollinator interactions on a community level is through examining pollination networks. A pollination network is a bipartite mutualistic network in which plants and pollinators are the nodes, and the pollination interactions form the links between these nodes.

Many network estimates can be made when pollination is studied by this method. Some estimates are at species level while others are on the level of the whole network. One important network metric estimate for the whole network is nestedness (Bascompte *et al.*, 2003; Joppa & Pimm, 2010). Nestedness is the tendency of the specialized species (for example a plant visited by few pollinators) to interact with a subset of the interaction partners of a more generalized species (a plant with more interaction partners) illustrated in figure 1 (Bascompte and Jordano, 2007). The nested structure may minimize interspecific competition and therefore enhance coexistence of a higher number of species (Bastolla *et al.*, 2009) Furthermore it is found that the species that contribute most to the nested structure of the network are also the most vulnerable to extinction (Saavedra *et al.*, 2011). This shows that it might be important to use a network approach in studying plant/pollinator interactions as the network structure may be important in determining species diversity, and some species can be more important than others in the preservation of overall species diversity.

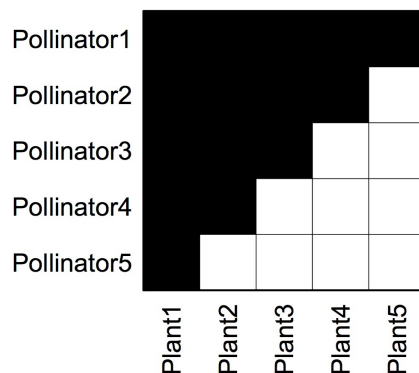


Figure 1: An illustration of a theoretical network matrix with a perfect nested structure.

A network approach for pollination networks may also be applied on a species scale. The level of generalization for each species is a network measure on the species scale. Generalization may be important since specialist species often interact with, and rely on, generalist species (Potts *et al.*, 2010; Bascompte *et al.*, 2003). In this way the generalist species are especially important within the pollination network. It is hypothesised that generalist species are the least vulnerable to change, since they rely on many interaction partners; this is supported by the finding that generalists have prospered while specialists have decreased in the current pollinator diversity decline (Biesmeijer *et al.*, 2006). On the other hand generalist species can be more threatened by factors like diseases and pesticides (Gill *et al.*, 2012; Fürst *et al.*, 2014). Specialization may be defined and measured in many different ways (Dormann, 2011). The classical and simplest way is just in the number of interactions a species has, but more complex measures may often be more meaningful. One way developed (Blüthgen *et al.*, 2006) of looking at specialization is in how much a species deviates from an opportunistic interaction pattern (interacting most with common species).

Pollination in Norway

In Norway there have been relatively few studies on pollination, but a report by Totland *et al.* (2013) states some characteristics of pollination in Norway. The only pollinating animals in the Norwegian fauna are insects. Of wild pollinators bumblebees have a relatively high species richness and abundance in Norway, while in contrast solitary bees seem to have a low abundance and species richness. It can be assumed that flies (especially; hoverflies, houseflies and danceflies (Empididae)) replace solitary bees in Norway and other northern countries. Large differences between northern and southern areas and lowland and mountain areas, render it difficult to make comparisons

between Norwegian pollinator fauna and that of other countries.

Totland et al's (2013) report also state that; most Norwegian plants are generalists in terms of how many interaction partners they have, but specialists do also exist. These often have a zygomorphic shape and a long corolla. Long tongued bumblebees such as *B. hortorum* and *B. consobrinus* are important pollinators of these plants. The proportion of long tongued bumblebees has decreased in Swedish red clover fields, indicating that they may be declining in parallel with the shift in bumblebee community. The production of red clover seeds in Sweden has dropped in production and stability (Bommarco *et al.*, 2012a).

Cultural landscapes in Norway are threatened by overgrowth (Fyhri *et al.*, 2009). and this regrowth, could be having a detrimental effect on the pollination networks. Seen in the context of the global decline of pollinators in which habitat loss, fragmentation and degradation are important factors, this may potentially be a significant threat to the Norwegian pollinator fauna. If the networks are affected this may therefore have consequences for the dynamics of the succession of these landscapes, and might further threaten some species indirectly through this change in pollination dynamics.

Aims

Totland et al.'s (2013) report about the status for Norwegian pollination emphasizes the need for further pollination studies in Norway to improve knowledge in this area. The probable decline of pollinators and the possible harmful effects on plants, seen in conjunction with the economic and ecological importance of pollination, further emphasizes the importance of pollination studies. This thesis will therefore try to investigate pollination with specific respect to Norway. Since many studies have shown that a network approach may be useful in studying pollination, this will be the main approach for this study.

The importance of hayfields for pollination and the fact that this landscape type is threatened (Lindgaard and Henriksen, 2011), makes this habitat especially important to study. The first part of this thesis will therefore consist of a field study of a hayfield. In addition this thesis will also study plant and pollinator interactions on a national scale. For the national scale study, data was obtained from the internet portal artsobservasjoner.no. The portal could provided pollination data from the whole of southern Norway, which mad useful for studying pollination. The use of internet portal

will also be evaluated in the study.

Totland et al.'s report states that there has been no systematic mapping of which pollinators visit which flowers in Norway. This study will emphasize bumblebees and hoverflies, two important pollinating taxa in Norway both of which are relatively easy to identify at species level. As they also are frequently reported on the internet portal artsobservasjoner.no, a large amount of data is available. This study will use both this data and field observations to map which plants these pollinator taxa visit in Norway, to examine if plants and pollinators have preferences in their interaction partners, and if so what particular preferences seem to be common?

Since specialisation is important for to determine how vulnerable species are, another aim of the study is to investigate how specialized plants and pollinators are in their interactions. Do they have many interaction partners or only a few, and to what extent do species deviate from being opportunistic? In addition is there variation in how specialized the species are, and which species are the most specialized?

Materials and Methods

Study site

Sampling for the field pollination network took place in the summer of 2013 (May-August) at Havråtunet on Osterøy, Hordaland, Norway (60.440282°N, 5.574369°E). Havråtunet is an old cluster of farms in a steep south facing slope with a maintained cultural landscape (["http://www.muho.no/havratunet/,"](http://www.muho.no/havratunet/)2013.). The climate is of a typical western Norwegian oceanic type with high precipitation and relatively cold summers and warm winters. The annual mean temperature is 6.9°C (["eKlima,"](#) 2013.), and monthly mean temperatures range from 15.8°C in the warmest month (July) to 0.8°C in the coldest month (February) (Moe and Botnen, 1997). Precipitation levels are at an annual mean of 2 060 mm (estimated from the years 1930-60).



Figure 2: The field location on Havråtunet, with the two sampled transects marked in red (Transect 1) and blue (Transect 2). This is an aerial photo retrieved from ut.no/kart 10.02.14

Field sampling and taxonomic identification

Pollinators were sampled using standardized transect sampling a method that is reviewed by (Gibson *et al.*, 2011). Two approximately 30 m long transects (T1 and T2) located above the farm houses in a steep meadow were visited and sampled throughout the season (Figure 2). A transect walk consisted of walking along the transect for about one hour at a slow pace, and collecting all observed plant-pollinating insects within approximately 1.5 meters distance from the transect. A plant-pollinator interaction was defined as an insect being in contact with the reproductive parts of the plant and hence possibly pollinating the plant. The insects were caught using an aspirator. When an insect was caught it was immediately put in a glass with 70% ethanol for preservation and labelled with the plant species with which it had been interacting. The strategy used for catching the insects was to approach them stealthily during their flower visit. In some cases the pollinator managed to escape. In such cases attempts were made at catching insects in flight immediately after their flower visits, however in most cases these attempts were unsuccessful.

In total, the site was sampled six times for pollination interactions. When it was possible both transects were sampled, but mowing removed all flowers from T1 during the middle of the sampling period and as a result T1 could not be sampled any more. T2 was partially mowed later on during sampling season, thereby shortening this transect by a bit. Sampling of T2 was also partially inhibited by bad weather on one sampling day. In total T1 was sampled 3 times and T2 was sampled fully 5 times. The meadows in T1 and T2 differ in their management regime. T1 was mowed in early June by hand with the use of a scythe, while T2 was mowed by machine in July. Removal of mowed plants for drying was done after mowing in T1, while in T2 the mowed plants were either not removed or removed some weeks later.

Data concerning flower density for the flowering plant species was collected on each sampling day for each sampled transect. Plant sampling was done using a standardized square frame, which was divided into 25 square subplots. The frame was placed along the sampling transect at 10 different places for analysis. For randomization purposes the frame was simply thrown a few meters along the transect for each placing. In the all of the plots the number of subplots where a flowering plant occurred were was counted for each flowering plant species.

All pollinators collected in the field were identified under a stereo microscope. Hoverflies were

identified using the keys in Nationalnycklen (Bartsch, 2009; Bartsch and Binkiewicz, 2009). Bumblebees were identified using an online key (descriptions and illustrations found at <http://touch.artsdatabanken.no/#/Databank/Taxon/Bombus> (19.02.14)) All bumblebees and hoverflies were identified to species level. Other insects were identified to family or order with the use of the identification key by (Chinery, 1993). Plants were identified to species level in the field. Plant taxonomy in this thesis follows Norsk Flora (Lid *et al.*, 2005).

A national pollination network

To make a “national pollination network” for hoverflies and bumblebees, the internet portal artsobservasjoner.no was used. This web service is used by a large number of amateur and professional naturalists for sharing species observations. It was originally developed by the Norwegian Biodiversity Information Centre (Artsdatabanken) in collaboration with five major naturalist organizations, namely the Norwegian Ornithological Society (NOS), Norwegian Botanical Society (NBS), Norges sopp og nyttevekstforbund (NSNF), the Norwegian Zoological Society (NZS) and the Norwegian Entomological Society (NES) (artsobservasjoner.no/info/html, 30.01.13). The database currently comprises more than ten million species observations with information on locality and date for each record. Many of the observations also include photographs which in many cases enable other users to check and verify the identifications.

Possible pollination by bumblebees and hoverflies was identified using photographs in the database. As with the field survey pollination interaction was recorded when a hoverfly or bumblebee in an image was seen to touch the reproductive parts of a plant. The plant species being pollinated was identified to the lowest possible taxonomic level from the picture and from other information the observation contained, such as the location and date of the observation. Some observations also stated the plant species depicted in the image and this information was generally trusted. When recording these plant-pollinator interactions geographic information and the date of the observation were also noted down in addition to the plant and insect species. Identifications of insects in the photographs were controlled against the available literature. All photographs from southern Norway that depicted pollination interactions were used, in addition a few photographs of bumblebees in Nordland county were also included.

Statistics

The data was analysed statistically using the software R version 2.15.1 (GUI 1.52 Leopard build 32-bit (6188)) (R Core Team, 2013). The package “*bipartite*” (2.04) (Dormann *et al.*, 2008) was used for the network analysis. Ordination analysis was performed with the package “*vegan*” (2.0-10) (Oksanen *et al.*, 2013). The package “*splines*” (3.0.2) (R Core Team, 2013) was used for creating a natural cubic spline. For all statistics the standard level for statistical significance was used (P-value < 0.05).

To account for uncertain taxonomic identifications, the national network was analysed on the taxonomic levels of family for plants and genera for animals. This was necessary as many plants could only be identified to family level. Although pollinators mostly were identified reliably to species level, the genus level was used for analyses since many species were only recorded a few times and some species level identifications were still not possible to verify based on the photographs. The field network from Havråtunet was analysed on a species level as far as possible; with only non-hoverfly and non-bumblebee pollinators aggregated at higher taxonomic levels. A second version of the field network was also analysed, on the taxonomic levels of plant family and pollinator genus. The latter version would make comparison to the national network easier.

Before analysis of the networks, nodes with few observations were excluded. The purpose of this exclusion was twofold. Firstly, nodes with few observations are more likely to be wrong, and secondly, plots with fewer nodes are easier to interpret. In addition, nodes with many observations are probably the most important ones ecologically. The level for exclusion was set at three observations for the Havråtunet network and 10 observations for the national network. A smaller exclusion level for the Havråtunet network was used since a level of 10 observations would have reduced the networks too drastically and removed too many species.

To explore which plants and pollinators were associated with each other in terms of interactions, ordination analyses were conducted both for the national and for the Havråtunet network, using non-metric multidimensional scaling (NMDS). In the ordinations, the plant species were interpreted as sites and pollinators as species. The NMDS method was used since it gave the most interpretable plots compared with the following methods; Principal component analysis (PCA), Correspondence analysis (CA), Principal coordinates analysis (PCoA) with Bray Curtis distance, and all methods

with log transformed data.

Different network parameters were calculated for all pollination networks. The parameters used were the following:

- **Connectance:** A measure of how many of the possible interactions in the network that are actually observed, given on a 0 to 1 scale (Rivera-Hutinel *et al.*, 2012). In a bipartite pollination network, connectance (C) is given by the simple formula: $C=I/(P \times A)$ where I is observed interactions and A and P are the respective numbers of animal and plant species in the network (Rivera-Hutinel *et al.*, 2012). High connectance is assumed to indicate that a network is more stable and contains many generalists. Connectance is highly dependent on network size and will decrease with the size of the network. Comparing connectance between networks directly is therefore not possible.
- **Web-asymmetry:** Asymmetry in the number of animal and plant species in the network is given by the equation $A-P/(A+P)$ where A animals and P is plants (Blüthgen *et al.*, 2007). A positive number would therefore indicate more pollinator species than plant species. This metric has been shown to be correlated with asymmetry in specialization between plants and pollinators so that the least abundant group is the most specialized (Blüthgen *et al.*, 2007).
- **Links per species:** The mean number of qualitative links for all the species in the web. This is simply the mean number of species of the other group with which each animal or plant species in the network interacts.
- **D':** A measure for specialization on the species level developed by Blüthgen *et al.* (2006). The measure goes from 0 to 1 where 0 is the most generalized and 1 most specialized. The measure is uses the weighted interactions in the network to calculate specialization. It measures specialization as in how much a plant or pollinator discriminates in choice of interaction partners compared with which partners are actually available in total. For instance, a generalist would be an opportunistic plant or pollinator that interacts with species in accordance with their availability. The measure is comparable between networks.
- **H2':** Specialization index for the whole pollination network that is independent of network size; developed by Blüthgen *et al.*, (2006). H2' ranges between 0 and 1 and a high H2' corresponds with a specialized network (ie. a network with many species scoring high d' scores).
- **Specialization asymmetry:** Asymmetry between pollinators and plants in the degree of

specialization. Specialization is estimated for each species using the metric d' and weighted according to the species abundance as done by Blüthgen et al. (2007). Mean d' scores for plants is subtracted from the mean d' score of pollinators. A positive score would therefore correspond to pollinators being more specialized than plants, a negative score to the opposite and a score of zero would indicate plants and pollinators being equally specialized.

For completeness following network metrics were also given; nestedness (in form of nestedness temperature, NODF and weighted NODF), clustering coefficient, interaction diversity and interaction evenness. All these metrics are described in appendix (3).

To see if the networks were more specialized than expected by chance the chance alone H_2 scores were tested against null models. For completeness this was also done for all the nestedness measures. To do this, 1000 null models were created according with the method “vaznull” in R (after Vázquez et al. (2007) for both networks. This method generates random networks in which the marginal totals and the connectance of the original network are kept constant. For testing the natural networks against the null model networks, a standard T test was used.

To see if specialization bore any relationship to the abundance of the plants and pollinators in the network a simple linear regression was performed. This was done for both networks, using the specialization metric d' .

For bumblebees the d' specialization index in the national network was examined in relationship to tongue length, to see if the length of tongue bore any relationship to degree of specialization. The bumblebee species in the network were divided into two groups based on tongue length, following the long/short-tongued classification in <http://touch.artsdatabanken.no> (20.03.14). Specialization in the hoverflies species was examined in relationship to the length of flight season. Length of flight season was estimated from information on main flight period given by Bartsch & Binkiewicz (2009) and Bartsch, (2009). To see if the length of flight season had any effect, different regressions were performed. Different models were tested to see which could best explain most of the variation in the data. The model that did explain most of the variation in the data was a General Additive Model (GAM) with a natural cubic spline that used two degrees of freedom corresponding to one knot.

Results

Havråtunet Network

The pollination network from Havråtunet contained 17 different plant species, 50 different animal taxa and 262 interactions. The true number of pollinator species is likely to be higher than the number of taxa since some taxa that were analysed at family or genus level could contain multiple species. When the rare plants and pollinators were removed (less than 3 obs.) there were 11 plant species, 16 animal taxa left and 208 interactions remaining (figures 3,4). The three most common plant species in the network were *Geranium sylvaticum* (52 obs), *Hypochaeris radicata* (46 obs) and *Ranunculus acris* (46 obs.) (Figure 4). Hoverflies (67 obs.) and bumblebees (55 obs.) were the most abundant taxa of pollinators. Other Diptera families and other bees (*Andrena* and *Lasioglossum*) were also quite abundant with 56 individuals in total. The most abundant pollinator species was the hoverfly *Rhingia campestris* (Figure 3).

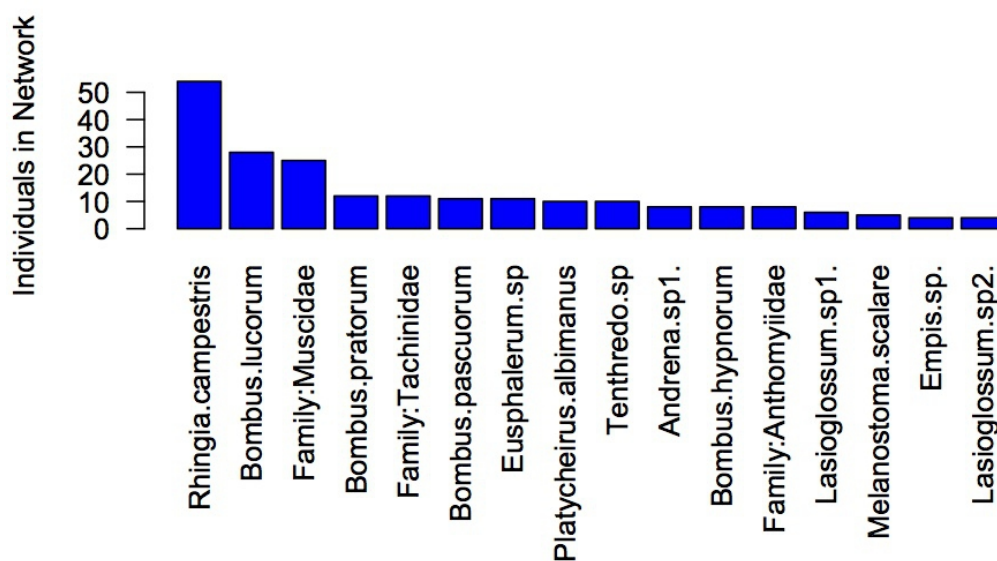


Figure 3: Barplot showing the interacting pollinator species at Havråtunet. Only pollinators with more than 3 observations are displayed.

Some differences were observed between the plant species present in the network and the overall presence of plant species at Havråtunet. *Alchemilla* sp for instance is much less present in the network than overall in the field (Figure 4). The plant species *G. sylvaticum* has an opposite pattern with much higher presence in the pollination network than overall (Figure 4).

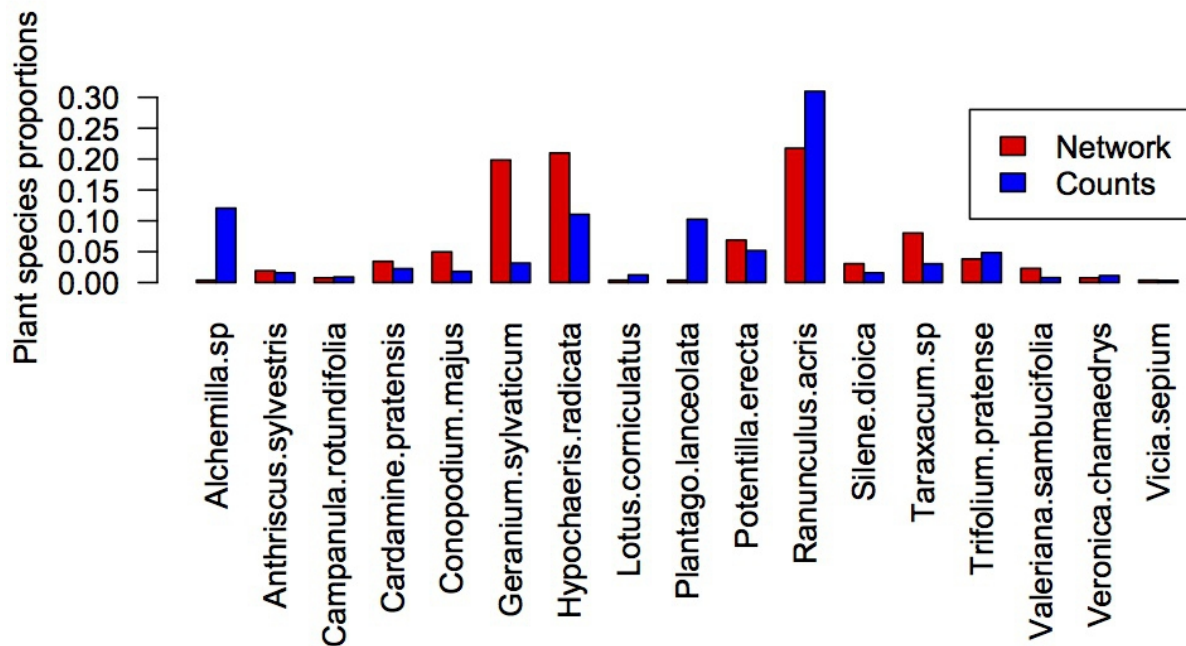


Figure 4: Bar plot of the proportions of plant species present at Havråtunet and in the Network from Havråtunet

Many of these were only observed in small numbers, seen as narrow interaction lines (Figures 5&6). The most common interactions in the network are between *R. campestris* and *G. sylvaticum* (Figure5). *Ranunculus acris* was most frequently visited by Muscidae and Anthomyiidae while *B. lucorum* was a frequent visitor of *H. radicata*.

The different bumblebee species do have similar interaction patterns, as seen by them clustering together on the NMDS plot (Figure7).

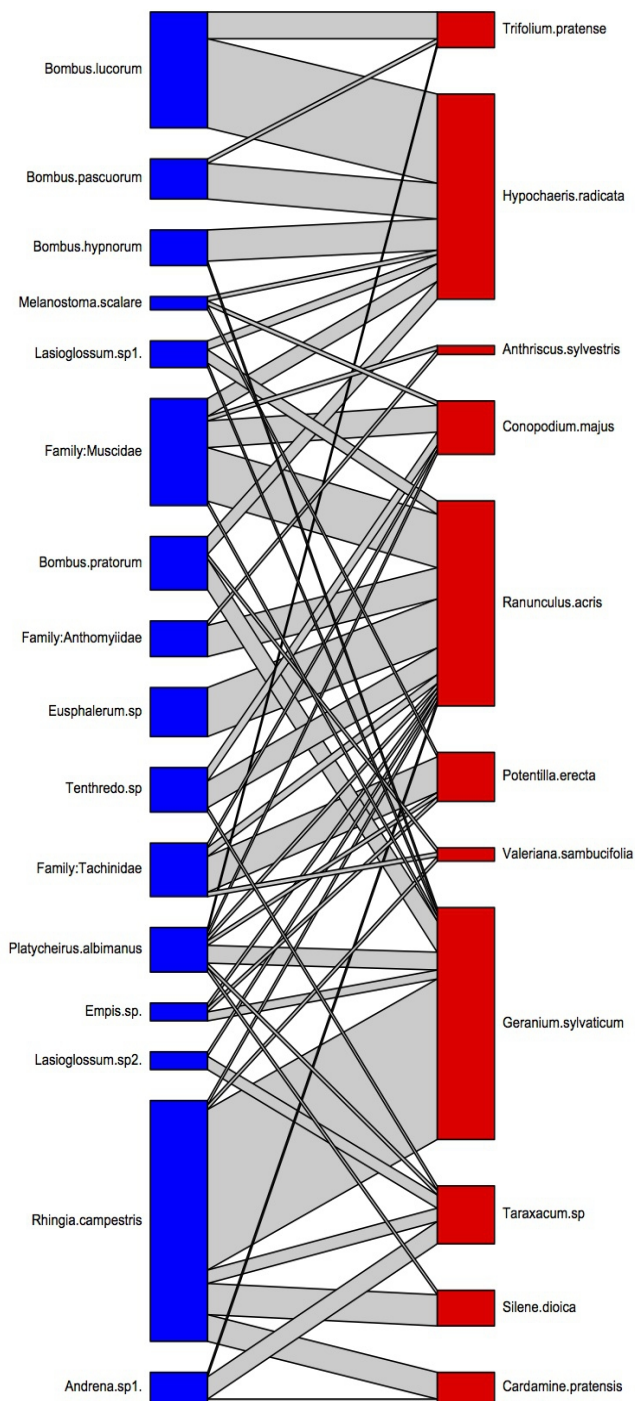


Figure 6: Pollination network from havråtunet. Pollinators are the blue boxes and plants the red.

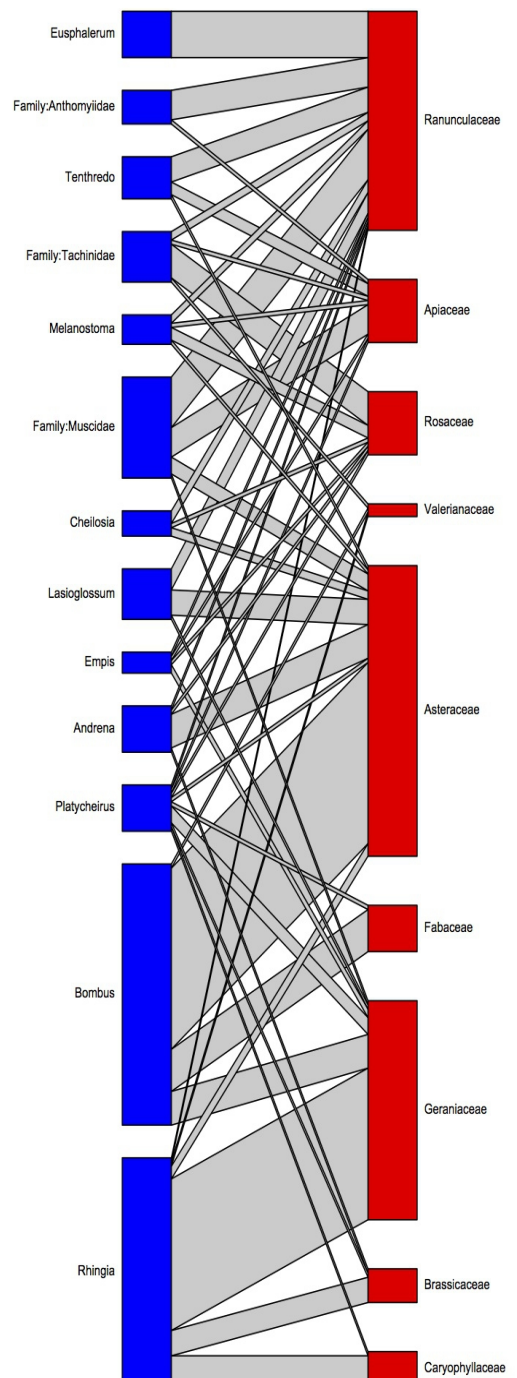


Figure 5: Pollination network from Havråtunet were higher taxa similar to the nation network are used (genera level for pollinators and family level for plants). Pollinators blue boxes and plants red

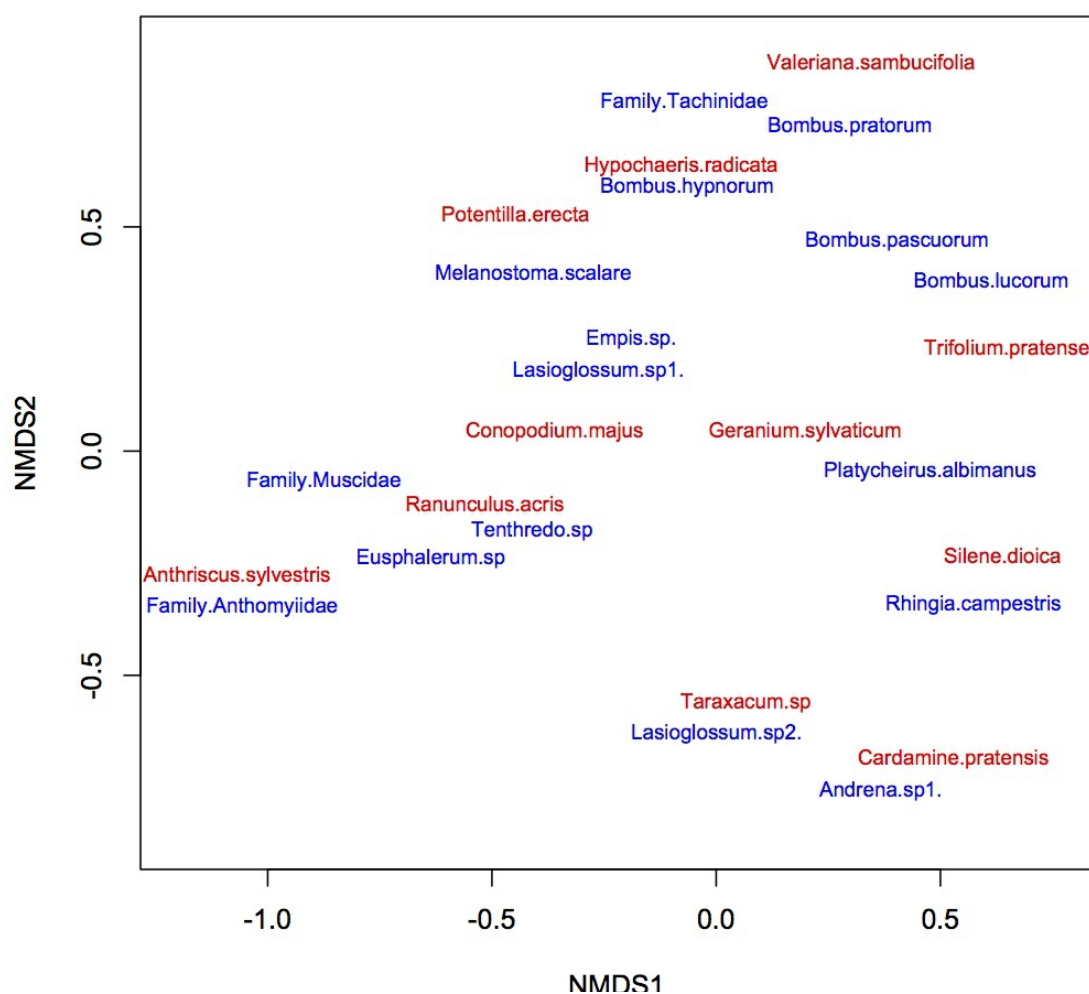


Figure 7: NMDS correspondence analysis of pollination network from Havråtunet, with species present in less than 3 observations removed. Pollinators (Blue) are analysed as columns and plants (Red) as rows.

The chi square test performed on the network matrix was highly significant ($p > 0.001$, $\chi^2 = 576.8$ with 150 df – ie. degrees of freedom), suggesting that the interaction patterns of the Havråtunet were not randomly allocated. The chi square test statistics were similar when the network was analysed on the taxonomic level of plant family and pollinator genera ($\chi^2 = 434.2$, p-value < 0.001 , df = 96). Testing against null models showed that, for all three nestedness measures the Havråtunet network was less nested than expected by chance. On the higher taxonomic level (using family for plants and genera for pollinators) the nestedness temperature measure showed that it was more nested than the null model networks, while the two other measures showed the opposite.

National network

In the national network consisted of 1880 interactions. When plants and pollinators with less than 10 observations were removed 1682 interactions remained in the data. The most common plant families in the dataset were Asteraceae (734 obs.), Apiaceae (223 obs.) and Rosaceae (161 obs) (Figure 9). Of the interacting animals, 372 individual bumblebees and 1310 individual hoverflies were recorded. Frequent genera besides *Bombus* were *Eristalis* (279 obs.) and *Heliophilus* (106 obs) (Figure8).

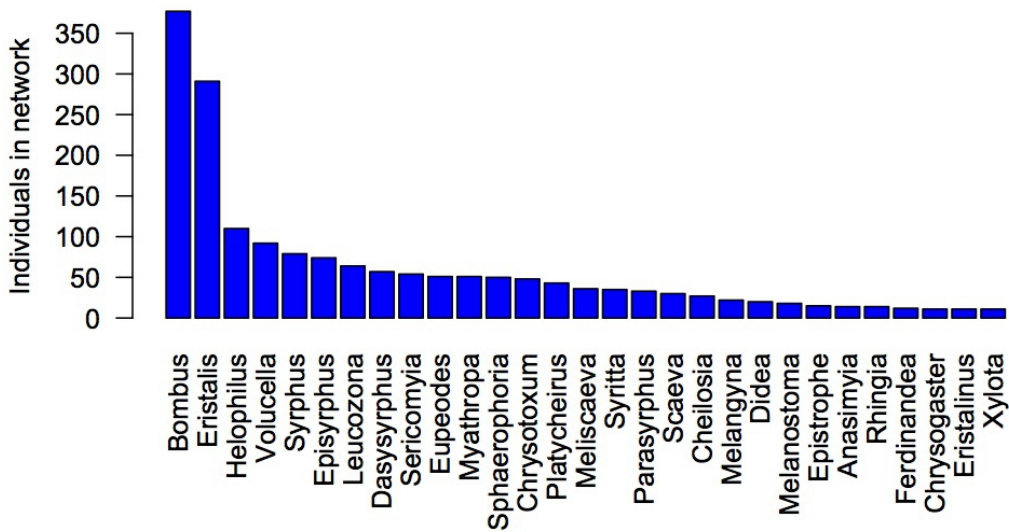


Figure 8: Barplot of pollinator genera in the national network. All genera with more than 10 entries are displayed.

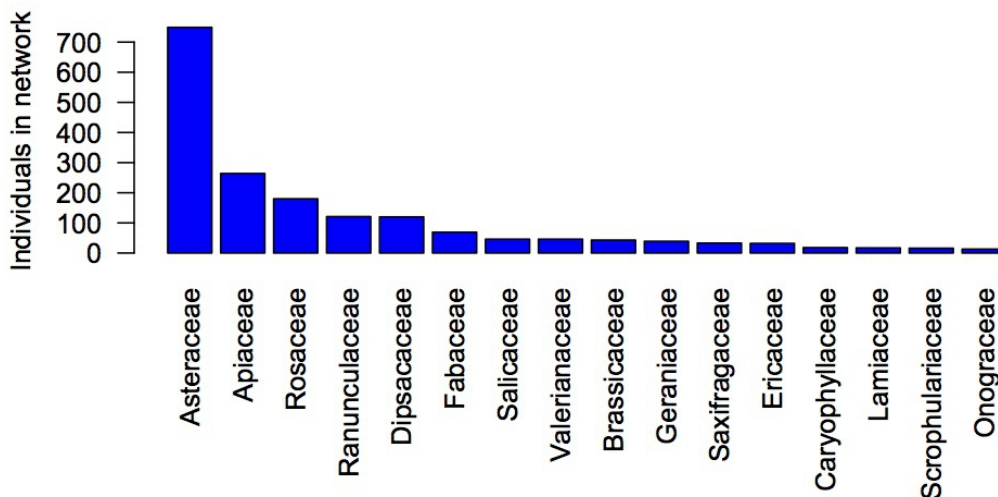


Figure 9: Barplot of plant families abundance in the national network. All families with more than 10 entries are displayed.

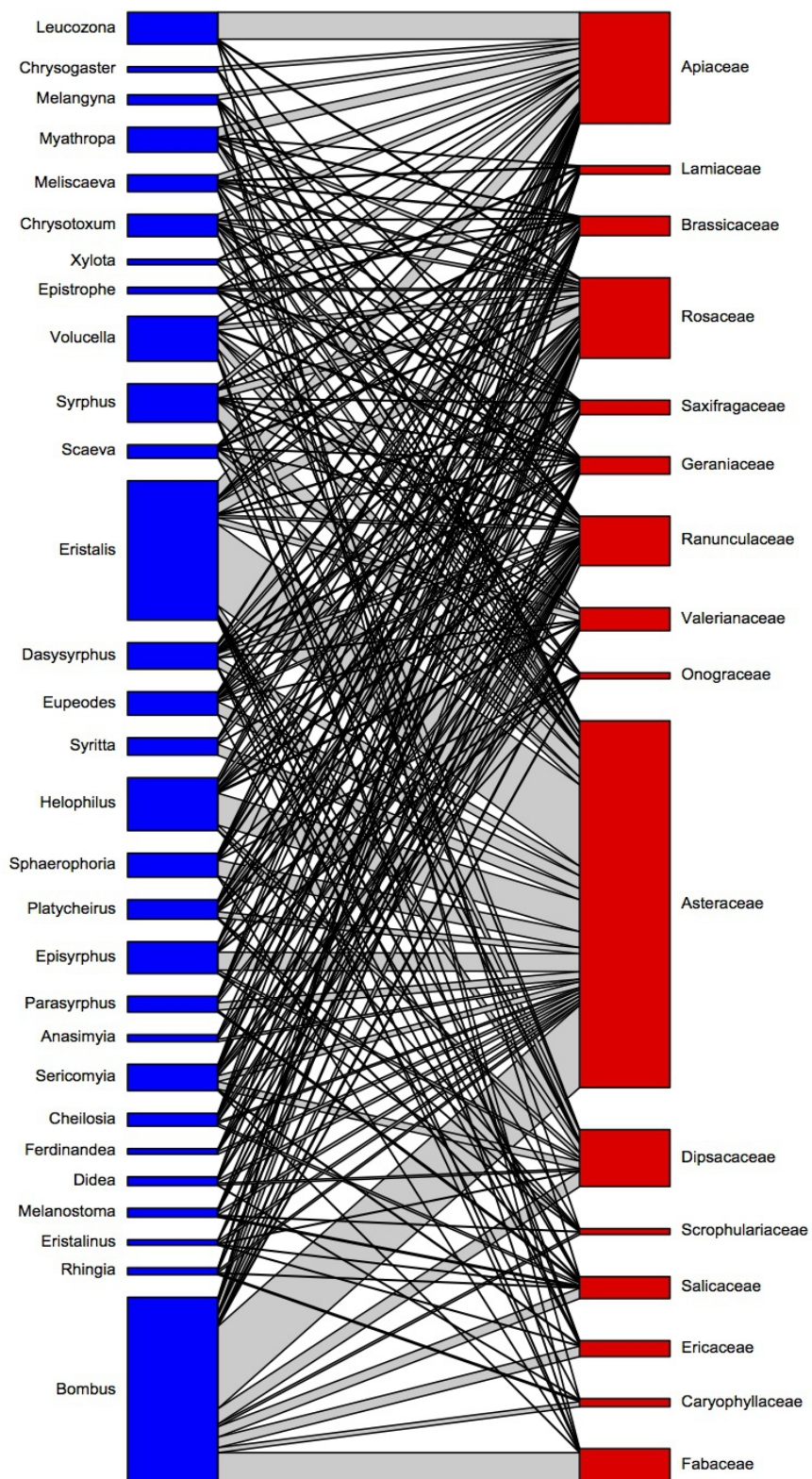


Figure 10: The national pollination network. Pollinators are the blue boxes and plants the red.

The pollination network between pollinator genera and plant families had many frequent interactions (Figure 10). The two most common interactions were between Asteraceae and *Bombus* and Asteraceae and *Eristalis*. In addition, the interactions between Fabaceae and *Bombus* and between Apiaceae and *Leucozona* were particularly interesting as they account for almost all of the interactions observed for one of the groups: 88.4% of Fabaceae's interactions were with bumblebees and 84.3% of all *Leucozona* interactions were with Apiaceae. Apiaceae was also a very dominant interaction partner for two other less frequent hoverfly genera, *Chrysogaster* and *Melangyna* (Figure 10). All interactions are listed in appendix 2.

The NMDS correspondence analysis shows that bumblebees are very closely associated with Fabaceae (Figure 11). The three largest plant families Asteraceae, Apiaceae and Rosaceae were also all closely associated (Figure 11).

Interaction in the national network were, as in the Havråtunet network, not randomly allocated. The chi square test was highly significant ($\chi^2=1809$, p-value <0.001, df=420). The national network furthermore was significantly less nested than the null model networks for all the nestedness measures.

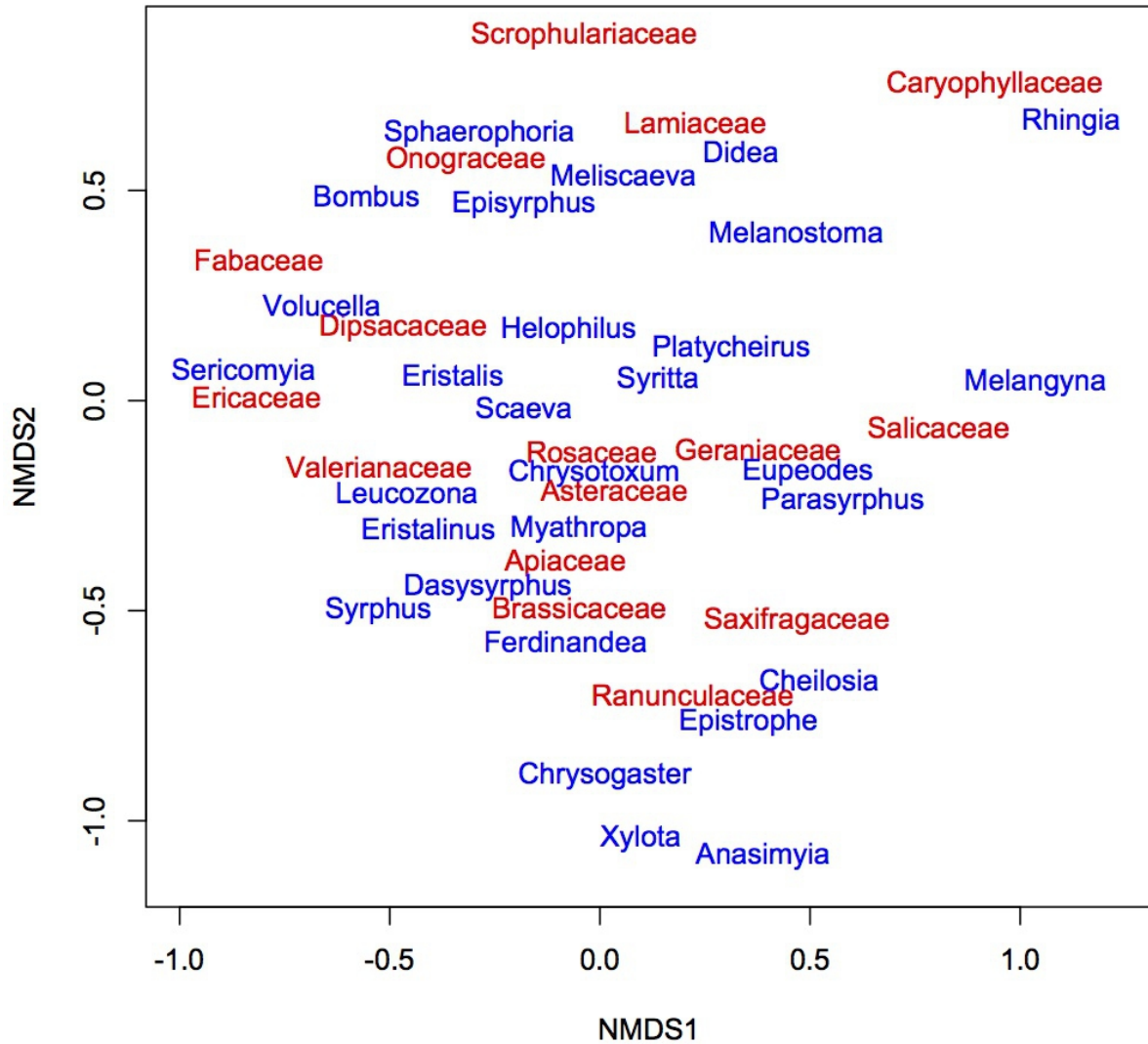


Figure 11: NMDS correspondence analysis of the National pollination network from *artsobservasjoner.no*. Groups observed fewer than 10 times have been removed. Plant families (red) are interpreted as sites and pollinator genera (blue) as species

Table 1: Network metrics from the national network, the Havråtunet network and the Havråtunet network with taxa at higher levels corresponding to the national network (ie. Plants at family level and pollinators at genus level).

Network-metric	Havråtunet network	Havråtunet network, with higher taxa levels	National network
Connectance	0.289	0.427	0.484
Web-asymmetry	0.185	0.182	0.288
Links per species	1.889	2.273	5.000
H2	0.549	0.467	0.190
Specialization asymmetry	-0.093	-0.041	-0.087
Cluster coefficient	0.464	0.759	0.990
Fisher alpha diversity for interactions	21.562	19.537	69.822
Shannon diversity for interactions	3.328	3.173	4.424
Shannon evenness for interactions	0.644	0.666	0.720
Alatalo interaction evenness	0.587	0.536	0.411
Nestedness temp.	35.303	20.565	29.060
NODF nestedness	40.5238095	61.734	67.503
Weighted NODF nestedness	9.648	13.742	28.081

All the networks had more animal taxa than plant taxa and this skewness was largest in the national network seen from the web-asymmetry numbers in table 1. A higher interaction diversity was also observed for the national network, which had higher values in both the Fisher alpha and Shannon diversity (table1).

Specialization

Plants in the Havråtunet network had very varying specialization scores. The most specialized plants were *Potentilla erecta* and *H. radicata*, while the least specialized plants were *Valeriana sambucifolium*, *Anthriscus sylvestris* and *Cardemine pratense* (Figure 12).

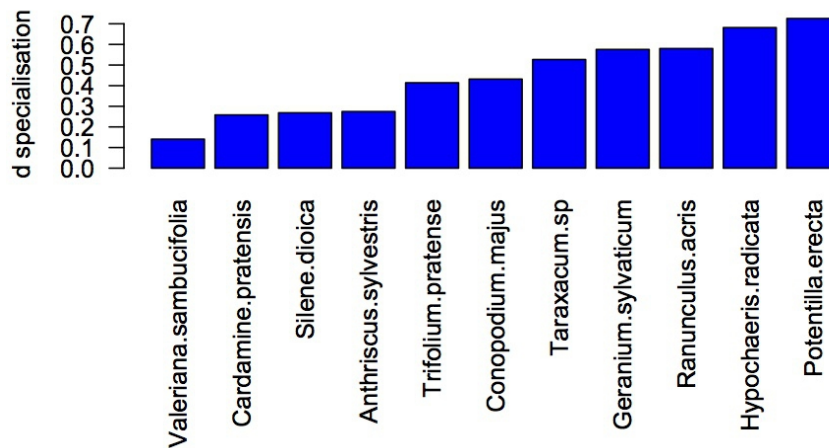


Figure 12: The d' specialization for plant species in the Havråtunet network

Pollinators at Havråtunet also had varying specialization scores. The species *Rhingia campestris* and *Bombus leucorum* clearly had the highest d' scores in the Havråtunet network while *Lasioglossum sp1* and *Platycheirus albimanus* had the lowest scores (Figure 13). The specialization asymmetry was -0.093, corresponding to plants being slightly more specialized than pollinators.

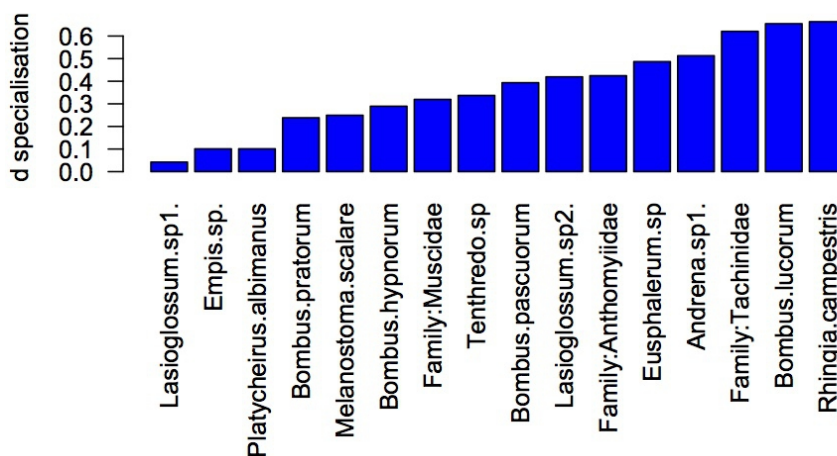


Figure 13: The d' specialization for pollinator species in the Havråtunet network

The plant families in the national network that had the highest d' specialization scores were Apiaceae, Fabaceae and Saxifragaceae, while Rosaceae, Scrophulariaceae and Asteraceae had lowest scores and came out as most generalist (Figure 14). It can be noted that compared with the plants in Havråtunet network, the two Asteraceae species *H. radicata* and *Taraxacum* sp were very specialized, contrasting to the low score for Asteraceae in the national network.

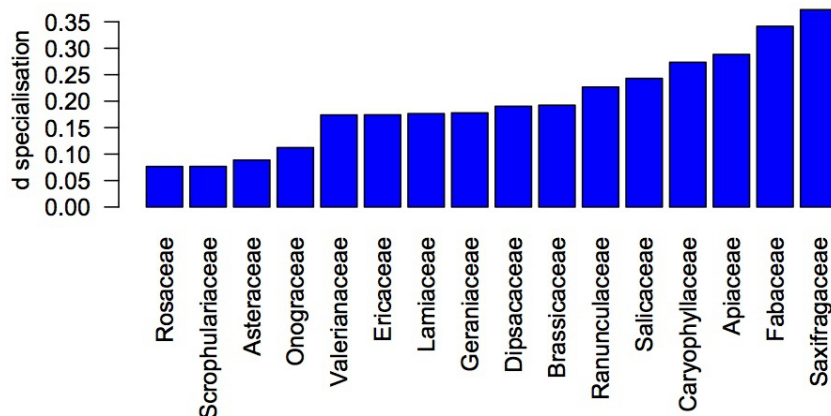


Figure 14: The d' specialization for plants in the national network

The pollinator genera *Leucozona*, *Xylota* and *Rhingia* had the highest d' scores in the national network, while *Scaeva*, *Syrphus* and *Eupeodes* had the lowest d' scores (Figure 15). Plants in the national network were slightly more specialized than pollinators with a specialization asymmetry score of -0.087.

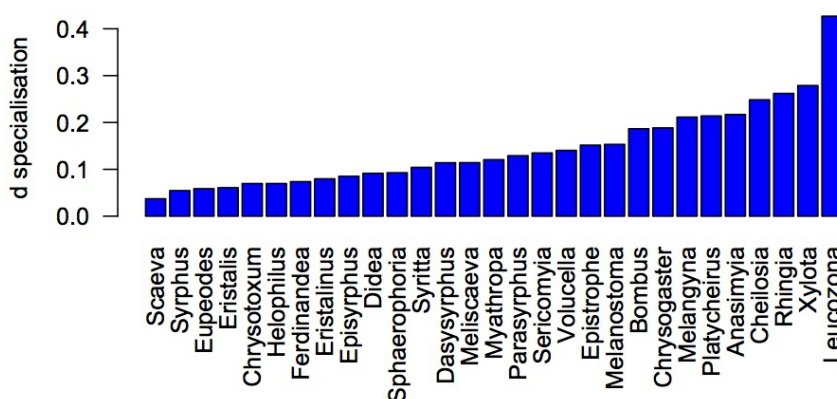


Figure 15: The d' specialization for pollinator genera in the national network.

Specialization scores for pollinators at species level in the national network were also estimated.

For bumblebees the species *B. consobrinus* had the highest d' score, by a large margin (Figure 16). *Bombus. leucorum*, which was one of the most specialized species in the Havråtunet network, had contrastingly a low d' score in the national network (Figure 16).

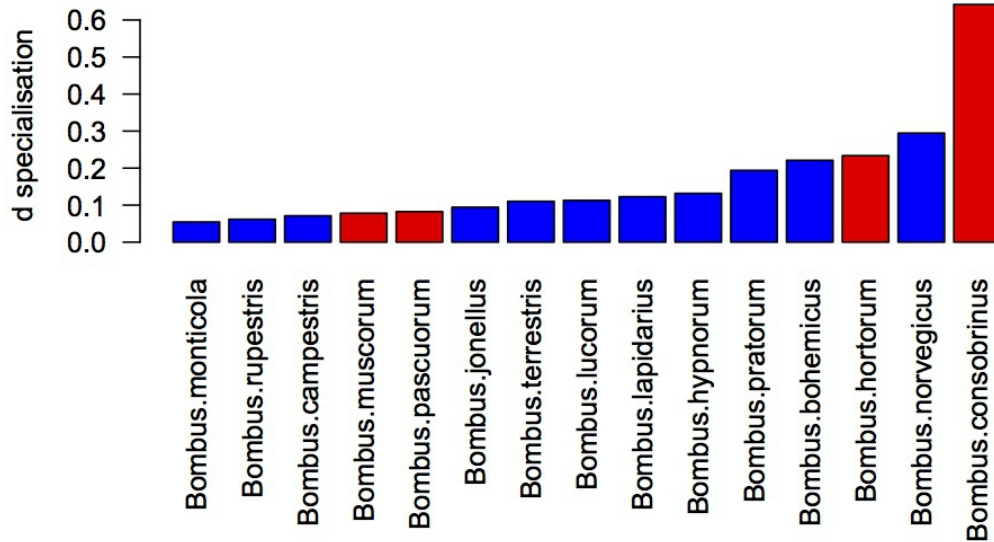


Figure 16: d' specialization of bumblebee species in the national network with more than 5 observations. Bumblebees with long tongues have red bars, while short-tongued bumblebees have blue bars

For the hoverflies the analysis at species level revealed that some genera with many species, such as *Syrphus* and *Eristalis*, had species ranging from the lowest d' scores (*S. vitripennis* and *E. arbustorum*) to medium-high d' scores (*S. torvus*, *E. tenax* and *E. intricaria*) (Figure 17). *Rhingia campestris* did have a high d' score, as it also did in the Havråtunet network. Mean d' scores for bumblebees and hoverflies were not statistically significantly different.

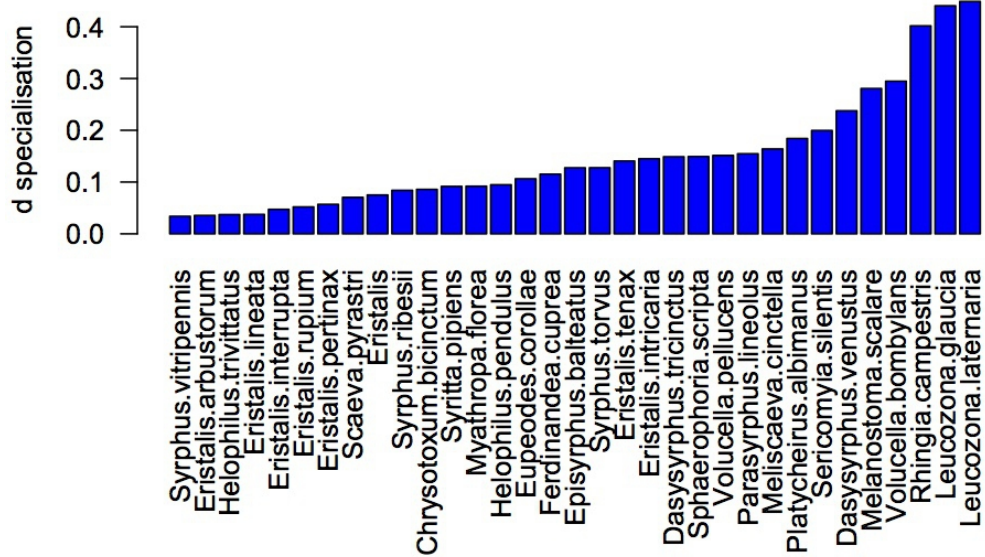


Figure 17: *d'* specialization for hoverfly species with more than 10 observations in the national network

The most specialized bumblebee, *B. consobrinus*, was a long tongued umblebee (Figure 16.). Despite this, bumblebees with a long tongue did not have a statistical significantly higher *d'* value than bumblebees with a short tongue, and it is therefore not possible on the base of this data to conclude that longer tongue lengths are automatically associated with higher degrees of specialization in bumblebees. It may be worth to noting that there were only 4 species of long-tongued bumblebees in the analysis (Figure 16) and that they had a higher variation in *d'* score than the short tongued bumblebees (Figure 18).

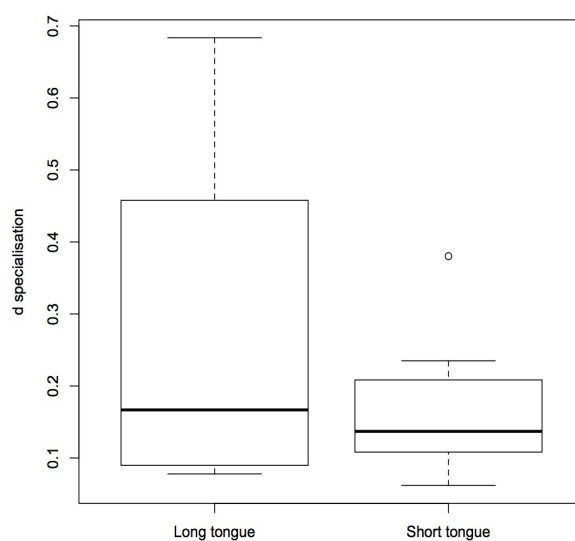


Figure 18: Boxplot indicating the level of *d'* specialization for short and long tongued bumblebees.

Specialization for hoverflies decreased with the length of the flight period. A GAM regression for this relationship showed that this relationship was statistically significant, with a p-value of 0.04. The adjusted R-square value of 0.145 suggests that the gam model explained about 14.5% of the variation in the data. The regression was only statistically significant for species with a flight period shorter than 4.75 months (where the model had its only knot) with a p-value of 0.012. The steepest part of the regression slope was also for flight periods shorter than 4.75. *Eristalis rupium* had a very low specialization level and as well as short flight period, deviating very much from the other species with similar short flight periods.

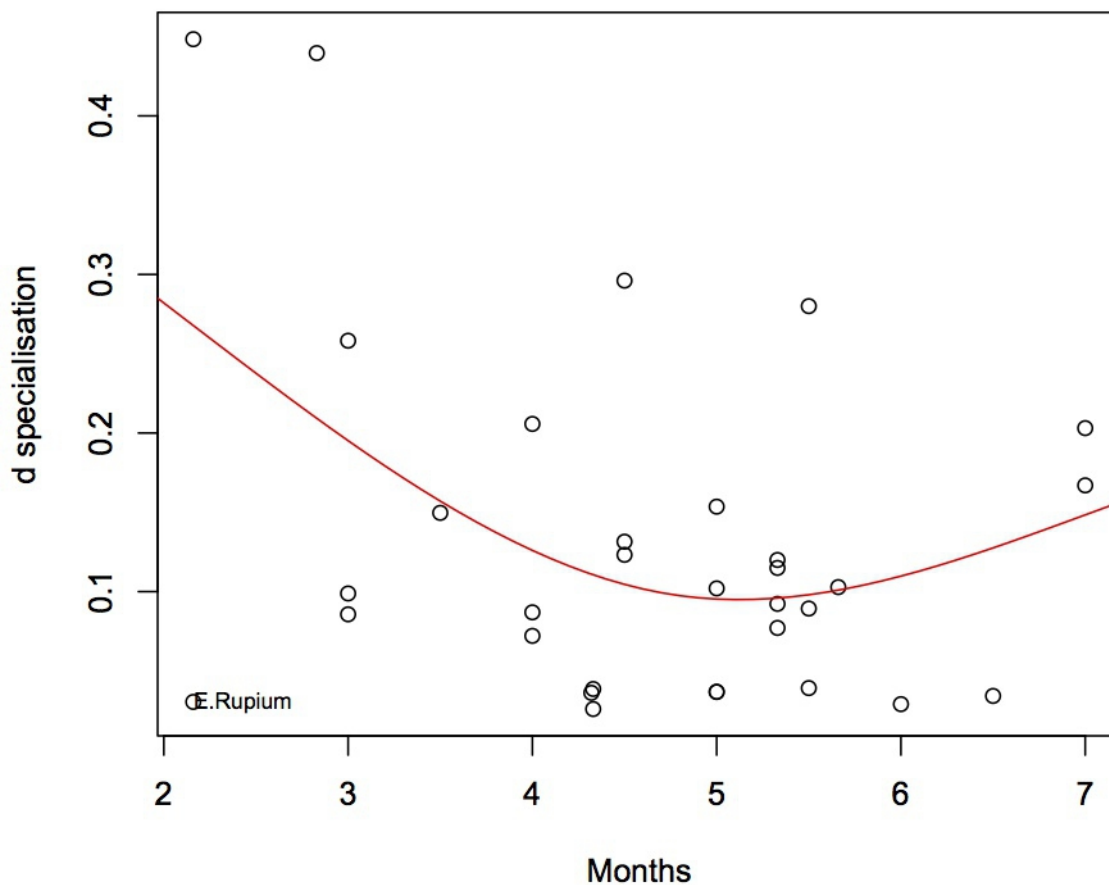


Figure 19: A plot showing length of main flight period (x axis) and d' specialization (y axis) for hoverflies in the national network. The red line is a gam regression line (with a natural spline and two df. used for the creation corresponding to one knot at 4.75 months).

The abundance of plants and pollinators had no statistical significant linear relationship with d' specialization in the national network. For the Havråtunet network, on the other hand, both plants (p -value=0.005) and pollinators (p -value=0.027) had a statistically significant linear relationship between abundance and d' specialization. Plants and pollinators were more specialized when they were more abundant in the network (Figure 20)

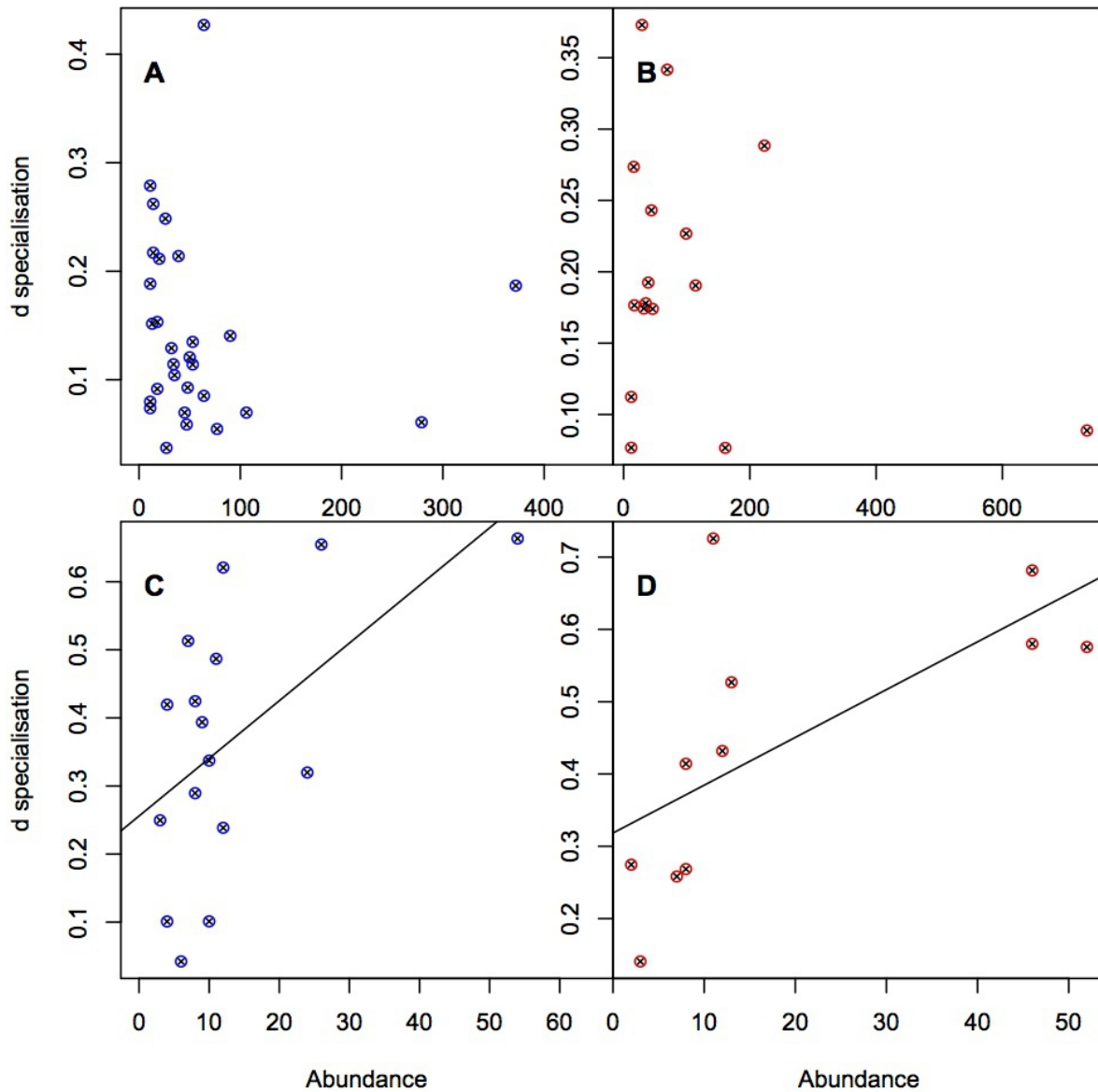


Figure 20: Plant and pollinator abundance plotted against d' specialization for the national and Havråtunet networks. Plot A and B is from the national network, while C and D is from the Havråtunet network. Blue dots are pollinators and red dots are plants. Linear regression lines are fitted when they were statistically significant.

The overall specialization for the networks are found in H2 in table 1. H2 was significantly higher for the national and the Havråtunet network (regardless of taxonomic level) than in their respective nullmodel networks. The Havråtunet network on a comparable taxonomic levels to the national network had a much higher H2 score (0.467 to 0.190). The simpler specialization related metric of links per species which does not take abundance into account, showed a similar pattern whereby the national network had more links per species (more generalised) than the comparable Havråtunet network (Table 1)

Discussion

Interactions

One of the goals of this thesis was to map the pollination interactions in Norway and this resulted in the figures (3, 4 and 10) and the interaction matrix in appendix (1,2). The local network map from the hayfield at Havråtunet and the national network have different properties. The interactions found at Havråtunet, are representative of what the plants and pollinators did at Havråtunet that year. However plants and pollinators may interact with different species in other places and other habitats. This is primarily because different species will be present there, but there are other factors which will also certainly influence interactions. Variations between years might also occur and studies have found a high year to year variation in species composition and interaction composition of pollination networks (Alarcón *et al.*, 2008; Dupont *et al.*, 2009; Petanidou *et al.*, 2008). The results from Havråtunet might therefore well have been a bit different if sampling had occurred in another year. Ideally sampling at Havråtunet should have been carried out over many years, but this was not possible within the frame of a master thesis. The National network will much better represent all the possible interactions a species can have, since it has data gathered from all of southern Norway over several years. The national network does not, however, represent a real-life network, since in reality species are restricted to more localised areas where only a subset of the interaction partners available in the national network are present.

Species in the networks did clearly have different preferences for interaction partners since their interactions were not randomly distributed. The chi square test showed this statistically, but so too did the pollination network figures (5, 6 and 10). That fact that different species exhibited variation in their preferences is not surprising. Seen in the light of global pollinator decline this means that species will respond differently to changes in the composition of the plants and pollinators they with which they interact.

One of the main findings in this study was that Fabaceae was almost exclusively pollinated by bumblebees in the national network. This trend was supported by findings from the Havråtunet network, where *Trifolium pratense* (a clover in the Fabaceae family) was almost only visited by bumblebees. That Fabaceae is largely bumblebee pollinated is expected since Fabaceae is known to be one of the principal pollen sources for bumblebees (Goulson *et al.*, 2005). Clover in particular is known to be pollinated mainly by bumblebees (Totland *et al.*, 2013) and clovers were very abundant

within Fabaceae in the networks. However, although Fabaceae was almost exclusively pollinated by bumblebees in the national network, Asteraceae by far represented the largest interaction path of bumblebees. This contradicts the idea that Fabaceae is the most important food resource for bumblebees (Goulson *et al.*, 2005). The drastic historic shift in bumblebee communities in Sweden, where short-tongued bumblebees have increased in abundance while long-tongued species have decreased (Bommarco *et al.*, 2012a), can also be a reason for this; the long-tongued bumblebees are thought to be the ones most strongly associated with Fabaceae species (Goulson *et al.*, 2005; Bommarco *et al.*, 2012a). The reduction of Fabaceae plants, particularly red clover fields, are hypothesised to be the reason behind this shift of bumblebees (Goulson *et al.*, 2005). A reduction of the abundance of Fabaceae plants would also in itself lead to fewer interactions with bumblebees.

Rhingia campestris was the most common pollinator in the Havråtunet network. This species has long mouthparts and is said to frequently visit plant species that are hard to access for other hoverflies (Bartsch, 2009). At Havråtunet no such patterns were found, but this can be due to the lack of such flowers at Havråtunet. *Geranium sylvaticum*, which was the dominant interaction partner for *R. campestris*, is known to be partially hoverfly pollinated and is therefore probably not hard to access for other hoverflies (Asikainen and Mutikainen, 2005). It nevertheless seems likely that *G. sylvaticum* is an important food resource for *R. campestris* at Havråtunet. *Rhingia* spp, along with *Platycheirus* spp, are thought to be important pollinators of *Silene dioica*, since they carry relatively much pollen and move frequently between plants (Westerbergh and Saura, 1994). *Silene dioica* was also present in the network at Havråtunet, and was visited predominantly by *R. campestris*, but also by *Platycheirus albimanus*. For *S. dioica* and maybe also *Cardamine pratensis* (which also had its visits dominated by *R. campestris*) it seems likely that *R. campestris* was the main pollinator. The same may also be true for *G. sylvaticum*, but then this plant was also visited by bumblebees, known to be highly efficient pollinators (Totland *et al.*, 2013). Indirectly *G. sylvaticum* may contribute positively to pollination of *S. dioica* and *C. pratensis* through attracting high numbers of *R. campestris*, some of which may “spill over” to the other plants. On the other hand, *G. sylvaticum* could negatively affect *S. dioica* and *C. pratensis* through attracting *R. campestris* away from them. However *C. pratensis* does normally bloom before *G. sylvaticum* so in this particular case this is unlikely. Both such positive and negative interactions between plants occur in natural pollinator systems (Hegland *et al.*, 2008).

Hypochaeris radicata, in the Asteraceae family, was mainly visited by bumblebees, and was the most frequently visited plant by all bumblebees except for *B. pratorum* (where it was second most frequent). It therefore seems that *H. radicata* was mainly bumblebee-pollinated at Havråtunet and that it also served as an important food resource for the bumblebees. *Hypochaeris radicata* and bumblebees started appearing at the same time later in the season in high numbers, when other plants and pollinators started to be more infrequent. This match in appearance, in combination with the decline of other species may be a reason for why bumblebees and *H. radicata* did interact so frequently.

Plants at Havråtunet differed substantially between their representation in the network and at the site itself. *Geranium sylvaticum* was for instance very common in the network despite being relatively rare at the site, while the opposite was true for *Alchemilla* sp. Most *Alchemilla* spp. are apomictic plants reproducing by parthenogenesis (Czapik, 1996), and therefore have little need for pollinators, resulting in poor attraction of pollinators and hence few interactions. *Geranium sylvaticum* on the other hand is dependent on pollination and is also pollen-delimited (Asikainen and Mutikainen, 2005). This is, however, probably the case for many other plants in the network, since pollen limitation is very common (Burd, 1994). Why *G. sylvaticum* was such a particularly good attractor of pollinators could potentially be due to its relatively large corolla, a trait known to increase pollinator attraction (Conner and Rush, 1995). The difference in network abundance and site-level abundance of flowering plant species suggests that site-level abundance is a poor predictor of a plants importance for pollinators.

Specialization

Based both on specialization for plants and pollinators was calculated, as was also the total degree of specialization for the networks, there was clearly variation in how specialized plants and pollinators were. Why some species were more specialized than others can be due to many factors, both ecological and morphological. In this study, length of flight period for hoverflies and tongue length for bumblebees were investigated as possible factors contributing to specialization.

Most species in the network had a substantial degree of d' specialization. The networks also had relatively high H_2 scores which were significantly higher than the null model scores. This means that species were not opportunistic in their interaction pattern and supports the observation that

plant and pollinators have preferences regarding the species with which they interact. The classical way of thinking of specialization, is just purely the number of species a species interacts with, and does therefore not take the dimension of opportunism into account. This study therefore does not disagree with the many authors who emphasises generalization in pollination networks (Waser *et al.*, 1996; Jordano *et al.*, 2003; Ghazoul, 2005). The results here also support the view that, while many species have many interaction partners, this does not mean that most species are opportunist. Fründ *et al.* (2010) study has also emphasised the lack of opportunism in pollination networks. How this lack of opportunism relate to the plasticity of pollination networks is important for determining the redundancy of the pollination networks. A lack of plasticity in the general preferences in plants and pollinators may make species, previously considered generalist, vulnerable.

Hoverflies in the national network became more specialized with shorter flight periods (figure 19). That specialization did increase with shorter flight period is expected since fewer plant species would be available in a shorter time span. The same trend is also found for butterflies in the Mediterranean (Stefanescu and Traveset, 2009). The level of generalization seems, however, to reach a plateau at a certain length of flight period, where the pollinators did not become more generalised.

Since a long tongue is a physiological adaption for flowers with long corollas, it can be hypothesized that long-tongued bumblebees would be more selective and hence more specialized than short-tongued ones. However, long-tongued bumblebees were not significantly more specialized than short-tongued ones in the national network and the data from the national network could therefore not support the hypothesis. However the very long-tongued species *B. hortorum* and *B. consobrinus* (*B. pascorum* and *B. muscorum* only have medium to long tongues) (Sikora and Kelm, 2012; Goulson *et al.*, 2005), were very specialized species. This indicated that tongue length indeed can be associated with specialization, but that a certain threshold length is required. Precise tongue length for all species was not possible to find for all the species in this study (although measures were found for many of the species) and therefore a simple approach, with only the two categories of “long” and “short” tongue, was chosen. To investigate more fully the relationship between specialization and tongue length future studies should measure tongue length on the bumblebees, and use mean tongue length for all species.

Both *B. hortorum* and *B. pascorum* are among the long-tongued species that declined in Sweden (Bommarco *et al.*, 2012a). The results from the national network would suggest that specialization is not the reason for *B. pascorum*'s decline. A possible other reason for the decline of *B. pascorum* is that the species has a relatively short foraging range that can make it more vulnerable to habitat fragmentation (Knight *et al.*, 2005; Dupont *et al.*, 2011). For *B. hortorum* however the results suggest that specialization could have made the species more vulnerable. Many studies point to that long-tongued bumblebees are more dependent on Fabaceae plants and clover fields (Knight *et al.*, 2005; Bommarco *et al.*, 2012; Dupont *et al.*, 2011), and this is another probable reason for the decline of both these species.

B. consobrinus is a known super-specialist of *Aconitum* spp, in Norway most importantly *A. lycoctonum*. This dependence can be seen in *B. consobrinus*' distribution, which follows closely the distribution of *Aconitum* spp. (Løken, 1973, 1950; Lavery and Plowright, 1988). It was therefore no surprise that *B. consobrinus* was the most specialized species in the data set, and this could be seen as an indication that the internet portal indeed can be used to reveal ecological phenomena. The fact that this relationship is well known (the Norwegian common name of this bumblebee species is even named after this relationship) could also lead observers to specifically look for, or at least photograph, the species at *A. lycoctonum*. Therefore the data in this network may be biased towards giving *B. consobrinus* an artificially high specialization score. While this is probably is not the case for *B. consobrinus*, ecological patterns revealed by analysis of artsobservasjoner.no or similar databases should nevertheless be controlled against field studies for this kind of bias.

Two of the most frequent plants in the Havråtunet network, *Ranunculus acris* and *H. radicata* came out as very specialized (figure 12), despite having many interaction partners (figure 5). For *Valeriana sambucifolia* the opposite was true as it only had three links and emerged out as the least specialized plant species (figure 5 and 12). This may seem counterintuitive and is a result of the abundance of both the species itself and of the species it is interacting with, which the d' index is designed to take into account (Blüthgen *et al.*, 2006). *Valeriana sambucifolium* was rare in the network and, in relation to its abundance, interacting with many abundant pollinators. Thus, the low numbers of interactions seemed to be a result of low sampling or the rarity of the species, not necessarily a sign of specialization. However it cannot be ruled out that *V. sambucifolium* actually only interacts with the three species and in reality is indeed a specialist. This in any case

demonstrates that the d' index is weak regarding rare species, and that the results from *V. sambucifolium* have a very high margin of error. The opposite pattern would then be true for the species *R. acris* and *H. radicata*. As both *H. radicata* and *R. acris* did not interact and only weakly interact with the most abundant pollinator *R. campestris*, this will therefore have given them higher specialization scores.

Rhingia campestris was the most specialized pollinator in the Havråtunet network. Its lack of interactions with *H. radicata* and *R. acris* contributes strongly to its high d' scores. A mismatch in the time of flowering and the peak time for the *R. campestris* flight period might be an explanation for why these species did not interact. *Taraxacum* sp., an Asteraceae species with very similar flower morphology to *H. radicata*, was visited by *R. campestris*; suggesting that *H. radicata* and *R. campestris* would have interacted had they been present at the same time. Even if this is not the case, *H. radicata* and *R. campestris*, appear to be a so called “forbidden interaction” which therefore imposes a bias regarding how well d' specialization mirrors the degree of opportunism. For the case of *R. acris* and *R. campestris*, however, the lack of interactions may simply be due to preference. This illustrates that specialization can be an attribute both of a species' selectivity and the availability of interaction partners. The genus *Rhingia* was very specialized also in the national network, supporting the findings from Havråtunet. This could be due to the long mouthparts of the species, enabling it to utilize resources efficiently from flowers that are difficult to reach for other species; giving it an advantage in preferring these plants.

Fabaceae and Saxifragaceae were the most specialized plant groups in the national network. The specialization of Fabaceae was expected because Fabaceae plants have relatively complicated flowers that require some specific adaptations on the part of pollinators. Saxifragaceae had many interactions, and was relatively rare, so it therefore would have been reasonable to expect Saxifragaceae to score low at d' specialization. The reason for this actually not being the case is that Saxifragaceae does not interact with species in the network on a scale commensurate with those species' relative abundance, but rather exhibits equal amounts of interactions with regard to many different pollinators. Saxifragaceae is therefore a specialized family by disfavoursing the most common pollinators.

There were differences in how specialized the same species were in the two different networks.

Bombus lucorum was specialized in the Havråtunet network, but not in the national. In the literature, *B. lucorum* is normally considered to be a generalist species (Power and Stout, 2011; Goulson and Darvill, 2004). It is therefore relatively unexpected that the species should emerge as a specialist, and especially in comparison with the other bumblebee species as well. Another mismatch between the networks was that the Asteraceae in the Havråtunet network scored a relatively high d' score while in the national network the score was low. This comparison is, however, problematic since there were only two Asteraceae species present in the Havråtunet network.

There was a significant positive linear relationship between specialization and plant and pollinator abundance in the Havråtunet network, while no such relationship was found in the national network. Meaning that plants and pollinators did get more specialized as they did get more abundant. Blüthgen et al. (2007) also found such a positive correlation for pollinators. Resource partitioning by the most abundant pollinators was a suggested reason for this. For plants, however, Blüthgen et al. (2007) found an opposite pattern: namely a negative correlation between plant abundance and specialization, conflicting with the results from Havråtunet. Even if the relationships found were significant one should be careful to interpret their biological meaning since the d' index is a conservative index that is weak for species with low abundances.

Both versions of the Havråtunet network were more specialized than the national network. The standardized version of the Havråtunet network actually had a H_2 score more than double that of the national network. Since the H_2 measure is independent of network size (Blüthgen 2006) it can be used for cross-network comparisons. Comparing the networks may still, however, pose some problems, mainly since they are sampled in very different ways. Whereas the national network consisted of only hoverflies and bumblebees, the Havråtunet network comprised all observed pollinating insects. So even though the national network was more generalized than the Havråtunet network, this could simply mean that hoverflies and bumblebees are more generalized than other pollinators. This trend was not supported by the findings in the Havråtunet network, where most bumblebees and the abundant hoverfly *R. campestris* were relatively specialized. A more likely reason for the difference is that the Havråtunet network only has data from one year, and that there are known to be large inter-annual fluctuations within pollination networks. Other research, for example (Lázaro *et al.*, 2010; Petanidou *et al.*, 2008), has concluded that specialization in plant

pollinator networks from short time periods can be overestimated to a large degree because some species tend to be specialists in one year and are generalists in another year. It can therefore not be concluded that the Havråtunet network is more specialized than the national network. To make such a conclusion the Havråtunet network would need to be resampled over several years to account for the inter-annual fluctuations.

Possible biases

Asteraceae was by far the most abundant plant family in the national network, followed by Apiaceae and Rosaceae. This result can be expected since many species of the Asteraceae family are common and abundant in Norway (Lid *et al.*, 2005). Species of this family were also very abundant at Havråtunet. Bias in the abundances of plant families in the national network may occur if some plants are favoured or disfavoured when observers take pictures for reporting species observations. Since the observers reported the pollinator species, but not the plant species it seems unlikely that they would favour or disfavour any plants. However if there are any systematic differences in accessibility of the plants then easily accessible plants are likely to be overrepresented. Many Asteraceae plants are popular garden plants and can therefore be regarded as easily accessible, meaning that it is possible that the Asteraceae family may be over-represented in the national network. If Asteraceae is very over-represented in the network this could explain why Asteraceae was the dominating interaction partner for bumblebees.

Looking at which pollinators were most common in the national network has to be done with the source of the data in mind. The observers are not sampling indiscriminately, and some species are probably being reported with frequencies quite disproportionate to their incidence of regularity in reality. Bumblebees were the most common pollinators in the national network at the taxonomic level of genera, but overall far more hoverflies were in the network. This does not indicate that hoverflies are more common visitors to flowers than bumblebees, but only that they have been more frequently reported to artsobservasjoner.no. Why bumblebees should have been less frequently reported than hoverflies could be due to many reasons. One possibility might be that hoverflies are more abundant than bumblebees and therefore more often reported. Another, and maybe more likely, reason for this is that hoverflies for various reasons are more popular to report than bumblebees. The proportion of bumblebees and hoverflies at Havråtunet was about equal. A bias towards under-reporting small and common hoverflies seemed to occur in the national

network. The small-bodied genera *Platycheirus* and *Melanostoma* were relatively infrequent in the national network, but are two of the most common and abundant hoverfly genera in Scandinavia (Bartsch & Binkiewicz, 2009). In the Havråtunet network, only *Platycheirus*, *Melanostoma* and another small genus *Cheilosia* were observed in addition to the larger *R. campestris*. A likely reason for this under-representation might be that smaller flies may be harder to discover and photograph, and possibly that observers find these small and common flies uninteresting, since they are common and maybe not as aesthetically appealing. In addition, smaller flies may be harder to identify taxonomically, especially from photographs, and observers will therefore not report them.

A bias towards rare species can be expected since observers are likely to be more interested in reporting and photographing these species. However, none of the species analysed present at more than 10 observations are listed on the Norwegian red list for species (Kålås *et al.*, 2010). This may indicate that this bias is not very extreme, although it must also be assumed that species not on the red list may still be rare.

The degree of specialization and the interaction pattern in pollination networks is known to have inter-annual fluctuations (Lázaro *et al.*, 2013; Petanidou *et al.*, 2008). This variation may be so large that the degree of specialization one year does not necessarily have any relationship with that of the following year (Lázaro *et al.*, 2013; Petanidou *et al.*, 2008). The specialization degrees from Havråtunet, based as they are on data from just one year, have therefore to be interpreted with this in mind.

Conclusion

Plants and pollinators in the network clearly did have preferences for interaction partners. One clear example was the Fabaceae preference for bumblebees in the national network and similarly *T. pratenses* preference for bumblebees in the Havråtunet network. The specialization scores in the network showed that plants and pollinators were generally not very opportunistic in their interactions, and that there was variation in how specialized different plants and pollinators were. Of the three different variables that were tested for their relationship to specialization, only tongue length in bumblebees did not give any significant results. Abundance did exhibit a positive relationship to specialization on the part of both plants and pollinators. A shorter flight period for hoverfly species in the national network corresponded to a higher degree of specialization, just as it was hypothesised due to less availability of interaction partners. The use of the internet portal

artsobservasjoner.no did give yield some useful results indicating that its use may be convenient for pollination studies, however there are many possible biases so data from the portal needs to be interpreted with extra care. Different preferences for interaction partners means that species will respond differently to changes in the abundance of their interaction partners. This in combination with the fact that species often were specialized probably has implications for how we should think of redundancy in pollination networks, the plasticity of p.

References

- Abrol, D. P. (2012). *Pollination Biology: Biodiversity Conservation and Agricultural Production*. Springer, New York, United States,. doi:10.1007/978-94-007-1942-2.
- Alarcón, R., Waser, N. M. and Ollerton, J. (2008). Year-to-year variation in the topology of a plant-pollinator interaction network. *Oikos*, 117 (12), p.1796–1807. doi:10.1111/j.0030-1299.2008.16987.x.
- Almeida-Neto, M., Guimaraes, P., Guimaraes Jr, P. R., Loyola, R. D. and Werner, U. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos*, 117 (8), p.1227–1239. doi:10.1111/j.2008.0030-1299.16644.x.
- Norwegian Metrological Institute (2013). eKlima[Online]. Available at: http://sharki.oslo.dnmi.no/portal/page?_pageid=73,39035,73_39080&_dad=portal&_schema=PORTAL [Accessed: 12 April 2013a].
- Museumssenteret I Hordaland. (2013) [Online]. Available at: <http://www.muho.no/havratunet/> [Accessed: 8 April 2013b].
- Asikainen, E. and Mutikainen, P. (2005). Pollen and resource limitation in a gynodioecious species. *American journal of botany*, 92 (3), p.487–494. doi:10.3732/ajb.92.3.487.
- Bartsch, H. (2009). *Tvåvingar : blomflugor: Diptera: Syrphidae: Eristalinae & Microdontinae*. ArtDatabanken, Sveriges lantbruksuniversitet, Uppsala, Sverige.
- Bartsch, H. and Binkiewicz, E. (2009). *Tvåvingar : blomflugor: Diptera: Syrphidae: Syrphinae*. ArtDatabanken, Sveriges lantbruksuniversitet, Uppsala, Sverige.
- Bascompte, J. and Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 38 (1), p.567–593. doi:10.1146/annurev.ecolsys.38.091206.095818.
- Bascompte, J., Jordano, P., Melián, C. J. and Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100 (16), p.9383–9387. doi:10.1073/pnas.1633576100.
- Bastolla, U., Fortuna, M. a, Pascual-García, A., Ferrera, A., Luque, B. and Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, 458 (7241), p.1018–1020. doi:10.1038/nature07950.
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, a P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. and Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313 (5785), p.351–354. doi:10.1126/science.1127863.
- Blüthgen, N., Menzel, F. and Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC ecology*, 6, p.9. doi: 10.1186/1472-6785-6-9.

- Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. and Blüthgen, N. (2007). Specialization, constraints, and conflicting interests in mutualistic networks. *Current biology*, 17 (4), p.341–346. doi:10.1016/j.cub.2006.12.039.
- Bommarco, R., Lundin, O., Smith, H. G. and Rundlöf, M. (2012a). Drastic historic shifts in bumble-bee community composition in Sweden. *Proceedings of the Royal Society: Biological sciences*, 279 (1727), p.309–315. doi:10.1098/rspb.2011.0647.
- Bommarco, R., Marini, L. and Vaissière, B. E. (2012b). Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia*, 169 (4), p.1025–1032. doi:10.1007/s00442-012-2271-6.
- Burd, M. (1994). Bateman's principle and plant reproduction: The role of pollen limitation in fruit and seed set. *The Botanical Review*, 60 (1), p.83–139. doi:10.1007/BF02856594.
- Chinery, M. (1993). *Insects of Britain & Northern Europe*. HarperCollins, London, UK.
- Conner, J. K. and Rush, S. (1995). Effects of flower size and number on pollinator visitation to wild radish, *Raphanus raphanistrum*. *Oecologia*, 105 (4), p.509–516. doi:10.1007/BF00330014.
- Cresswell, J. E. and Thompson, H. M. (2012). Comment on “A common pesticide decreases foraging success and survival in honey bees”. *Science*, 337 (6101), p.1453. doi:10.1126/science.1224618.
- Czapik, R. (1996). Problems of apomictic reproduction in the Families Compositae and Rosaceae. *Folia Geobotanica*, 31 (3), p.381–387. doi:10.1007/BF02815382.
- Dormann, C. (2011). How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, 1 (1), p.1–20.
- Dormann, C., Gruber, B. and Fründ, J. (2008). Introducing the bipartite package: analysing ecological networks. *R News*, 8 (October), p.8–11.
- Dupont, Y. L., Damgaard, C. and Simonsen, V. (2011). Quantitative historical change in bumblebee (*Bombus* spp.) assemblages of red clover fields. *PloS one*, 6 (9), p.e25172. doi:10.1371/journal.pone.0025172.
- Dupont, Y. L., Padrón, B., Olesen, J. M. and Petanidou, T. (2009). Spatio-temporal variation in the structure of pollination networks. *Oikos*, 118 (8), p.1261–1269. doi:10.1111/j.1600-0706.2009.17594.x.
- Elle, E., Elwell, S. L. and Gielens, G. A. (2012). The use of pollination networks in conservation. *Botany*, 90 (7), p.525–534. doi:10.1139/b11-111.
- Fründ, J., Linsenmair, K. E. and Blüthgen, N. (2010). Pollinator diversity and specialization in relation to flower diversity. *Oikos*, 119 (10), p.1581–1590. doi:10.1111/j.1600-0706.2010.18450.x.

- Fyhri, A., Jacobsen, J. K. S. and Tømmervik, H. (2009). Tourists' landscape perceptions and preferences in a Scandinavian coastal region. *Landscape and Urban Planning*, 91 (4), p.202–211. doi:10.1016/j.landurbplan.2009.01.002.
- Fürst, M. a., McMahon, D. P., Osborne, J. L., Paxton, R. J. and Brown, M. J. F. (2014). Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature*, 506 (7488), p.364–366. doi:10.1038/nature12977.
- Gallai, N., Salles, J.-M., Settele, J. and Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, 68 (3), Elsevier B.V., p.810–821. doi:10.1016/j.ecolecon.2008.06.014.
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. a, Bommarco, R., Cunningham, S. A, Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S. K., Kennedy, C. M., Krewenka, K. M., Krishnan, S., Mandelik, Y., Mayfield, M. M., Motzke, I., Munyuli, T., Nault, B. A, Otieno, M., Petersen, J., Pisanty, G., Potts, S. G., Rader, R., Ricketts, T. H., Rundlöf, M., Seymour, C. L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tschardtke, T., Vergara, C. H., Viana, B. F., Wanger, T. C., Westphal, C., Williams, N. and Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339 (6127), p.1608–1611. doi:10.1126/science.1230200.
- Ghazoul, J. (2005). Buzziness as usual? Questioning the global pollination crisis. *Trends in ecology & evolution*, 20 (7), p.367–373. doi:10.1016/j.tree.2005.04.026.
- Gibson, R. H., Knott, B., Eberlein, T. and Memmott, J. (2011). Sampling method influences the structure of plant-pollinator networks. *Oikos*, 120 (6), p.822–831. doi:10.1111/j.1600-0706.2010.18927.x.
- Gill, R. J., Ramos-Rodriguez, O. and Raine, N. E. (2012). Combined pesticide exposure severely affects individual- and colony-level traits in bees. *Nature*, 491 (7422), p.105–108. doi:10.1038/nature11585.
- Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., Pretty, J., Robinson, S., Thomas, S. M. and Toulmin, C. (2010). Food security: the challenge of feeding 9 billion people. *Science*, 327 (5967), p.812–818. doi:10.1126/science.1185383.
- Goulson, D. and Darvill, B. (2004). Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? *Apidologie*, 35 (1), p.55–63po. doi:10.1051/apido:2003062.
- Goulson, D., Hanley, M. E., Darvill, B., Ellis, J. S. and Knight, M. E. (2005). Causes of rarity in bumblebees. *Biological Conservation*, 122 (1), p.1–8. doi:10.1016/j.biocon.2004.06.017.
- Goulson, D., Lye, G. C. and Darvill, B. (2008). Decline and conservation of bumble bees. *Annual review of entomology*, 53, p.191–208. doi:10.1146/annurev.ento.53.103106.093454.

- Hegland, S. J., Grytnes, J.-A. and Totland, Ø. (2008). The relative importance of positive and negative interactions for pollinator attraction in a plant community. *Ecological Research*, 24 (4), p.929–936. doi:10.1007/s11284-008-0572-3.
- Henry, M., Béguin, M., Requier, F., Rollin, O., Odoux, J.-F., Aupinel, P., Aptel, J., Tchamitchian, S. and Decourtye, A. (2012). A common pesticide decreases foraging success and survival in honey bees. *Science*, 336 (6079), p.348–350. doi:10.1126/science.1215039.
- Joppa, L. and Pimm, S. (2010). On nestedness in ecological networks. *Evolutionary Ecology Research*, 12 (1), p.35–46.
- Jordano, P., Bascompte, J. and Olesen, J. M. (2003). Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters*, 6 (1), p.69–81. doi:10.1046/j.1461-0248.2003.00403.x.
- Kearns, C. A., Inouye, D. W. and Waser, N. M. (1998). Endangered mutualisms: The Conservation of Plant-Pollinator Interactions. *Annual Review of Ecology, Evolution, and Systematics*, 29 (1998), p.83–112.
- Kevan, P. G. and Baker, H. G. (1983). Insects as Flower Visitors and Pollinators. *Annual Review of Entomology*, 28 (1), p.407–453. doi:10.1146/annurev.en.28.010183.002203.
- Klatt, B. K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. and Tschamntke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society: Biological sciences*, 281 (1775), p.20132440. doi:10.1098/rspb.2013.2440.
- Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. a, Kremen, C. and Tschamntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society: Biological sciences*, 274 (1608), p.303–313. doi:10.1098/rspb.2006.3721.
- Knight, M. E., Martin, a P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, R. A. and Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular ecology*, 14 (6), p.1811–1820. doi:10.1111/j.1365-294X.2005.02540.x.
- Kålås, J. A., Viken, Å., Henriksen, S. and Skjelseth, S. (eds.). 2010. *The 2010 Norwegian Red List for Species*. Norwegian Biodiversity Information Centre, Oslo, Norway.
- Larson, B., Kevan, P. and Inouye, D. (2001). Flies and flowers: taxonomic diversity of anthophiles and pollinators. *The Canadian Entomologist*, 133 (4), p.439–465. doi:10.4039/Ent133439-4.
- Laverty, T. M. and Plowright, R. C. (1988). Flower handling by bumblebees: a comparison of specialists and generalists. *Animal Behaviour*, 36 (3), p.733–740. doi:10.1016/S0003-3472(88)80156-8.
- Laycock, I., Lenthall, K. M., Barratt, A. T. and Cresswell, J. E. (2012). Effects of imidacloprid, a neonicotinoid pesticide, on reproduction in worker bumble bees (*Bombus terrestris*). *Ecotoxicology*,

21 (7), p.1937–1945. doi:10.1007/s10646-012-0927-y.

Lázaro, A., Jakobsson, A. and Totland, Ø. (2013). How do pollinator visitation rate and seed set relate to species' floral traits and community context? *Oecologia*, 173 (3), p.881–893. doi:10.1007/s00442-013-2652-5.

Lázaro, A., Nielsen, A. and Totland, Ø. (2010). Factors related to the inter-annual variation in plants' pollination generalization levels within a community. *Oikos*, 119 (5), p.825–834. doi:10.1111/j.1600-0706.2009.18017.x.

Lebuhn, G., Droege, S., Connor, E. F., Gemmill-Herren, B., Potts, S. G., Minckley, R. L., Griswold, T., Jean, R., Kula, E., Roubik, D. W., Cane, J., Wright, K. W., Frankie, G. and Parker, F. (2013). Detecting insect pollinator declines on regional and global scales. *Conservation biology: The journal of the Society for Conservation Biology*, 27 (1), p.113–120. doi:10.1111/j.1523-1739.2012.01962.x.

Lid, J. 1886-1971, Lid, D. T. 1903-1998, Elven, R. and Alm, T. 1957-. (2005). *Norsk flora*. Samlaget, Oslo, Norway.

Lindgaard, A. and Henriksen, S. (2011). *Norsk rødliste for naturtyper 2011*. Norwegian Biodiversity Information Centre, Trondheim, Norway.

Løken, A. (1950). Bumble bees in relation to *Aconitum septentrionale* in Western Norway (Eidfjord). *Norsk Entomologisk Tidsskrift*, 8, p.1–17.

Løken, A. (1973). Studies on scandinavian bumble bees (Hymenoptera, Apidae). *Norwegian Journal of Entomology*, 20 (1).

Meeus, I., Brown, M. J. F., De Graaf, D. C. and Smagghe, G. (2011). Effects of invasive parasites on bumble bee declines. *Conservation biology: The journal of the Society for Conservation Biology*, 25 (4), p.662–671. doi:10.1111/j.1523-1739.2011.01707.x.

Moe, B. and Botnen, A. (1997). A quantitative study of the epiphytic vegetation on pollarded trunks of *Fraxinus excelsior* at Havrå, Osterøy, western Norway. *Plant Ecology*, 129 (2), p.157–177.

Müller, C. B., Adriaanse, I. C. T., Belshaw, R. and Godfray, H. C. J. (1999). The structure of an aphid-parasitoid community. *Journal of Animal Ecology*, 68 (2), p.346–370. doi:10.1046/j.1365-2656.1999.00288.x.

Neff, J. L. and Simpson, B. B. (1993). *Bees, pollination systems and plant diversity. Hymenoptera and biodiversity*, CAB International, Tucson, USA.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H. (2013). *vegan: Community Ecology Package*.

Ollerton, J., Winfree, R. and Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, 120 (3), p.321–326. doi:10.1111/j.1600-0706.2010.18644.x.

- Opsahl, T. (2013). Triadic closure in two-mode networks: Redefining the global and local clustering coefficients. *Social Networks*, 35 (2), p.159–167. doi:10.1016/j.socnet.2011.07.001.
- Osborne, J. L. (2012). Ecology: Bumblebees and pesticides. *Nature*, 491 (7422), p.43–45. doi:10.1038/nature11637.
- Petanidou, T., Kallimanis, A. S., Tzanopoulos, J., Sgardelis, S. P. and Pantis, J. D. (2008). Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology letters*, 11 (6), p.564–575. doi:10.1111/j.1461-0248.2008.01170.x.
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, 25 (6), p.345–353. doi:10.1016/j.tree.2010.01.007.
- Power, E. F. and Stout, J. C. (2011). Organic dairy farming: impacts on insect-flower interaction networks and pollination. *Journal of Applied Ecology*, 48 (3), p.561–569. doi: 10.1111/J.1365-2664.2010.01949.X.
- R Core Team. (2013). *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
- Rivera-Hutinel, A., Bustamante, R. O., Marin, V. H. and Medel, R. (2012). Effects of sampling completeness on the structure of plant–pollinator networks. *Ecology*, 97 (7), p.1593–1603.
- Sikora, A. and Kelm, M. (2012). Flower Preferences of the Wrocław Botanical Garden Bumblebees (*Bombus* spp.). *Journal of Apicultural Science*, 56 (2), p.27–36. doi:10.2478/v10289-012-0021-y.
- Stefanescu, C. and Traveset, A. (2009). Factors influencing the degree of generalization in flower use by Mediterranean butterflies. *Oikos*, 118 (7), p.1109–1117. doi:10.1111/j.1600-0706.2009.17274.x.
- Stout, J. C. and Morales, C. L. (2009). Ecological impacts of invasive alien species on bees. *Apidologie*, 40 (3), p.388–409. doi:10.1051/apido/2009023.
- Saavedra, S., Stouffer, D. B., Uzzi, B. and Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature*, 478 (7368), p.233–235. doi:10.1038/nature10433.
- Totland, Ø., Hovstad, K. A., Ødegaard, F. and Åström, J. (2013). *Kunnskapsstatus for insektpollinering i Norge-betydningen av det komplekse samspillet mellom planter og insekter*. Norwegian Biodiversity Information Centre, Trondheim, Norge.
- Traveset, A. and Richardson, D. M. (2006). Biological invasions as disruptors of plant reproductive mutualisms. *Trends in ecology & evolution*, 21 (4), p.208–216. doi:10.1016/j.tree.2006.01.006.
- Vázquez, D. P., Melián, C. J., Williams, N. M., Blüthgen, N., Krasnov, B. R. and Poulin, R. (2007). Species abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116 (7), p.1120–1127. doi:10.1111/j.2007.0030-1299.15828.x.

Waser, N. M., Chittka, L., Price, M. V, Williams, N. M. and Ollerton, J. (1996). Generalization in pollination and systems, why it matters. *Ecological Society of America*, 77 (4), p.1043–1060.

Watts, D. J. and Strogatz, S. H. (1998). Collective dynamics of “small-world” networks. *Nature*, 393 (6684), p.440–442. doi:10.1038/30918.

Westerbergh, A. and Saura, A. (1994). Gene Flow and Pollinator Behaviour in *Silene dioica* Populations. *Oikos*, 71 (2), p.215. doi:10.2307/3546269.

Whitehorn, P. R., O’Connor, S., Wackers, F. L. and Goulson, D. (2012). Neonicotinoid pesticide reduces bumble bee colony growth and queen production. *Science*, 336 (6079), p.351–352. doi:10.1126/science.1215025.

Winfree, R. (2010). The conservation and restoration of wild bees. *Annals of the New York Academy of Sciences*, 1195, p.169–197. doi:10.1111/j.1749-6632.2010.05449.x.

Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G. and Aizen, M. A. (2009). A meta-analysis of bees’ responses to anthropogenic disturbance. *Ecology*, 90 (8), p.2068–2076. doi:10.1890/08-1245.1. Winfree, R., Bartomeus, I. and Cariveau, D. P. (2011). Native Pollinators in Anthropogenic Habitats. *Annual Review of Ecology, Evolution, and Systematics*, 42 (1), p.1–22. doi:10.1146/annurev-ecolsys-102710-145042.

Appendix 3:

Network metrics that are given in table 1 for completeness and not used in the discussion:

- **Nestedness:** Defined as the tendency of the specialized species (for example a plant visited by few pollinators) to interact with a subset of interaction partners of the more generalized species (a plant with more interaction partners)(Bascompte and Jordano, 2007). Nestedness can be measured in different ways. Here the following Nestedness measures were used:
 - Nestedness temperature: Measures nestedness in degrees from 0-100 where 0 is cold and perfect nestedness, 100 hot and no nestedness.
 - NODF: Measures nestedness in values 0-100, but here values are opposite to the temperature measures in that 100 is perfect nestedness and 0 is no nestedness. The measure was proposed by (Almeida-Neto *et al.*, 2008).
 - Weighted NODF: Same as NODF, but here the number of interactions in the links are incorporated (Almeida-Neto *et al.*, 2008).
- **Clustering coefficient:** The clustering coefficient is given for the whole network as the average of the local clustering coefficients for all the nodes in the network. The coefficient was introduced by Watts and Strogatz (1998) for unipartite networks. For a node in a unipartite network the local coefficient is defined as realized links between the neighbouring nodes (the node and all nodes linked with it) divided by all the possible links between these nodes. The coefficient aims to measure how strongly nodes cluster together in densely connected groups. For bipartite networks the coefficient cannot be directly used as in unipartite networks. However, different methods for adapting the coefficient exist; in this study the method proposed by Opsahl (2013) is used.
- **Interaction diversity:** The diversity of the network entries is represented using by both the Shannon diversity and Fisher alpha diversity indices.
- **Interaction evenness:** Shannon–evenness for interaction entries. Zeros are treated as no data. Interaction evenness is also given as Alatalo interaction evenness as proposed used by (Müller *et al.*, 1999).