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Nitrogen deposition linked to changes in flowering plant and wild bee diversity

Marianne Strand Torvanger

Master of Science in Ecology



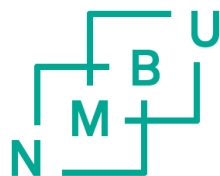
Leafcutter bees (*Megachile spp.*) collecting nectar from *Lotus corniculatus*, july 2021.

PREFACE

The completion of this thesis marks the end of five wonderful years at NMBU. My work on the thesis has overall been a great learning experience.

Firstly, I would like to thank my supervisors Markus A. K. Sydenham (NINA) and Katrine Eldegard (NMBU). Markus, thank you for all guidance with study design and data analysis, and draft feedback. Also, thank you for letting me in at your lab in Oslo to work on bee species identifications! Katrine, thank you for your guidance, detailed text edits and feedback. I am grateful to everyone who contributed to the data collection; Yoko, L. Dupont, Jens M. Olesen, Claus Rasmussen, Gry Liljefors, Kaj-Andreas Hanevik, Daniel I.J. Skoog, and Markus A.K. Sydenham, for assistance with fieldwork. Anders Gunnar Helle, Kaj-Andreas Hanevik, Daniel I.J. Skoog, and Lise Lauridsen contributed with vegetation surveys. Field and lab work was funded by The Research Council of Norway [Proj. no. 302692] as part of the project ‘MetaComNet: Linking metacommunity dynamics to the structure of ecological networks and ecosystem functioning’.

I must thank everyone who contributed to the completion of this fire thesis. Many thanks to Øyvind S. Nyheim and Mikaela E. G. P. Olsen for detailed, constructive feedback on my text. Also, thank you Mikaela for teaching me to prepare bees, and great company during lab work. Thank you to Micah and the ForBio-course students for helpful comments on the draft, and Hilde and Louise for statistical input. I would like to thank Hans Zimmer and Adrian von Ziegler for providing lit background music during intense R and writing sessions, and Monster for keeping a sleepy master student caffeinated. Lastly, thank you to my roomies Kaia and Undis, the rugby team, the gaming club, and my family, I highly value your company and support.



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TABLE OF CONTENTS

Preface	ii
Abstract	v
1 Introduction	1
2 Methods	4
2.1 Study site	4
2.2 Data collection	6
2.2.1 Vegetation surveys	6
2.2.2 Field data collection	6
2.2.3 Wild bee sampling	7
2.2.3 Environmental data	7
2.2.4 Plant species traits information	8
2.2.4 Bee species traits information	9
2.2.5 Plant and bee community weighted means	10
2.3 Statistical modelling	11
2.3.1 Preliminary analyses	11
2.3.2 Plant occurrence models (models 1 and 2)	12
2.3.3 Bee occurrence models (models 3 and 4)	12
2.3.4 Model validations.....	13
2.3.5 Bee species predictions	13
3 Results	14
3.1 Plants.....	14
3.1.1 Legumes	15
3.1.2 Longevity	16
3.1.3 Nitrophilous vs non-nitrophilous plants.....	17
3.2 Bees.....	17
3.2.1 Effects on bees associated with legumes	18
3.2.2 Bee responses to changes in plant trait composition.....	20
3.2.3 Bee species predictions	22
4 Discussion.....	24
4.1 Trait-specific effects of N deposition on plant occurrence	24
4.2 N deposition reduced occurrence of solitary legume specialists	26
4.3 Effects of N deposition on bees associated with asters.....	28

4.4 Study limitations	29
4.5 Synthesis and applications	31
5 Conclusion	32
References	33
Supplementary Information.....	i
A. Overview over all variables included in analyses	i
B. Species information	iv
C. Correlations between environmental variables.....	xi
D. Odds Ratios	xiii
E. Table overview of models (GLMMs).....	xv

ABSTRACT

Nitrogen (N) deposition from anthropogenic activities is a major threat to plant biodiversity, but few studies have investigated effects of N deposition on higher trophic levels, such as on flower-visiting insects. N deposition causes nutrient enrichment to ecosystems, resulting in a reduction of legumes (Fabaceae), which is an important insect-pollinated family, particularly for wild bees. In Europe, there has been a decline of long-tongued and specialist bees, and changes in land management – including increased N fertilization – has been identified as a major driver of pollinator decline. However, the impact of atmospheric N deposition on pollinators – including wild bees – is still poorly known.

Here, I used standardized and representative samples of flowering plants and wild bees from 70 sites in Denmark and Norway to assess the effect of N deposition on flowering plant and bee diversity. I explored whether the occurrence of plant and bee species changed in response to increased N deposition, and if the response depended on functional and ecological traits, including plant longevity, bee tongue lengths and floral preferences. I also assessed how bee species occurrences were affected by changes in plant community composition of life-history and soil N preferences with increased N deposition. I hypothesized that plant and bee species responses would be dependent on their ecological and functional traits. In particular, I expected a decline of legumes and their associated pollinators with increasing N deposition.

I found evidence that N deposition had a negative effect on occurrence of perennial plants and legumes. For bees, there was evidence that occurrence of solitary legume specialists decreased with N deposition, both in Norway and the whole region. Bees that increased in occurrence with increased N deposition were generalist species associated with Asteraceae. Contrary to my hypothesis, the probability of legume pollinators occurring increased with N deposition in Norway. However, most of the recorded pollinators of legumes were bumblebees. Thus, bee responses were dependent on functional group and dietary breadth, where generalist bumblebees were not as affected by changes in N deposition and bee species specializing on legumes had the largest decrease in occurrence probability at higher N deposition.

My results indicate that N deposition causes a turnover of plant and bee species, where diversity of legumes and their specialist pollinators will decline in response to increased N deposition. Therefore, ensuring diversity of legumes and corridors for dispersal will be important management practices for the conservation of these species. For example, areas in early successional stages (e.g., roadsides) maintains legume diversity, and can therefore be used to mitigate the impact of N deposition on legume specialist bees. Since N deposition is predicted to increase in the future, my study provides valuable information about species of special conservation interest.

1 | INTRODUCTION

Nitrogen (N) is abundant in the atmosphere, making up almost 80% of the atmosphere's total mass (Galloway & Cowling, 2002). However, the chemical form of atmospheric N (N_2) is not available to most organisms (Galloway et al., 2003). In natural ecosystems, reactive N (i.e., N usable for most plants and animals) is limited, thus the world's ecosystems have adapted to low amounts of reactive N (Erisman et al., 2013). Additional inputs of reactive N to natural ecosystems have caused eutrophication and acidification of both aquatic and terrestrial ecosystems (Erisman et al., 2007), and is thus likely to cause bottom-up effects across trophic levels. During the Holocene, anthropogenic input of reactive N has approximately tripled the amount of N to the ecosystems (Rockström et al., 2009), as a result of human demands for food and energy (Bobbink et al., 2010). Reactive N includes inorganic reduced N (e.g., ammonia), inorganic oxidative N (e.g., NO_x) and organic compounds such as urea (Bobbink et al., 2010). Producing energy creates oxidative N, as a result of combustion of fossil fuels (Galloway & Cowling, 2002). Overall, anthropogenic production of reactive N has accelerated since 1860, and the increase is expected to continue in the future (Galloway et al., 2008).

Major ecological effects of N deposition on plant diversity have been described, including reduced plant species richness in grasslands, where abundance of grasses increases and angiosperms decrease (Duprè et al., 2010). N deposition typically leads to biodiversity loss in plant communities in European grasslands (Vellend et al., 2017). More specifically, N deposition have reduced legume abundance and diversity (Tognetti et al., 2021), which are zygomorphic flowers especially important for oligolectic pollinators (i.e., specialists using fewer flower taxa as food source) (Cole et al., 2022; Yoder et al., 2020). N deposition reducing legume diversity can therefore be a possible driver of the ongoing pollinator decline. A recent study of grasslands in Northern Europe found a decrease of insect-pollinated plants from 2004-2014, where plants with specialist pollinators of zygomorphic flowers have declined in all habitats (Ehlers et al., 2021). Major drivers of pollinator decline are changes in land management (including fertilizer use) and pesticide use (Dicks et al., 2021). However, impacts of atmospheric N deposition on pollinators have received little attention (Harrison & Winfree, 2015; IPBES, 2016; Stevens et al., 2018), and further research is required to assess its potential effect (IPBES, 2016).

Bees (Apoidea: Apiformes) are the dominant taxon of pollinating insects (Ollerton, 2017), and are essential for providing pollination ecosystem services, thereby maintaining wild plant diversity (Potts et al., 2010; Wei et al., 2021). Wild bees face numerous threats from anthropogenic activity, including habitat loss, pesticide use, introduction of non-native species, and climate change (Goulson et al., 2015; LeBuhn & Luna, 2021; Potts et al., 2010). In the UK, bees that have declined the most are less mobile, specialist species, and especially solitary oligolectic species (Biesmeijer et al., 2006). The ongoing decline of wild bees raises concern about whether the biodiversity within natural ecosystems can be

maintained, including plant diversity. There is an urgent need for a better understanding of the causes of pollinator decline in general and the relative steeper decline among specialist bees (Potts et al., 2010).

The main predictor of local wild bee diversity is flower availability (Roulston & Goodell, 2011). Pollinators of plants that are negatively affected by increased N deposition should therefore be expected to decline in tandem with their host plants. Legumes (Fabaceae) are important food sources for bees, especially long-tongued bees (including bumblebees). Pollen from legumes is the major pollen source for bumblebees, and pollen from red-clover (*Trifolium pratense*) is a clear favorite of bumblebees in the UK (Goulson et al., 2005). Both the abundance and species richness of legumes was reduced in response to increased N deposition (Tognetti et al., 2021), raising concern about potential bottom-up effects on pollinators with strong preference for legumes, and the possible negative feedback loop on legume fitness. There has been a decrease of legumes in response to increased N deposition in nine European countries, causing a reduction in pollination (Helsen et al., 2014). Thus, the decline of long-tongued bees in the Netherlands (Biesmeijer et al., 2006) might be connected to N deposition, as the Netherlands is a hot-spot for N deposition in Europe (European Environment Agency, 2007). Furthermore, plant species adapted to infertile soils decline at high N deposition, while nitrophilous grasses increase (Stevens et al., 2004). If nitrophilous angiosperms (e.g., *Taraxacum spp.* and *Tanacetum vulgare*) show the same response as grasses to N deposition, the occurrence of pollinators of nitrophilous plants, such as many polylectic species (i.e., pollen generalists) might also increase.

Only a few published studies have investigated the effect of atmospheric N deposition on pollinators (Carvalho et al., 2020; Stevens et al., 2018). Stevens et al. (2018) found a decrease of plants pollinated by larger bees and plants with yellow flowers, and larger bees showed a negative response when N deposition increased in acidic grasslands in the UK. However, Stevens et al. (2018) only analyzed species records, and did not conduct representative and standardized sampling. Carvalho et al. (2020) also used data on species records – which do not follow standardized sampling schemes, leading to considerable bias (Isaac & Pocock, 2015) – to investigate the effects of soil eutrophication on pollinators. Furthermore, experimental studies that have investigated N pollution rates on plants and bees have assessed the effects of N levels that are higher than in real-life ecosystems influenced by human land use (e.g., Hoover et al., 2012). Therefore, the effects of N deposition across trophic levels should be studied in a natural system with standardized sampling, to predict how pollinator communities respond to realistic pollution concentrations (Ryalls et al., 2022). Specifically, we need empirical evidence of effects of N deposition on wild bees, from large-scale ecological studies, with standardized sampling of plant and bee communities.

Here, I investigated the effects of real-life rates of N deposition on representative plant and bee communities in Denmark and Norway. I investigated responses on different plant and bee species traits, by including interactions between N deposition and species traits. Plant traits were chosen as either having a possible impact of their response to N deposition, where interactions were included to explore whether a plant species response to N deposition was dependent on their family (including legumes) and differences in soil N preference. Other plant traits were included to control for species distributions in a disturbed area, including mowing preference. Bee traits were chosen as being important predictors of responses to habitat disturbance, where I included interactions to explore whether a bee species response to N deposition was dependent on floral preference and functional group (relating to sociality and tongue length). Other bee traits were included to control for their effect on bee diversity, which included plant and landscape diversity. I tested the hypothesis that both i) the occurrence of flowering-plant species and ii) the occurrence of wild bee species will depend on the amount of N deposition, and iii) that the species responses will be modulated by different species traits. Specifically, I explored whether the effect of increased N deposition on bee species occurrence depended on tongue length and floral preference, and if changes in bee occurrence corresponded to changes in plant community composition (plant traits). I predicted that if flowering-plant and wild bee responses to N deposition is dependent on their ecological and functional traits, (1) the occurrence of both legume plant species and their pollinators would decline with increased N deposition, and (2) nitrophilous plant species (including species of Asteraceae) and the occurrence of bees associated with Asteraceae will increase with N deposition.

2 | METHODS

2.1 | STUDY SITE

Fieldwork was conducted from May to July in 2021 along 71 roadsides in Norway and Denmark (Fig. 1). At each location, a 50m x 3m long transect with vegetation was established and sampled just next to a roadway, sidewalk, roundabout, or intersection. To get a standardized measure of each site (transect), 50 m was set as a fixed length (following Potts et al., 2020; Woodcock et al., 2013). The width of the transect was set as 3 meters, as recommended by the Proposal for an EU Pollinator Monitoring Scheme (Potts et al., 2020).

The study sites were selected as part of the ‘MetaComNet’ project (Sydenham et al., 2021), where selection criteria included having at least three different plant families in the transect, of which at least two are insect pollinated. To prevent overgrowth, all sites are mowed several times each year. An early-successional stage is therefore maintained at the sites, with grasses and forbs (including angiosperms) adapted for frequently disturbed habitats. During the sampling season of this study, sites were not mowed.

My study sites were in the Nordic region in the Northern Hemisphere, where the latitudinal range of the sites were 55 - 57° in Denmark, and 59 - 60° in Norway. The climate was boreo-temperate, where annual mean temperatures ranged from 7.2 - 7.7 °C at sites in Denmark, and 4 - 6.6 °C at sites in Norway (Fick & Hijmans, 2017). Annual mean precipitation ranged from 579 - 766 mm in Denmark, and 719- 824 mm in Norway (Fick & Hijmans, 2017). The transects were surrounded by a variety of land cover types including semi-natural landscapes, croplands, urban areas, coniferous, and deciduous forests.

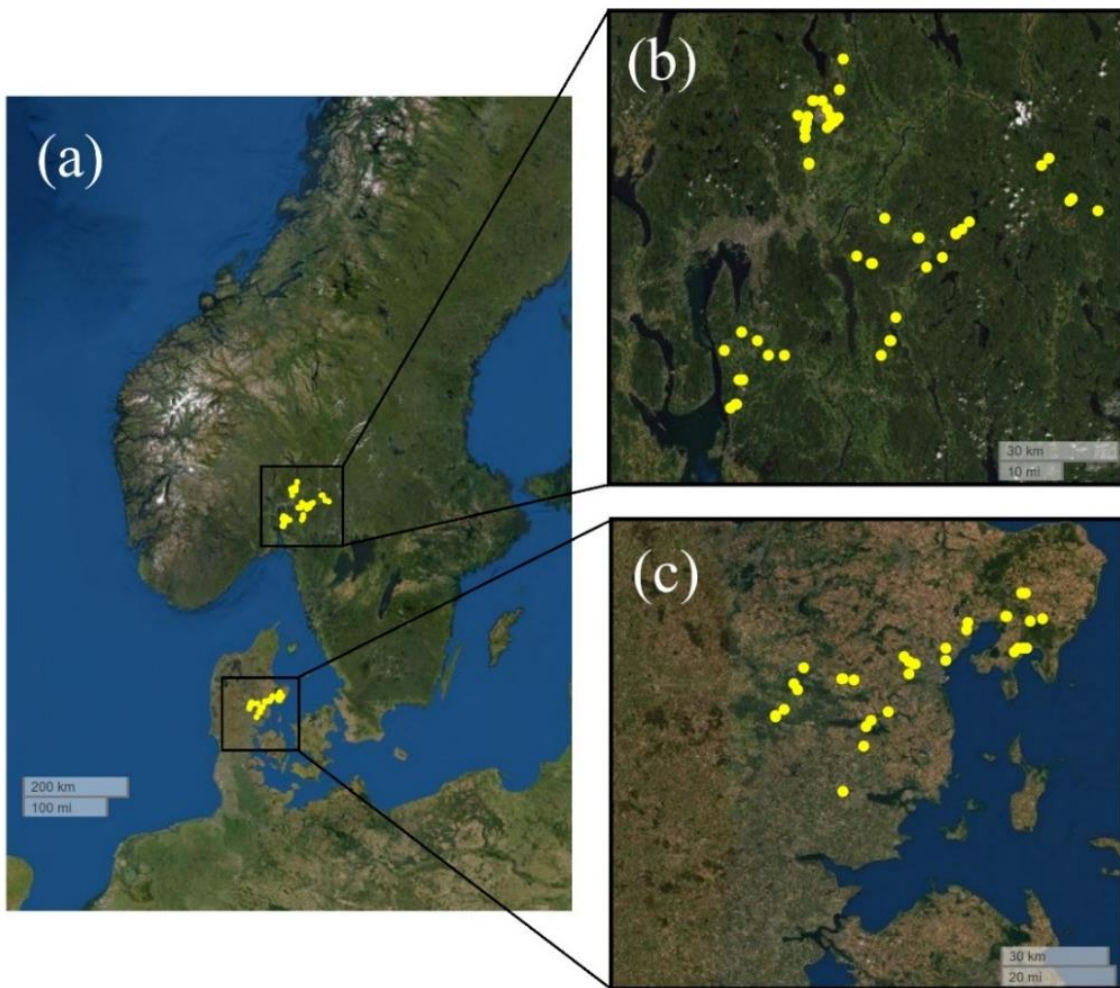


Figure 1. Map showing the location of each study site in Scandinavia (a). There are 71 sites in total, where 42 are in South-East Norway (b), and 29 sites in the Central Denmark Region (c).

2.2 | DATA COLLECTION

2.2.1 | VEGETATION SURVEYS

To estimate the richness of all flowering plant species present, we conducted a vegetation survey for each site between June 16 and July 2, 2021. At each site, ten 1x1-m plots were evenly placed, with approximately five meters distance between each plot (Fig. 2). Further, each 1 m² plot was divided into four square subplots of equal size. Inside each subplot we registered which flowering plant species were present. As a result, the abundance of each species was between 0 and 4 in each plot.

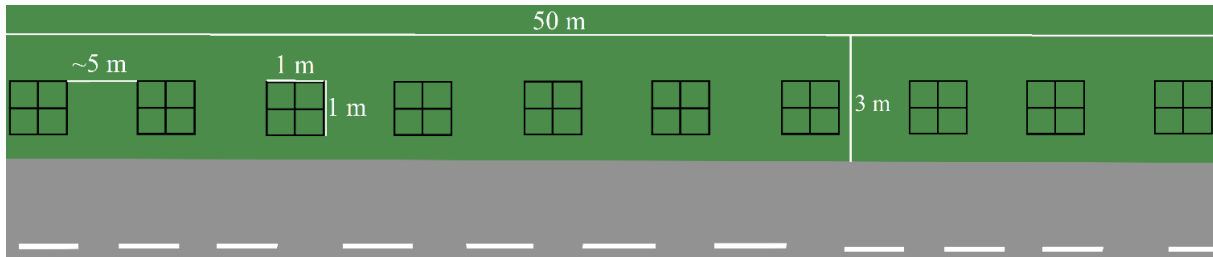


Figure 2. Schematic overview over the vegetation survey's study design. Each transect (roadside) was 50 meters long and 3 meters wide. The black squares are the 1 m² plots, consisting of four subplots where angiosperm occurrence was registered. The plots were placed randomly along the 3-meter edge.

2.2.2 | FIELD DATA COLLECTION

Flower-visiting wild bees were sampled three times, from May to July 2021, using standardized transect walks. Standardized transect walks with netting of bees have been found to be an efficient method for collecting bees, giving a good indicator of overall species richness (Westphal et al., 2008), while also providing specific information about bee forage plant. The first collection was timed to the blooming of dandelions (*Taraxacum* spp.), when the spring community of bees was active. The second and third round of collection was conducted approximately three to four weeks after the previous round. To sample all target species when they were active, the exact sampling period was restricted to days with temperatures above 15°C, wind speeds under 5 m/s, and little to no cloud cover. We were four observers collecting bees in Norway, and two observers in Denmark, sampling bees from separate sites. Each sampling took place approximately between 10:00 and 18:00 (for specifics, see Fig. S5), when bees were actively flying to collect pollen and/ or nectar. We spent 30 minutes walking slowly through the transect, while collecting all flower-visiting wild bees present. Bees were netted directly from the flower, using an entomological sweep net (Fig. 3). We registered the plant species each bee was netted from. After 30 minutes, we added 30 seconds per sampled specimen to the sampling time to account for handling time. The reason for this was to avoid under sampling sites with a lot of activity, thereby avoiding under sampling rare bees. We stored the collected bees in plastic containers (falcon tubes) filled with 96% ethanol, and with a label indicating site name, date of sampling, time of sampling, and plant photographs on which bees were sampled (Fig. 3).

2.2.3 | WILD BEE SAMPLING

I pinned and prepared the bees for identification in lab at the Norwegian University of Life Sciences (NMBU). The bee specimens were identified to species level by using taxonomic literature based on morphological traits. Solitary bee species sampled in Norway were determined by Markus A. K. Sydenham (Norwegian Institute for Nature Research, NINA), while bumblebee species were determined by Arnstein Staverløkk (NINA). Species belonging to the *B. lucorum* complex (*B. cryptarum*, *B. lucorum* and *B. magnus*, *B. terrestris*) were all put in the same subgenus *Bombus sensu strictu*, as species identification is not possible studying only morphological characteristics (Carolan et al., 2012).

Bees sampled in Denmark were identified by Henning B. Madsen at Copenhagen University, who also identified one specimen from Norway. The collection of bees was stored at NINA, Oslo. Plant species visited by bees were either determined in field by the observers, or confirmed by a specialist (Anders Often, NINA) studying pictures taken at the site. However, these data on plant species visited by individual bees were not used in my master's thesis.

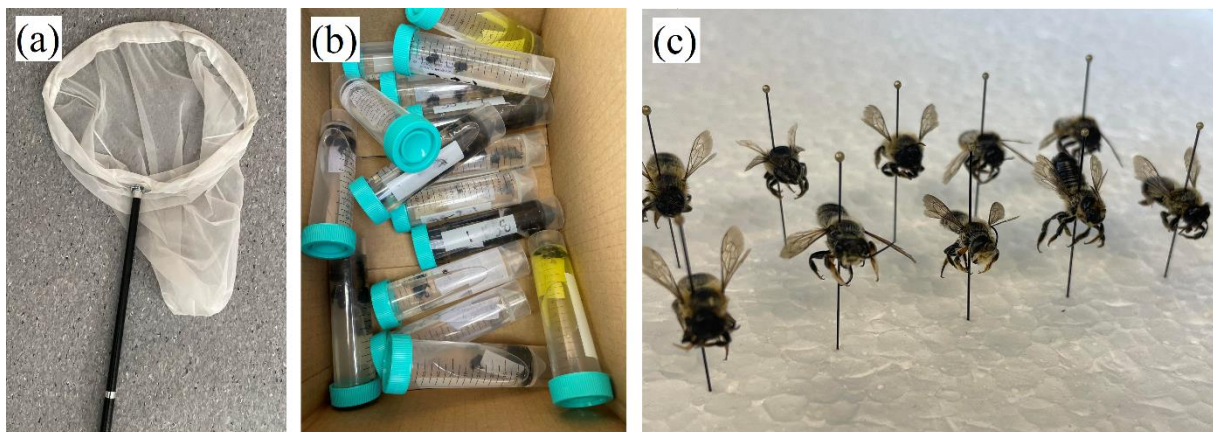


Figure 3. Impressions of field and laboratory work; entomological sweep net used for the collection of bees (a). Next, collected bees stored in falcon tubes, with labels specifying date and plant species visited (b). Finally, pinning and drying of bees, as a preparation for species identification (c).

2.2.3 | ENVIRONMENTAL DATA

I carried out all data extraction and calculations in R version 4.1.2. (R Core Team, 2021). Weather, soil, and landscape data are assumed to be important predictors of plant and bee species distributions (Kammerer et al., 2021; Kreft & Jetz, 2007), and were therefore included to control for their effect on bee and plant diversity. The variables included mean annual temperature and precipitation (Fick & Hijmans, 2017), soil quality (Fischer et al., 2008), and coverage of landscape attributes (Venter & Sydenham, 2021) (detailed description of all variables included in Table S1). Furthermore, data on total (wet + dry) annual N deposition (MET Norway, 2019; Tørseth et al., 2012) was included to investigate the impact of N deposition on species occurrences. The climate variables were extracted from raster maps using the function *GetData* from the package ‘raster’ (Hijmans, 2022). The data of N deposition

and soil quality was downloaded as raster maps from websites (see Fischer et al., 2008; MET Norway, 2019) and extracted using the function *extract* from packages ‘raster’ and ‘sp’ (Pebesma & Bivand, 2005).

2.2.4 | PLANT SPECIES TRAITS INFORMATION

The three traits (plant longevity plant mowing and/or grazing criteria, and Ellenbergs N indicator value; Table S2) were derived from a recent publication on trait values for all vascular Swedish plant species (Tyler et al., 2021). The genus *Taraxacum* was omitted from the dataset since there were no trait values available of the genus. Plants belonging to genera *Alchemilla*, *Hieracium*, *Crataegus*, and *Rubus* were not identified to species, as species identification was not possible in field. The trait values of species only identified to genera, and other species determined to genus within a site, were calculated by taking the average values of all species present in each genus from Tyler et al. (2021).

I selected plant traits relevant for growth and reproduction in disturbed areas (such as roadsides, as in this study), which included plant mowing and/or grazing criteria (hereafter: **mowing**). I chose the trait ‘mowing’ since the distribution of plant species in a roadside location with frequent mowing (e.g., removal of above-ground biomass) is determined by the species’ resistance to mowing, as grazing selects plants with ruderal strategy (Diaz et al., 2007).

Plant response to N deposition might depend on their longevity, where shorter-lived (ruderal) plants are more adapted to disturbance (Diaz et al., 2007). I divided longevity into three categories, where I classified plants with longevity = 1 (Tyler et al., 2021) as **annuals**, plants with longevity = 2 (Tyler et al., 2021) as **biennials**, plants with longevity ≥ 3 (Tyler et al., 2021) were classified as **perennials**.

Ellenberg N indicator has previously been used to assess the effect of N deposition on terrestrial plants (Falkengren-Grerup & Schöttelndreier, 2004; Tyler et al., 2021). I classified Ellenberg N in two categories, following the same classification as Öckinger et al. (2006) and Carvalheiro et al. (2020); plants either being **nitrophilous** (Ellenberg N > 5) or **non-nitrophilous** (i.e., Ellenberg N ≤ 5). Nitrophilous species are indicators of N rich soils, while non-nitrophilous (i.e, nitrophobous) species are indicators of infertile soils.

To separate the response of legumes from other angiosperm families, I also included a trait that separated **legumes**, **asters**, and **other** angiosperm families. I separated legumes and asters specifically as they are of interest relating to the responses of bees with different dietary niches, since legumes are a large group of zygomorphic flowers, and asters are a large group of actinomorphic flowers.

2.2.4 | BEE SPECIES TRAITS INFORMATION

As bee responses to environmental change depend on their trait characteristics (Williams et al., 2010), I selected traits of bees that are likely important predictors of response to habitat disturbance, including tongue length (Fig. 4), and floral preference (dietary niche), which are both linked to local habitat occurrence. I also included floral preference community weighted mean, and whether the species was a known legume visitor (Table S3). To investigate the effect of N deposition on bees, I created a **functional group** of four categories relating to sociality and tongue-length (Fig. 4), as these four groups differ in both sociality, body size, and habitat requirements (including flower preference and nesting site requirements), thus important for determining their responses to changes in the environment (Williams et al., 2010).

Tongue (i.e., proboscis) length of solitary bees was either classified as long (families Apidae and Megachilidae, with proboscis mean length > 4 mm) (see Cariveau et al., 2016) or short (other families, with proboscis mean length < 3 mm) (see Cariveau et al., 2016). Proboscis lengths of bumblebees show great variation (Cariveau et al., 2016), and was therefore separated in two groups (long or short), based on lengths from Wood et al. (2021). Bumblebees with proboscis length ≥ 7.9 mm were classified as long tongued. Bumblebees with proboscis length < 7.9 mm were classified as short tongued. I chose to separate at exactly 7.9 mm, since 7.9 mm separated bumblebees that are strongly associated with legumes in Goulson et al. (2005).

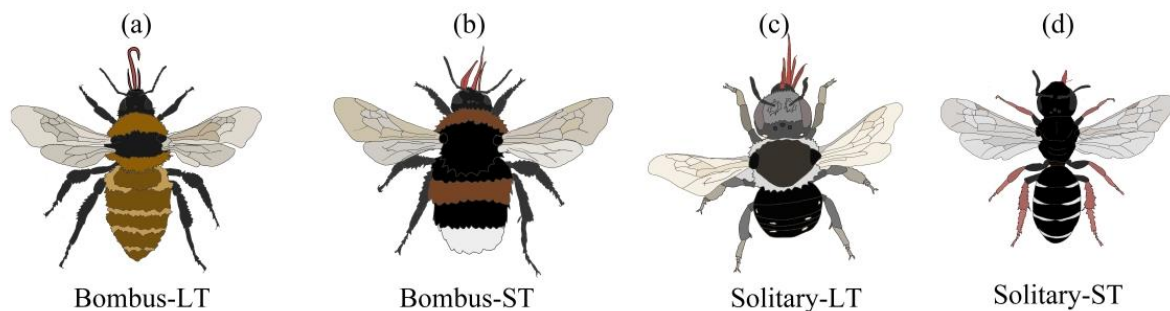


Figure 4. Wild bees were divided into four functional groups, according to their sociality (solitary or eusocial) and length of proboscis. Bumblebees with proboscis length ≥ 7.9 mm were classified as long-tongued (a). Bumblebees with proboscis length < 7.9 mm were classified as short-tongued (b). Long tongued solitary bees (c) are solitary bees of families Apidae and Megachilidae. Short-tongued solitary bees (d) are species belonging to other families (i.e., Andrenidae, Colletidae, Halictidae, and Mellitidae).

Bee foraging preference has traditionally been classified in three categories; monolectic (single host species), oligolectic (few related hosts), and polylectic (many hosts) (Cane & Sipes, 2006), with the latter being highly generalized, and does not provide information about what plant families are preferred. For example, both *Andrena lathyri* and *Andrena humilis* are oligolectic, but visit entirely different plant families (e.g., *A. lathyri* on Fabaceae, see Bees Wasps & Ants Recording Society (BWARS) (2022b), and *A. humilis* on Asteraceae, see Bees Wasps & Ants Recording Society (BWARS) (2022a)).

Therefore, I performed a detrended correspondence analysis (DCA), which provides a more specific classification of the **floral preference niche** of each species, on a continuous scale (Table S3). I created a matrix with one row for each plant family and one column for each bee species, and cell numbers containing information on the number plant genera within plant families that bees are known to visit (Rasmussen et al., 2021). The family Orchidaceae had a single observation of *Chelostoma campanularum*, which is oligolectic on family Campanulaceae (Bees Wasps & Ants Recording Society (BWARS), 2022e), and was thus a strong outlier. Therefore, I removed the plant family Orchidaceae from the matrix. The Western honeybee (*Apis mellifera*) is a domesticated species and was also removed from the matrix. Next, I ran the DCA using function *decorana* from package ‘vegan’ (Oksanen et al., 2020), which created two linear combinations (DCA1 and DCA2, see Fig. S1). I selected the first linear combination (DCA1) as the floral preference niche score, since it separated pollinators associated with zygomorphic flowers (including legumes) from pollinators associated with actinomorphic flowers (including asters). As a result, the niche score (DCA1) measured the functional diversity of the dietary breadth of bees, where bee species with similar host plant preferences obtained similar scores (Fig. S1).

2.2.5 | PLANT AND BEE COMMUNITY WEIGHTED MEANS

To investigate the effect of changes in plant trait composition on bee occurrences along the N deposition gradient, I used **community weighted means** (CWMs) to get an estimate of overall distribution of plant traits in each species community.

The community weighted mean values (CWM) were calculated by:

$$CWM = \sum_{i=1}^S p_i x_i$$

where p is the relative abundance of species i , and x is the trait value for species i ($i = 1, 2, \dots, S$) (Garnier et al., 2004; Ricotta & Moretti, 2011). I calculated plant community weighted means for longevity, mowing, and Ellenberg N for each site, where x was the trait value for each plant species, and r the frequency of a plant species at each study site.

Furthermore, to investigate the effect of changes in bee community floral preferences to N deposition, I calculated the bee community composition of flower preferences (CWM for bees). The CWM for bees was calculated for each site, where the x was the niche score (DCA1) and r the frequency of a species at each study site.

2.3 | STATISTICAL MODELLING

All statistical modeling were carried out in R version 4.1.2. (R Core Team, 2021). Kleptoparasites (cuckoo bees) were excluded from all statistical analyses, as their distribution is dependent on their hosts (Williams et al., 2010). This included species belonging to the genera *Sphecodes*, *Nomada*, and *Epeolus*, and social parasites of *Bombus* (*B. bohemicus*, *B. norvegicus*, *B. campestris*, and *B. sylvestris*). The Western honeybee (*Apis mellifera*) was also excluded since it is a domesticated species.

2.3.1 | PRELIMINARY ANALYSES

I performed data exploration following Zuur et al. (2010), and checked for outliers, violations of homoscedasticity or normality, and multicollinearity. When two variables were highly correlated (Pearson's correlation coefficient > 0.5), one was excluded from the analysis. This included multiple environmental variables (which correlated highly with N deposition) and forest cell cover and crop cell cover (correlated with Shannon landscape diversity). I selected N deposition since it was of study interest, and Shannon landscape diversity as it is a measure of landscape heterogeneity, and therefore provides information on the amount of edge habitats (e.g., forest edges) in a landscape.

To investigate the correlative relationships between the predictors, I ran a principal component analysis (PCA) including the environmental variables (i.e., N deposition, temperature, precipitation, latitude, elevation, and Shannon landscape diversity) using the function *prcomp* (base R function). The two first linear combinations explained 91.1% of the total variation, where N deposition and temperature (bio1) explains the same variation (Pearson correlation > 0.9) and was almost completely negatively correlated with precipitation (bio12), latitude and elevation. (Fig. S5). When only investigating the environmental variables from Norway, I found weaker correlations with precipitation and latitude N deposition (Fig. S6). Thus, to account for the latitudinal effect of N deposition, I carried out four different tests. This included two models on plant occurrence (model 1 was based on the entire dataset, while model 2 was based on a subset of the data; i.e., only the data from Norway) and two models on bee occurrence (model 3: entire dataset, model 4: Norway). In addition, the collection of bees was not entirely standardized between the two countries, because of the timing of the first round of collection, which missed most of the blooming of *Taraxacum spp.* in Norway). Running one test just for Norway also accounted for this bias.

I fitted generalized linear mixed effect models (GLMMs) using the function *glmer* from the package 'lme4' (Bates et al., 2015). I chose mixed models as they allowed me to interpret predictor variables as either fixed or random effects (Henderson Jr, 1982), since my study design was nested with sites within a country, occurrences within sites, and occurrences within species (i.e., some species are naturally more rare than other species). My response variable 'occurrence' (presence within a plot or site) was binary, and I therefore chose a logit link (binary outcome) function.

2.3.2 | PLANT OCCURRENCE MODELS (MODELS 1 AND 2)

To analyze changes in plant species occurrence across sites with different rates of N deposition, two generalized linear mixed-effects models (GLMMs) were fitted, with plant presence/ absence within a plot ('plant occurrence') as response variable. To account for differences in species individual sizes, the response variable 'plant occurrence' was species presence/ absence in each 1 m² plot (i.e., subplots were discarded). I used data for the whole region for the first model (model 1), and data from Norway in the second model (model 2).

I included interaction terms between N deposition and all plant traits selected, to test for trait-group specific responses to N deposition. The full model included the fixed effects to control for plant distributions (mowing criteria, soil quality, landscape diversity, and urban landscape cover), and interactions between N deposition and plant traits (family of the species, longevity, and Ellenberg N criteria). The fixed effect mean annual precipitation was also included as a control in model 2, since Pearson's correlation between N deposition and precipitation was less than five in Norway.

To avoid pseudoreplication for plant species observed at the same sites, and to adjust for collector bias, site, and collector identity were included as random effect terms (Fig. S10). Country was also included as random effect in model 1 but was later removed since the probability of detecting species occurrence at a site was independent of country (the variance component of the random effect 'country' was 0). All non-significant predictors were removed using backwards-stepwise selection, and the significance of variables were tested using likelihood ratio tests. I created diagnostic plots (i.e., residuals against fitted values and QQ plots) to verify that the model assumptions associated with binomial models were met using function *plotResiduals* from package 'DHARMA' (Hartig, 2022). I found a residual problem with soil quality and urban landscape cover, and both variables were therefore omitted from the final (reduced) models.

As N deposition was highly correlated with the other environmental variables in model 1 (Fig. S2), a similar model was built but with temperature as predictor instead of N deposition, and an *anova* test (function from base R) was run for comparison. The test revealed no significant differences between the two models since the effect of temperature was equal to the effect of N deposition on plant occurrence (Table S6).

2.3.3 | BEE OCCURRENCE MODELS (MODELS 3 AND 4)

To analyze changes in occurrence of bee species across sites with different rates of N deposition, two generalized mixed-effects models (GLMMs) were fitted, with bee presence/ absence within a site ('bee occurrence') as response variable. I used data for the whole region for the first model (model 3), and data from Norway in the second model (model 4). Before analysis of the subset data (model 4), I omitted all the species only found in Denmark.

The full models included N deposition, bee traits (tongue length and floral preferences), floral preference CWM, plant CWMs, plant Shannon diversity, and landscape diversity as fixed effects. Interactions added in the full bee model were functional group with plant CWMs, N deposition with plant CWMs, N deposition with functional group, floral preference CWM, and floral preference niche score (DCA1). Mean annual precipitation was also included as a control in model 4, since Pearson's correlation between N deposition and precipitation was less than five in Norway.

To account for nested effects (e.g., dependence for bees collected at the same site and time) bee species and site was included as random effects in both models. I used backwards-stepwise selection to remove all non-significant predictors and tested the final model for significance using likelihood ratio tests. Non-important predictor variables were removed until the final model included predictors to control for their effect on bee diversity, and significant interactions between N deposition and bee traits.

2.3.4 | MODEL VALIDATIONS

The final models were based on the Bayesian Information Criterion (BIC), i.e., the one with lowest BIC value provide the best fit to the data. For all four models, I used the R package 'car' (Fox & Weisberg, 2019) to create variance inflation factors (function *vif*) and made sure they were less than 5 for the final model to avoid multicollinearity. I created diagnostic plots (i.e., residuals against fitted values and QQ plots) to validate homoscedasticity and normality of residuals, using function *plotResiduals* from package 'DHARMA' (Hartig, 2022). No major violations of model assumptions were detected. I obtained R² values using the package 'MuMIn' (Barton, 2020). The *drop1* function (from base R) with Chi square test was used to get one p-value for each interaction. The final model predictions were extracted using the function *allEffects* from package 'effects' (Fox & Weisberg, 2018; Fox & Weisberg, 2019).

2.3.5 | BEE SPECIES PREDICTIONS

I predicted the occurrence of each bee species along a N deposition gradient using the final bee occurrence model (model 4) with the function *predict* (base R function). The response variable was standardized by dividing each occurrence value by the maximum occurrence value, thus visualizing each species response to N deposition, independent of how rare or common the species was. I used bee species as a random effect in the prediction, and the bee species traits included was floral preference niche score (DCA1), if the species was a documented visitor of legumes or not ('RegFabaceaeVisitor', Table S2), and the species functional group relating to sociality and tongue length ('GroupTL', Table S2).

3 | RESULTS

3.1 | PLANTS

The number of sites and plots sampled were 70 and 700, respectively. One site was mowed during the sampling season and the data from that site was therefore discarded. One hundred ninety angiosperm species were registered in the study area. The plant species with highest occurrences (i.e., presence in a plot = n) were *Achillea millefolium* (n = 316, sites = 56), *Vicia cracca* (n = 195, sites = 47), and *Ranunculus acris* (n = 186, sites = 35) (Table S4). The two families with highest occurrences were asters (Asteraceae) and legumes (Fabaceae), with 1181 (of 25 900 possible) and 991 (of 14 700 possible) occurrences, respectively. In total, 47% of observed species were either legumes or asters. Relating to the longevity of the species observed, 28 were annuals, 11 were biennials, and 155 were perennials. The total number of plant species with registered bee visitors were 97, and the most visited plant species was red clover (*Trifolium pratense*) with 227 visitors.

Important predictors of plant occurrence in the whole region (model 1) were plant mowing criteria and Shannon landscape diversity, where there were higher occurrences of plants adapted for mowing (Table 1, $p = 0.009$, odds ratio = 1.35, Fig. S6), and Shannon landscape diversity reduced plant occurrences (table 1, $p = 0.004$, odds ratio = 0.83, Fig. S6). The fixed effect terms in Model 1 explained 6.7 % of the variation in plant occurrences (Table 1).

The analysis of the data from Norway (model 2) revealed that annual precipitation, mowing and Shannon landscape diversity were not important predictors of plant occurrences. The fixed effect terms in model 2 explained 8.7 % of the variation in plant occurrences (Table 1).

Table 1. Likelihood ratio tests for the final model (GLMM) on plant occurrence from the whole region (Norway and Denmark, model 1), and the final model (GLMM) on plant occurrence from Norway (model 2). The models were fitted with site, plant species and collector as random effects. The fixed effect ‘Ellenberg N’ was a non-significant predictor in model 1 that was omitted during backwards-stepwise selection. Annual precipitation created high VIFs and was not included in model 1.

	Model 1: Plant occurrence (Full data; NO + DK)			Model 2: Plant occurrence (Subset data; NO)		
Predictors	<i>df</i>	<i>LRT</i>	<i>p-value</i>	<i>df</i>	<i>LRT</i>	<i>p-value</i>
N deposition x Longevity	2	371.44	< 0.001	2	6.1897	0.0453
N deposition x Family	2	17.12	< 0.001	2	5.9741	0.0504
N deposition x Ellenberg N				1	5.2158	0.0224
Mowing	1	6.89	0.0087	1	1.8977	0.1683
Shannon Landscape Diversity	1	8.39	0.0038	1	3.6993	0.0544
Mean annual precipitation				1	0.63323	0.6332
Random effects	<i>Variance and Std. Dev.</i>					
Plant species (n = 194)	$\sigma^2 = 2.23682, \sigma = 1.4956$			$\sigma^2 = 5.98586, \sigma = 2.4466$		
Site (model 1: n = 70, model 2: n = 41)	$\sigma^2 = 0.16093, \sigma = 0.4012$			$\sigma^2 = 0.17132, \sigma = 0.4139$		
Collector (model 1: n = 4, model 2: n = 3)	$\sigma^2 = 0.04727, \sigma = 0.2174$			$\sigma^2 = 0.06285, \sigma = 0.2507$		
Observations	135 800			79 540		
Marginal R²/ Conditional R²	0.067 / 0.677			0.087 / 0.476		

3.1.1 | LEGUMES

I found strong evidence for different responses to N deposition between the plant families investigated ($p < 0.001$, Fig. 5, Table 1). Specifically, the predicted probability of occurrence of a legume species was 2.7 % at sites with 460 mg N/ m² per year, and 2.2 % at sites with 1200 mg N/ m² per year, albeit with much variation (Fig. 5a, odds ratios = 0.84, Fig. S6). For asters and other species, there was no significant change in occurrence with N deposition (Fig. 5 b-c). Overall, this finding is consistent with my hypothesis that legumes are more affected by N deposition than other angiosperms. For the analysis of the data from Norway (model 2), other families decreased in occurrence with increased N deposition, but the interactive effect was weak (Table 1, $p = 0.0504$, Fig. S7).

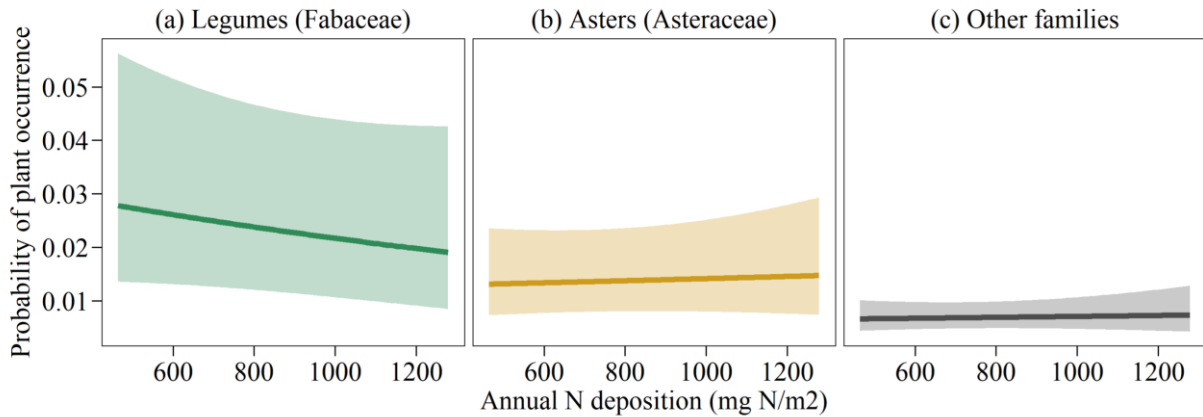


Figure 5. The effect of N deposition on the occurrence of angiosperms was dependent on their family (model 1: $p < 0.001$). There was a significant difference in predicted occurrence (model 1: $p < 0.001$) depending on if the plant belongs to Fabaceae (a), Asteraceae (b), or another family (c). The solid lines represent the model prediction (model 1). The shaded areas are 95% confidence intervals.

3.1.2 | LONGEVITY

I found strong evidence that the effect of N deposition on plant occurrence was dependent on plant longevity ($p < 0.001$, Table 1). The probability of occurrence of shorter-lived plant species increased with N deposition (Fig. 6 a-b, Table S6), while perennial plant occurrence decreased significantly with N deposition (Fig. 6c, odds ratios = 0.35, Fig. S6). Specifically, the probability of perennial occurrence decreased from 1.3 % to 0.8 % along the N deposition gradient (Fig. 6c). Due to fewer observations of annuals and biennials, there is greater uncertainty in the estimates for shorter-lived plants (Fig. 6 a-b). For the analysis of the data from Norway (model 2), the same pattern was observed, but the evidence was weak (Table 1, $p = 0.0453$, Fig. S7).

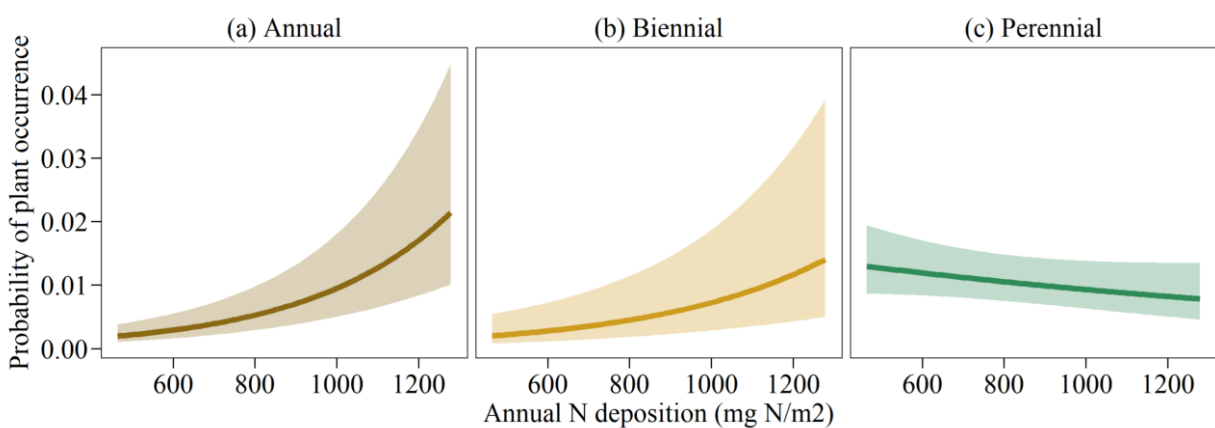


Figure 6. The effect of N deposition on the occurrence of angiosperms was dependent on life history type (model 1: $p < 0.001$). The occurrence of shorter-lived (a, b) plants increased with N deposition, while longer-lived plants (perennials) decreased with N deposition (c). The solid lines represent the model prediction (model 1). The shaded areas are 95% confidence intervals.

3.1.3 | NITROPHILOUS VS NON-NITROPHILOUS PLANTS

Contrary to my expectations, I found no evidence that the effect of N deposition was dependent on N soil preference (Ellenberg classification) in Norway and Denmark. There was no significant difference in the response of non-nitrophilous and nitrophilous plants along the N deposition gradient ($p = 0.20$). For plant occurrence in Norway (model 2), there was moderate evidence that nitrophilous plants and non-nitrophilous plants had different response in occurrence with increased N deposition (table 1, $p = 0.022$). However, the effect was marginal: the odds ratios was 1.11 (Fig. S7), indicating that the odds of nitrophilous plants occurring at a site is only slightly different from the odds of non-nitrophilous plants occurring at a site.

3.2 | BEES

The total number of wild bees collected was 1918, and when kleptoparasites and social parasites were omitted, 1891 bees remained, which included 1221 bumblebees, and 670 solitary individuals. More specifically, 1379 specimens were collected in Norway, and 512 were collected in Denmark. Eighty species (excluding kleptoparasites and social parasites) were collected in total, in which 23.8% only occurred at one site ($n = 1$). Both species richness and abundance of bees varied among sites (richness: mean = 11.9, sd = 4.3; abundance: mean = 27.4, sd = 19.1). The bumblebee species and the solitary species with the highest occurrences were *Bombus pascuorum* ($n = 58$) and *Halictus tumulorum* ($n = 25$) (Table S5).

The two final models on bee occurrence revealed different drivers of wild bee occurrences between regions (Table 2). I focused on the effects captured by both models, as these results are the most robust and least biased. This is because for model 3 I had issues with multicollinearity and did not control for important predictors of bee diversity such as precipitation. Model 4 was therefore the better model, and results from this model will also be reported. The fixed effect terms in model 3 explained 21.3 % of the variation in wild bee occurrences and the fixed effect terms in model 4 explained 21.7% of the variation in wild bee occurrences.

For both models, N deposition had a different response on the floral preference niche score of bees (DCA1), where legume specialists declined. Furthermore, the interaction between Shannon landscape diversity and bee functional group was a significant predictors of bee occurrence (table 2, model 3: $p < 0.001$, model 4: $p = 0.0021$). Landscape diversity increased occurrence of all functional groups, except short-tongued bumblebees. In Norway (model 4), the strongest driver of wild bee occurrence was annual precipitation (Table 2, $p < 0.001$). Occurrences declined with precipitation (odds ratios = 0.71, Fig. S9), and increased with landscape diversity (odds ratios = 2.23, Fig. S9). Plant Shannon diversity had a significant positive effect on solitary bee occurrence ($p = 0.0046$, odds ratios [SolitaryST] = 2.08, odds ratios [SolitaryLT] = 2.03), while bumblebees were not affected by changes in plant diversity (Fig. S9)

Table 2. Likelihood ratio tests for the final model on bee occurrence from the whole region (Norway and Denmark, model 3), and the final model on bee occurrence from Norway (model 4). The models were GLMMs (generalized linear mixed effect models) fitted with site and bee species as random effects. Empty cells are non-significant variables that were omitted during backwards-stepwise selection.

	Model 3: Bee occurrence (Full data; NO + DK)			Model 4: Bee occurrence (Subset data; NO)		
Predictors	<i>df</i>	<i>LRT</i>	<i>p-value</i>	<i>df</i>	<i>LRT</i>	<i>p-value</i>
N deposition x Niche score (floral preference; DCA1)	1	22.04	< 0.001	1	4.934	0.026
N deposition x Bee CWM [floral preference]	1	4.682	0.03			
N deposition x Registered visitor of Fabaceae				1	4.158	0.041
Registered visitor of Fabaceae	1	4.489	0.034			
Bee functional group x Shannon landscape diversity	3	19.16	< 0.001	3	14.7	0.0021
Bee functional group x Plant CWM [Longevity]	3	39.99	< 0.001			
Plant CWM [Longevity]				1	8.41	0.0037
Bee functional group x Plant Shannon diversity	3	5.96	0.11	3	13	0.0046
Bee functional group x Plant CWM [Ellenberg N]				3	13.22	0.0042
Annual precipitation				1	12.81	< 0.001
Random effects	<i>Variance and Std. Dev.</i>					
Bee species (model 3: n = 80, model 4: n = 57)	$\sigma^2 = 0.9823, \sigma = 0.9911$			$\sigma^2 = 1.036, \sigma = 1.018$		
Site (model 3: n = 70, model 4: n = 41)	$\sigma^2 = 0.1774, \sigma = 0.4212$			$\sigma^2 = 0.084, \sigma = 0.290$		
Observations	5600			2337		
Marginal R²/ Conditional R²	0.213 / 0.418			0.217 / 0.416		

3.2.1 | EFFECTS ON BEES ASSOCIATED WITH LEGUMES

I found that as bees floral preference niche scores increased (i.e., as bees became more specialized on zygomorphic flowers), N deposition had a stronger negative impact on bee occurrence, and this pattern was found in both models (Fig. 7, Model 3: $p < 0.001$, odds ratios = 0.73, Fig. S8. Model 4: $p = 0.026$, odds ratios = 0.82, Fig. S9). The probability of occurrence of a bee species associated with Asteraceae and Apiaceae (DCA1 = -1) increased from 10.8% at 460 mg N/ m² per year in Norway, to 21.7% at 720 mg N/ m² per year in Norway (Fig. 7a). In contrast, the probability of occurrence of legume specialist (DCA1 = 2) occurrence had the strongest negative response to N deposition (Fig. 7g), where their probability of occurrence was reduced from 11.8% at sites with 460 mg N/ m² per year, to 2.1% at sites with 720 mg N/ m² per year in Norway. Similarly, analysis of the whole region (model 3) revealed that the probability of occurrence of legume specialists (DCA1 = 2) was reduced from 6.6 % (460 mg N/ m² per year) to 0.05% (1300 mg N/ m² per year) along the N gradient (Fig. 7h). This finding is consistent

with my hypothesis that N deposition reduced occurrence of legume specialists, and that polylectic bees and bees associated with asters have no response or positive response to N deposition.

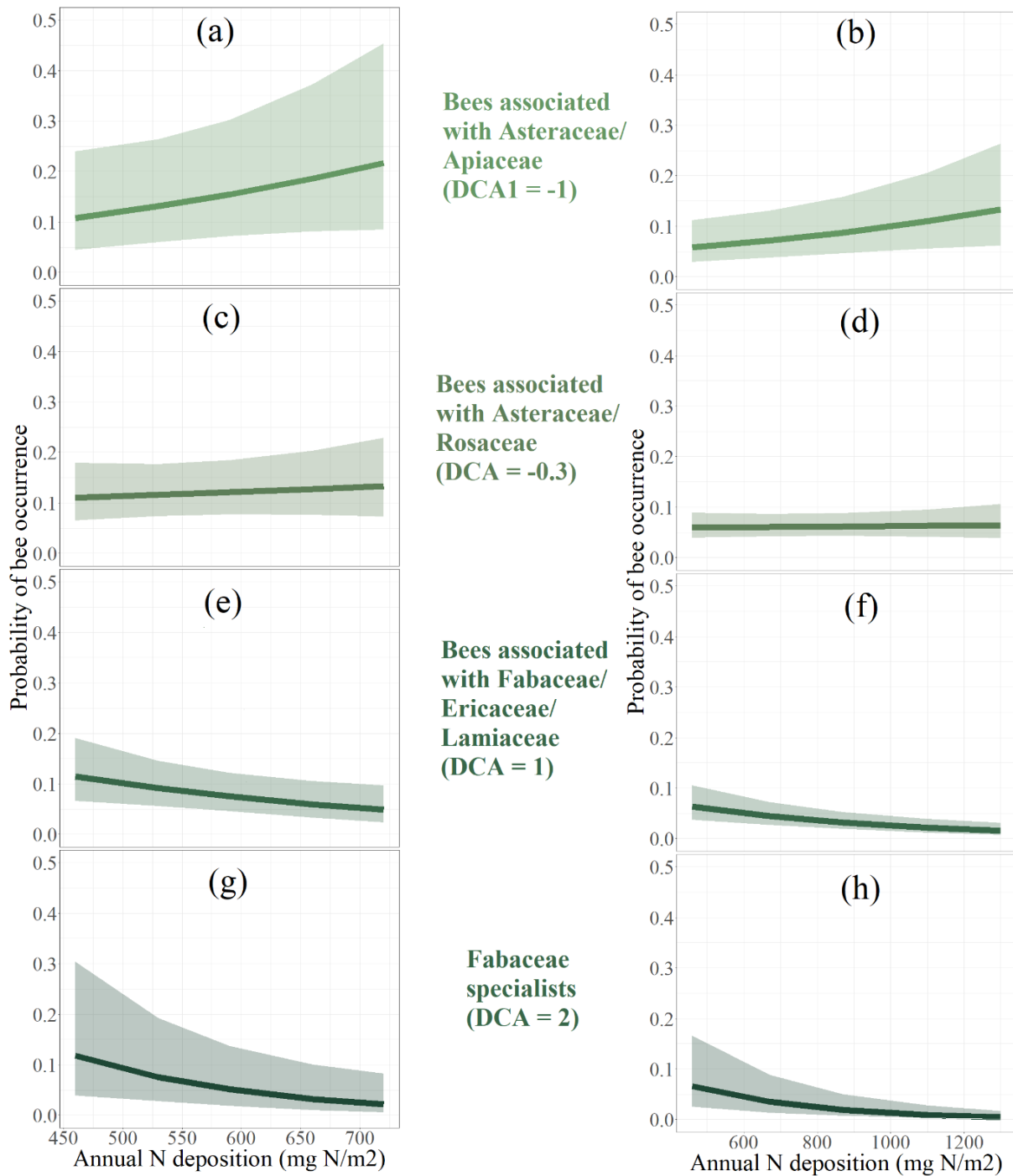


Figure 7. Bee species had different response to N deposition, according to their flower preference niche score (DCA1). Bees associated with actinomorphic flowers (a-d) increased in occurrence, while bees associated with zygomorphic flowers (e-h) decreased in occurrence. The effect was captured by both models: left-side plots (a, c, e, g) shows the response from the model based on the subset data from Norwegian sites (model 4, $p = 0.026$), while the right-side plots (b, d, f, h) shows the response from the full bee model (model 3, $p < 0.001$).

In Norway, the effect of N deposition on bee occurrence depended on whether the species was a documented visitor of legumes or not (i.e., never found on Fabaceae) (Fig. 8). There was moderate evidence that bee species known to visit Fabaceae increased with higher N deposition (table 2, $p = 0.041$, odds ratios = 1.39, Fig. S9).

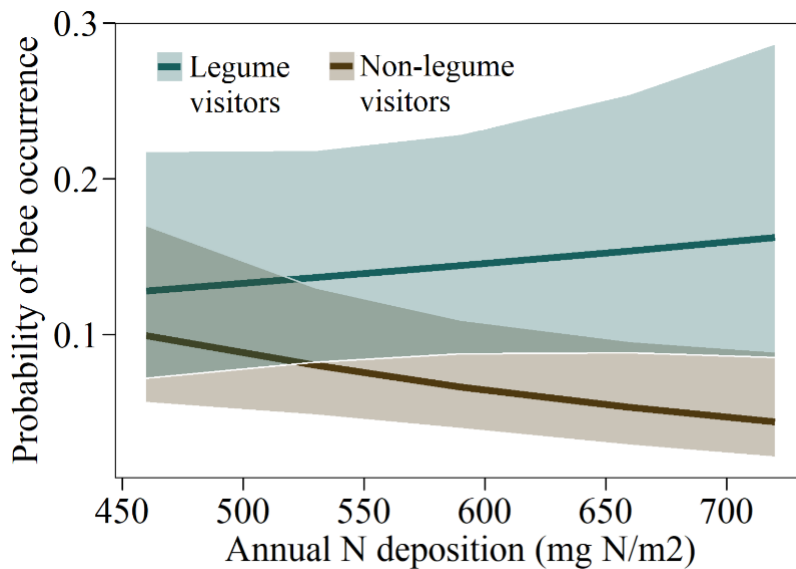


Figure 8. The effect of N deposition on bee occurrence in Norway significantly depended on if the species is a documented visitor of legumes, or a non-legume visitor (model 4, $p = 0.041$). When N deposition increased, legume visitor occurrence increased, while visitors of other plant families decreased.

3.2.2 | BEE RESPONSES TO CHANGES IN PLANT TRAIT COMPOSITION

The change in plant community composition relating to life-history had a significant impact on bee occurrence in Norway, where there was moderate evidence that plant longevity was an important predictor of bee occurrence (model 4, $p = 0.0037$, Fig. 9). Specifically, as perennial plants became more dominant in a community, the probability of bee occurrence increased (Fig. S9, odds ratio = 1.38). Furthermore, there was moderate evidence that the effect of plant CWM [Ellenberg N indicator] on the occurrence of bee species was dependent on functional group relating to sociality and tongue length ($p = 0.0042$, Table 3). Specifically for short-tongued bees, occurrence decreased when the plant community was dominated by nitrophilous plants (Fig. 10, odds ratios [BombusST]= 0.36, odds ratios [SolitaryST] = 0.69). The effect was not significant for long-tongued bees.

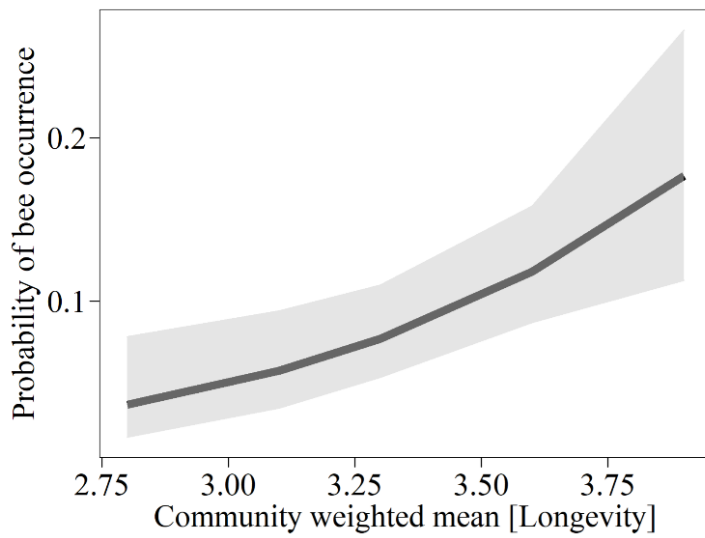


Figure 9. Predicted effect of plant CWM (longevity) on bee occurrence in Norway (model 4, $p = 0.0037$). The probability of bee occurrence increased significantly when there was an increase in longer-lived (perennial) plants in the community (odds ratios = 1.38). The shaded areas are 95% confidence intervals.

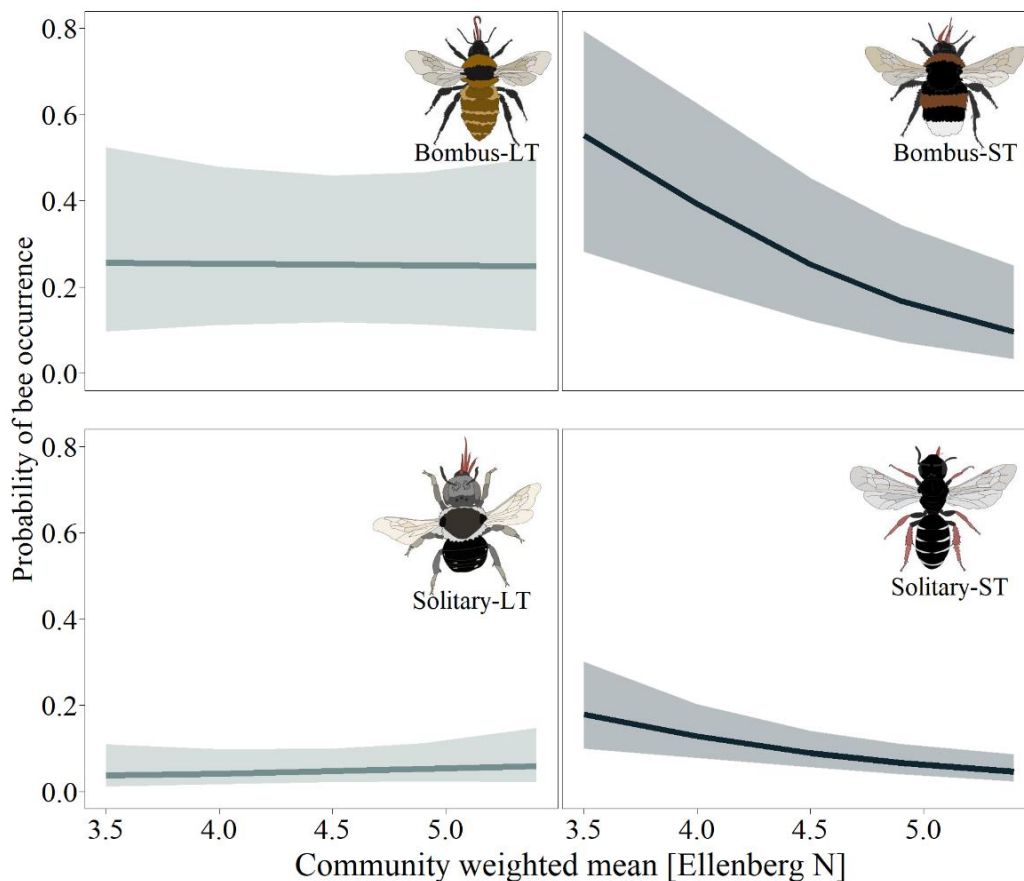


Figure 10. The predicted effect of change in plant community composition of N soil preference (Plant CWM: Ellenberg N indicator) on bee occurrence was dependent on bee functional group (relating to sociality and tongue length) in Norway (model 4, $p = 0.0042$). The occurrence of short-tongued bees (right side plots) decreased significantly with increased domination of nitrophilous plants in the plant community. The effect was not significant for long-tongued bees (left side plots).

3.2.3 | BEE SPECIES PREDICTIONS

To investigate the impact of N deposition on each bee species in Norway, I predicted the probability for occurrence of each bee species at 100 new sites with different rates of N deposition (model 4, Fig. 11).

The prediction revealed that most bee species were negatively affected by N deposition, including all legume (Fabaceae) specialists (e.g., *Andrena lathyri* and *Eucera longicornis*) and some Asteraceae-specialists (e.g., *Andrena denticulata* and *Colletes similis*). Bumblebees mostly associated with zygomorphic flowers (long-tongued bumblebees and *B. wurflenii*) showed a negative response to increased N deposition.

Species that increased strongly in occurrence with N deposition (e.g., positive impact) belong to the genera *Bombus*, *Hylaeus* and *Halictus*. The occurrence of *Hylaeus hyalinatus* increased ~70% from sites with lowest to highest rates of N deposition. *Hylaeus hyalinatus* is polylectic on actionomorphic flowers, including Apiaceae and Asteraceae (Bees Wasps & Ants Recording Society (BWARS), 2022f). The species complex *Bombus sensu strictu* had the largest positive response to N deposition compared to other bumblebees. *Bombus sensu strictu* includes the common bumblebee *Bombus terrestris*, a highly polylectic species (Goulson et al., 2005).

A few species barely differed in their occurrence between low and higher N deposition sites, where the difference in occurrence was < 15% between the site with lowest and highest N deposition. These were the highly polylectic species *Bombus pascuorum*, *B. lapidarius*, *Andrena fucata*, and *Megachile versicolor*, and one polylectic species with preference for legumes (*Bombus distiguendus*, Bees Wasps & Ants Recording Society (BWARS) (2022c))

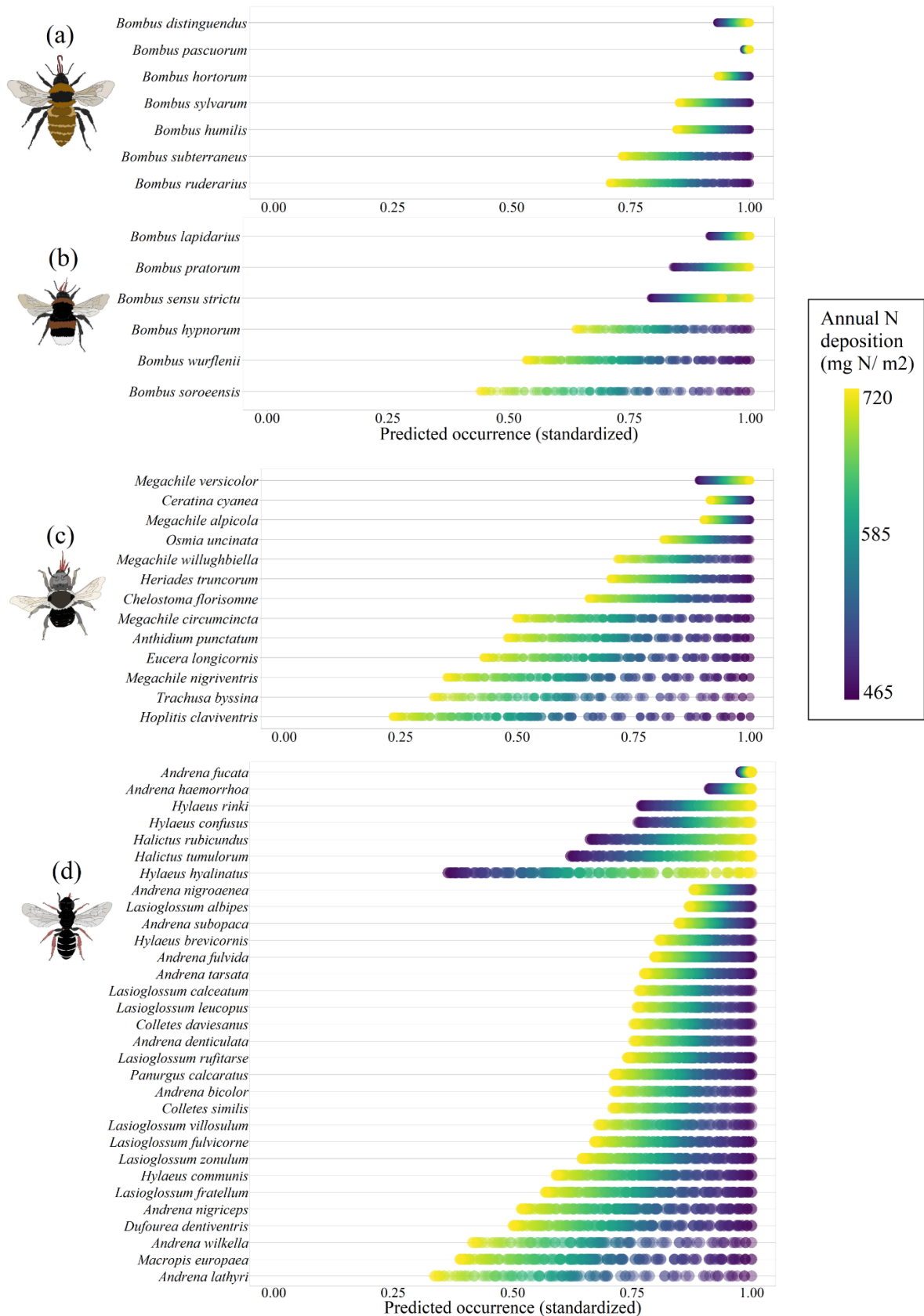


Figure 11. Model predictions of bee species occurrence along the N deposition gradient in Norway (ranging from 465-720 mg N/ m² per year). The prediction is based on model 4, i.e., bee occurrence in Norway. The figure is divided in four functional groups, with the predicted probability of occurrence of species that are long-tongued bumblebees (a), short-tongued bumblebees (b), long-tongued solitary bees (c), and short-tongued solitary bees (d).

4 | DISCUSSION

The aim of my study was to investigate the effect of N deposition on flowering-plants and wild bees and explore if their response was modulated by different ecological and life-history traits. I found evidence for my hypothesis that species occurrence depended on the amount of N deposition, and was determined by their traits. Specifically, I found that N deposition had a negative impact on legume and perennial plant occurrence. Since legumes and perennial flowering-plants provide important food resources for bees, bee species occurrences were overall reduced by the change in plant community composition. Furthermore, I found support for my predictions when separating bees by flower preferences. As expected, solitary legume specialists had the sharpest occurrence decline in response to N deposition. Although I found no support for my prediction that nitrophilous plant occurrence increases with N deposition, the occurrence of pollinators of actinomorphic flowers (i.e., flowers with shorter corolla, such as asters) increased with N deposition. Bee occurrences in Norway decreased with increased abundance of shorter-lived plants and nitrophilous plants, suggesting that disturbed habitats will have an overall negative impact on bee diversity. The high correlation between the environmental variables prevented me from assessing their individual effects on the plant and bee communities; the influence of N deposition was partly masked by the other environmental variables, and vice versa. However, the analysis of the subset of the data (from Norway) and the species predictions revealed a similar response to N deposition, where there was moderate evidence that the probability of occurrence of bees strongly associated with legumes was reduced.

4.1 | TRAIT-SPECIFIC EFFECTS OF N DEPOSITION ON PLANT OCCURRENCE

Analyzing plant occurrences in Norway and Denmark, I found that plant response to N deposition was dependent on the species' longevity. I found fewer perennial plants at higher N deposition, which suggests that perennial plants have a competitive advantage in low N environments, while shorter-lived plants have an advantage in higher N environments. A potential explanation for this pattern is that since plant survival is lower in disturbed areas, annual plants are selected for in disturbed areas (Friedman, 2020), which optimizes the plants reproduction. Previous studies have found a reduction of perennial forbs (Burkle & Irwin, 2010) and a loss of forb diversity (Payne et al., 2013; Stevens et al., 2006) with N addition, which corresponds with my findings. Also, and in line with my findings, previous studies have found that species with perennial life history were more likely to be lost than annuals with N addition (Suding et al., 2005). On the other hand, there has been a reported increase of hemicryptophytes (i.e., herbaceous perennials) with N deposition (Helsen et al., 2014). However, the shift in species composition was caused by an increase in graminoids, not angiosperms (Helsen et al., 2014). These results indicate that it is important to separate responses of grasses and flowering-plants. My study corroborates previous studies showing that perennial plants lose their competitive advantage in high N environments.

Temperature and water availability can also explain why a plant is annual or perennial (Friedman, 2020), and other environmental variables might therefore be important in explaining plant responses. Since N deposition correlated highly with other environmental variables (i.e., temperature, precipitation, and latitude) in my study, perennials occurrence can be modulated to multiple abiotic factors, including both nutrient (N) addition, water availability, and temperature. Midolo et al. (2019) found evidence for a steeper decline in plant species richness at warmer sites compared to colder sites. Thus, the combination of higher temperatures and higher N deposition rates can explain the steep response of perennial plants at the southern sites in my study. These findings might also explain why I overall had much fewer observations of shorter-lived plants than perennials. Furthermore, differences in management across the two countries (e.g., more frequent mowing in Denmark) might explain the different abundance of annuals and perennials, as annuals are favored by grazing (Díaz et al., 2007). These findings suggest that the occurrence of plants with different longevity depends on a combination of N deposition, temperature, and other human disturbances.

I found a significant decrease in legume (Fabaceae) occurrences with higher N deposition, supporting my hypothesis that legume occurrence is reduced with nutrient enrichment. This can possibly be explained by the longevity of the legumes observed in the study, where 67% were perennials. Another explanation is the presence of other species, where previous studies have found that the effect of N deposition on legumes depend on other plant species present (Skogen et al., 2011). Some asters (e.g., *Solidago canadensis*) get the competitive advantage in a nutrient rich environment, and have been reported to increase strongly in biomass with N deposition (Skogen et al., 2011). My finding is consistent with Silvertown et al. (2006), who found that the legume *Lathyrus pratensis* was favored in low-N environments, but are outcompeted by grasses because grasses have the advantage in competition for phosphorous in N rich environments. When nutrient availability increases, native species have been shown to have a higher probability of local extinction (Suding et al., 2005), while faster-growing, shorter-lived plants get the competitive advantage. Moreover, zygomorphic flowers (including legumes) can be affected by direct effects of soil acidification caused by N deposition (Stevens et al., 2018). Even though I only observed a small reduction in legume occurrence with N deposition, previous literature on global trends have found that N deposition has decreased both legume cover, richness, and biomass (Tognetti et al., 2021), also in line with my hypothesis. These results seem to indicate that legume diversity is reduced with increased N deposition, because of both their adaption to nutrient poor environments, and their longevity.

I found no difference in occurrences between nitrophilous and nitrophobous plants along the N deposition gradient in Norway and Denmark. This finding contradicts Carvalheiro et al. (2020), who found a decline in richness of nitrophobous plants at higher N deposition. However, Carvalheiro et al. (2020) studied richness changes in the Netherlands, where the amount of N deposition has exceeded critical loads drastically (European Environment Agency, 2007). Critical loads are measures of the

exceedance of pollution linked to a clear reduction in plant species richness (Bobbink et al., 2010). In European acidic grasslands, Payne et al. (2013) found that the plant community level threshold (i.e., largest change in species composition) was at the upper limit of the critical load of N deposition, which was 1420 mg N per m² annually. At this critical load, the plant species community changed to a more pollutant-tolerant species composition (Payne et al., 2013), which possibly included species that are indicators of N rich soils (i.e., nitrophilous species), which was found in the Netherlands (Carvalho et al., 2020). At my study sites, the mean and maximum annual loads of N deposition was 800 and 1279 mg N m², respectively. Since my study sites are under the threshold limits (found in Payne et al., 2013), my results indicate that Ellenberg N criterion is not an important trait in explaining plant species distributions in roadsides in Norway and Denmark.

It is important to mention that the studies I read on the effect of atmospheric N deposition on plants are from Europe, especially relating to European acidic grasslands in the UK (e.g., Stevens et al., 2004). My results indicate that N deposition also can have an effect of plant diversity in Nordic region in the Northern Hemisphere, where the background rate of atmospheric N deposition is much lower than in the UK (European Environment Agency, 2007). However, the evidence from Norway was weak, suggesting that the atmospheric N deposition level is too low to have an observed impact on the plant community. The lowest N deposition at which it is possible to identify any change is 700 mg N per m² annually (Payne et al., 2013), and maximum level of total annual N deposition from my sites in Norway was 720 mg N per m², thus explaining why the evidence of N deposition having an effect on plant occurrences in Norway was weak. Future studies are needed to investigate if these results are applicable on a more global scale.

4.2 | N DEPOSITION REDUCED OCCURRENCE OF SOLITARY LEGUME SPECIALISTS

As I hypothesized, the occurrence of bees strongly associated with legumes decreased along the N gradient, both in the whole region, and in Norway. Since floral resource abundance and temporal availability are the most important predictors of bee distributions (Roulston & Goodell, 2011), the observed reduction in legumes should reduce occurrences of their associated pollinators. The observed reduction in legumes with N deposition in my study, also in line with other studies (e.g., Tognetti et al., 2021) is a possible explanation of why legume specialists decreased at higher N deposition rates. Although my finding was limited by few solitary legume specialists (7 of 80 species had DCA1 > 1.5, see Table S3), these species use legumes as their only food source. In my study, 14 of 21 legumes were perennials, and their occurrence decreased significantly with N deposition. Legumes that are especially important for long-tongued bees (e.g., *Trifolium repens* and *Lotus corniculatus*) are long-lived perennials. There has been reported a decrease of long-tongued bees with N deposition (Stevens et al., 2018), corresponding well with my findings were the occurrence of 12 of 13 long-tongued solitary bees was reduced with N deposition. These findings are also in line with Burkle and Irwin (2010), who found

that N addition had an impact the pollinator visitation rates, were forbs (including legumes) in lower N environments had a significantly higher rate of visitors. N deposition has an indirect negative impact on long-tongued solitary bees and legume specialists, where fewer perennials and legumes explains their observed reduction along the N deposition gradient. Since zygomorphic flowers (e.g., legumes) have fewer potential species (Yoder et al., 2020), their decline will be more apparent than for flowering plants with generalist pollinators. These findings demonstrate that N deposition causes a negative feedback loop across trophic levels, negatively affecting both legume and legume pollinator fitness.

I found that several responses of bee species were dependent on their functional group, which relates to both sociality, tongue length, and body size. Previous studies have found a correlation between N deposition and bee diversity changes, in relation to their body size. An increase of smaller bees (Burkle & Irwin, 2010), and a decline of larger bees was linked to higher N deposition (Burkle & Irwin, 2010; Stevens et al., 2018). In contrast, my species predictions revealed that some smaller bees respond negatively to N deposition, depending on their floral preference. For example, the smaller bee *Andrena wilkella* decreases in occurrence with N deposition. *Andrena wilkella* has strong preferences for Fabaceae (Wood & Roberts, 2017). There is a positive correlation between body size and dispersal ability (Gathmann & Tschardt, 2002; Greenleaf et al., 2007). The steep reduction in smaller legume specialists might therefore be explained partially by their body size. On the other hand, since smaller bees require less energy, and may therefore be better able to maintain population size in a disturbed area with less resources (Williams et al., 2010). Overall, the effect of N deposition on bees with different body sizes remains unclear, and future studies should therefore account for body size of each species of study interest.

For bees associated with legumes, I found that oligolectic solitary bees had a stronger negative response than bumblebees to N deposition. When including all legume pollinators (both polylectic and oligolectic species, including *Bombus* spp.) occurrence increased along the N deposition gradient in Norway. However, these data were dominated by *Bombus* occurrences, and 12 of 14 of the recorded *Bombus* species were documented visitors of legumes. In my study, bees that were classified as legume specialists (DCA1 > 1.5) were either a long-tongued solitary bees (e.g., *Eucera longicornis*) or short-tongued solitary bees *Andrena lathyri* and *A. wilkaella*. Solitary bees could have responded more strongly to N deposition than bumblebees since they do not fly far away from their nest (Gathmann & Tschardt, 2002) and thus dependent on having food available in close proximity. Most bumblebees are generalists, and can pollinate a range of flowers (Wood et al., 2021). A possible explanation of the observed higher occurrences of *Bombus* species is that since social bees are associated with higher reproduction and foraging capacity, local landscape context affects solitary bees more than bumblebees (Steffan-Dewenter et al., 2002). Therefore, they might not be as impacted as solitary bees when there is a reduction in food resources at smaller scales (Bommarco et al., 2010) as a response to N deposition. It is well established that niche breadth and dispersal ability modifies the responses of wild bee species to

habitat change (Bommarco et al., 2010), and the traits associated with threatened species includes narrow niche breadth and poor dispersal ability (Kotiaho et al., 2005). These findings altogether explain why solitary legume specialists had the strongest decline in occurrence with N deposition. Because of fewer observations of legume specialists in my data, their response was masked by bumblebee occurrences when only separating documented legume pollinators and non-legume pollinators. Hence, my study highlights the importance of separating between sociality when studying bee responses to environmental disturbance.

4.3 | EFFECTS OF N DEPOSITION ON BEES ASSOCIATED WITH ASTERS

I found that bees strongly associated with Apiaceae (the carrot family) and Asteraceae (the aster family) (DCA1 between -1 and -0.8) increased with N deposition, and that other pollinators of actinomorphic flowers (DCA1 > -0.8, but < 0.3) were not affected by changes in N deposition. Bees strongly associated with Apiaceae and Asteraceae were *Colletes cunicularius* (DCA1 = -0.8), *Andrena fulva* (DCA1 = -0.8), and *Andrena chrysoseles* (DCA1 = -0.9). These species were only observed in Denmark on *Anthriscus sylvestris* or *Taraxacum spp.*, Further, *Andrena haemorrhoa* (DCA1 = -0.8) was observed in both Denmark and Norway, and was found on *Taraxacum spp.*, in 37 of 39 of the observations. This finding can possibly be explained by the availability of dandelions (*Taraxacum spp.*). I did not study the response of dandelions to N deposition, however since we missed the blooming of dandelions at many sites in Norway, many bees were collected on dandelions at sites with higher N deposition (i.e., in Denmark). Moreover, some nectar and pollen resources with high Ellenberg N scores and could respond positively to eutrophication, for example dandelions (*Taraxacum spp.*) (Stevens et al., 2018). In the Netherlands, bees preferring pollen from Rosaceae, Brassicaceae, and Asteraceae have remained stable, or increased (Scheper et al., 2014). This is consistent in my findings, where occurrences of bees associated with Asteraceae and Rosaceae were stable along the N deposition gradient. My study seems to indicate that the species not negatively affected by N deposition are highly polylectic species and/ or are species associated with Apiaceae and Asteraceae (e.g., dandelions).

The prediction of bee occurrence in Norway revealed that most pollinators of actinomorphic flower decreased in occurrence with N deposition. Contradictory to my predictions, only a few species had a predicted increase; *Hylaeus hyalinatus*, *Halictus rubicundus*, and *Halictus tumulorum* which are highly polylectic short-tongued solitary bees. For example *Andrena denticulata* who is broadly oligolectic on Asteraceae (Wood & Roberts, 2017) occurrence decreased with N deposition. In my study, *Andrena denticulata* was collected from tansy (*Tanacetum vulgare*). Tansy had only short-tongued visitors (e.g., *Colletes similis* and *Andrena denticulata*) and was classified as nitrophilous. However, nitrophilous plants did not increase with N deposition in my study. In the Netherlands, there was an increase in nitrophilous plants pollinated by bees when N deposition increased the most, between 1950 and 1990 (Carvalho et al., 2020). My findings indicates that nitrophilous plants does not increase with N

deposition at habitats with lower N inputs (here: Norway) and does not influence the majority of pollinators of nitrophilous plants in Norway.

There was less bee occurrences at sites with larger domination of short-lived plants in Norway. This finding is consistent with what I expected since most of the bees in my study were collected on perennial plants. However, the species complex *Bombus sensu strictu* increased in occurrence with N deposition, which can possibly be explained by their generalist preference. *Bombus sensu strictu* includes the common bumblebee *Bombus terrestris*, which is highly polylectic (Goulson et al., 2005). For example, all the recorded visitors of the biennial flowering plant *Cirsium palustre* (Asteraceae) in my study were polylectic bumblebees (n = 21). This finding demonstrate that N deposition causes an overall reduction in diversity across trophic levels, but highly generalist species (e.g., *Bombus terrestris*) increase in occurrence.

Since the location of nests affect bee responses to habitat change (Williams et al., 2010), another possible explanation of the observed response of bees with contrasting floral preferences is their differences in nesting site preference. I found that landscape diversity (Shannon index) had a strong positive effect on bee occurrence, except short-tongued bumblebees. Landscape diversity is a proxy for nesting site availability, since increased landscape heterogeneity increases landscape elements (e.g., rodent holes, roadsides, grasslands, pastures, and forest edges). Bee species richness increases with proximity to sandy sediments and forests (Sydenham et al., 2022), which in turn can favor some functional groups of bees. Overall, changes in availability of nesting resources can be predictors of bee community variance in richness (Murray et al., 2012). Since the sites in my study had a great variation in landscape diversity (min = 0.3, max = 1.5, mean = 1.1), my findings demonstrate that sites with similar nesting site availability should be studied to provide stronger evidence of the effect of N deposition on bee species occurrence.

4.4 | STUDY LIMITATIONS

The data I used N deposition might not have been detailed enough to capture the site-specific deposition rates, not providing accurate levels of N deposition rates at a local level. Roadsides are N deposition hot spots, where N inputs increases with proximity to roadside edges (Bettez et al., 2013). The data I used was annual averages in resolution approximately 10 km x 10 km radii, and therefore, my sites (roadsides) might contain more N deposition than what I used in my data. Furthermore, my sites had differences in traffic intensity, and air pollutants (dry deposition of N) have been shown to affect bees, where bee counts was significantly decreased with diesel exhaust (Ryalls et al., 2022). Another possibility is that there is a greater variation at local level due to different distances of agriculture (husbandry and fertilizers). Thus, there a possibility that N deposition does not correlate as highly with latitude at my sites. Future studies need to separate N deposition from other environmental variables, by including more site-specific measure of pollution, by for example adding distance to major N pollution sources

(e.g., agriculture and traffic intensity) as a proxy for N deposition, or measure soil N content at the site. Moreover, since the fixed effects in my models explained < 10 % of the observed variation in plant occurrence, future studies should aim to remove confounding factors to obtain a more robust conclusion on species responses to N deposition.

A challenge with ecological gradient studies is correlating variables. In my study, N deposition correlated strongly with other environmental variables (see figures S2 and S4), including annual means of temperature and precipitation, latitude, and elevation. Therefore, the impact of N deposition is overestimated caused by multicollinearity, and I was not able to make accurate conclusions that N deposition is the main predictor of the observed decrease in species occurrences. The N deposition gradient (400-1200 mg N/ m² a year) and PCA1 was a similar gradient (Fig. S4), thus N deposition and other factors might together explain the observed changes in species diversity. However, analyzing only the data from Norway, I was able to separate the effect of annual mean precipitation, and found similar (but weaker) trends, where for example there was a decline of solitary legume specialists. However, I did not isolate the effect of temperature. Specifically for Norway, solitary bee species richness decreases with latitude and elevation (Sydenham et al., 2022), which correlated with annual mean temperature in my study. Temperature has been found to have strong effects on bee distributions (Aguirre - Gutiérrez et al., 2017; Kammerer et al., 2021). Thus, the observed decline in legume specialists could partially be explained by temperature having a different impact on bees associated with legumes and asters, however this remains unknown. These findings suggest that we need more research on trait-specific responses of bees to environmental change.

In my study, 50 % of the plant species occurrences had Ellenberg N equal to four or five, and these species are indicators of moderate N poor to N rich soils, and moderately N-rich soils, respectively (Tyler et al., 2021). The cut-off I used to separate nitrophilous and nitrophobous might therefore be inaccurate. Moreover, the Ellenberg N indicator value is based on observations by experts, and not an actual measure of nutrient availability (N content) in the soil (Falkengren-Grerup & Schöttelndreier, 2004). Terrestrial plant responses has previously been found to be dependent on type of reactive N deposited, where for example nitrate (NO₃⁻) has increased plant allocation to above-ground tissues, and ammonia (NH₄⁺) enhanced below-ground growth (Yan et al., 2019). Similarly, Falkengren-Grerup and Schöttelndreier (2004) found that plants responses was dependent on soil N, where for example the common nettle (*Urtica dioica*) showed a positive growth response to ammonium, but a negative growth response to nitrate. Since atmospheric input of ammonia and nitrate are uneven in many areas (Yan et al., 2019), and I did not separate the different types of reactive N, my results suggest that plants with different soil criteria (measured by Ellenberg N) is dependent type of reactive N deposited. Future studies should therefore account for the type of N deposited to investigate if plant responses are dependent on soil N preferences.

4.5 | SYNTHESIS AND APPLICATIONS

Conservation of pollinator functional diversity is essential for maintaining pollination services and biodiversity (Fontaine et al., 2006). I found a strong positive relationship between habitat heterogeneity (landscape diversity) and wild bee occurrences. Plant diversity increased occurrence of solitary bees. Also, high disturbance selected for shorter-lived plants, reducing bee occurrences. My findings show that it is vital to maintain a diverse landscape and vegetation, with low disturbance, to maintain pollinator diversity. My study provides more evidence that anthropogenic disturbance (including N deposition) has an impact on the current pollinator declines, and major contributors to N deposition (including agricultural practices and industry) should aim to reduce emissions of N compounds (e.g., nitrate and ammonia). My results indicate that legume specialists are especially vulnerable to N deposition. Since small body size reduces dispersal ability (Greenleaf et al., 2007), smaller specialists like *Andrena lathyri* and *A. wilkaella* are especially vulnerable to environmental change. A combination of habitat fragmentation and N deposition, reducing nectar and pollen availability, will therefore be particularly detrimental for these species. Moreover, a decline in legume specialist species will entail a greater reduction in fitness of legumes compared to other species, since zygomorphic flowering plants have fewer pollinating species (Yoder et al., 2020). Conservation of specialists should therefore be a priority in the future.

Grasslands (including roadsides) are important for supporting pollinator communities (Ehlers et al. 2021) and can therefore mitigate the negative impact of N deposition on bee diversity. Even though roadsides are particularly exposed to pollution (particularly from vehicles), they can provide possible dispersal corridors for bees. Since I found perennial plants to increase wild bee occurrences, management should maintain perennial-rich roadsides, and prevent growth of shorter-lived plants. Since diesel exhaust repel bees (Ryalls et al., 2022), roadsides with less traffic should be prioritized in establishment of flower-rich roadsides. Furthermore, I found a significant increased occurrence of plant species adapted to frequent mowing. Since roadsides are being mowed frequently, maintaining an early successional stage, they can possibly provide a diversity of plants facilitating bee diversity, for example dandelions (*Taraxacum spp.*), and legumes *Trifolium pratense* and *Lotus corniculatus*, which are adapted to high frequency of mowing (Tyler et al., 2021). Moreover, researchers have stated that the cause of legume specialist declines is possibly loss of legume-rich grasslands (Goulson et al., 2005), and a decrease of agricultural use of legumes as fodder crops (Scheper et al., 2014). Conservation of sites with legumes and legume specialists should therefore be a priority to mitigate the negative impact of N deposition on their diversity.

5 | CONCLUSION

To my knowledge, this is the first study of a large-scale N gradient study based on standardized species communities, involving two trophic levels, i.e., flowering plants and wild bees. I found that N deposition had a different impact on bees relating to their niche breadth, where legume (Fabaceae) specialists had the strongest decline in occurrence. Thus, the reduction in legumes can partially be explained by the observed reduction in their associated pollinators. The bee species with predicted increase with N deposition were highly polylectic species, or species strongly associated with the aster family (Asteraceae) and the carrot family (Apiaceae). As N deposition was linked to a change in plant community composition, which in turn affected bee occurrences, my study emphasizes the importance of reducing N pollution for biodiversity conservation. The observed diversity changes in my study can lead to homogenization of flowering plant and wild bee diversity. Hence, my study reveals that it is important to assess the impacts of N deposition on higher trophic levels, to provide information about what pollinator groups are in special need of conservation. The change in community composition observed in this study predict future turnover of plant and bee species, where diversity of legumes and their specialist pollinators will have the greatest decline. My study also illustrates that functional and ecological traits provide valuable information when studying species-specific responses to global change and is vital to understand population declines and plan conservation strategies.

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SUPPLEMENTARY INFORMATION

A. OVERVIEW OVER ALL VARIABLES INCLUDED IN ANALYSES

Table S1. Overview over all environmental variables included in data analyses.

Explanatory variable	Code	Definition	Units	Source
Total annual deposition of nitrogen (N)	TotalNitrogenDep	Total deposition = Annual deposition of dry and wet reduced N + dry and wet deposition of oxidized N. Calculated as follows: Total annual N deposition = Total deposition of reduced nitrogen (= DDEP_RDN_m2Grid + WDEP_RDN) + total deposition of oxidized nitrogen (= DDEP_OXN_m2Grid + WDEP_OXN)	mg N /m ²	The Norwegian Meteorological Institute (MET Norway, 2019), (Tørseth et al., 2012), (EMEP Status Report, 2021)
Shannon landscape diversity	ShannonLandscape	Landscape composition, Shannon diversity	Shannon index	European ELC10 land cover map (Venter & Sydenham, 2021)
Crop cell cover	CropCells	Percentage of area covered by planted/cultivated crops.	Decimal	
Urban cell cover	UrbanCells	Percentage of area covered by artificial land, human-built constructions, and pavement.	Decimal	
Mean annual temperature	bio1	Mean annual temperature (from 1970-2000).	Average temperature (°C * 10) per 5 m	WorldClim database (Fick & Hijmans, 2017). The data was derived using function <i>getData</i> from package 'raster' (Hijmans, 2022) in R (R Core Team, 2021)
Mean annual precipitation	bio12	Mean annual precipitation (from 1970-2000).	Average precipitation (mm) per 5 m	
Elevation	Elevation	Elevation data in 25 m resolution.	Numeric	(European Environment Agency (EEA), 2021)
Latitude	Latitude	Latitude coordinate	Numeric	Measured at site

Soil quality 1	sq1	Describes the nutrient availability in the soil. This includes soil texture, soil organic C content, pH, and total exchangeable bases.	Categoric variable with four levels. 1-4	Harmonized World Soil Database v 1.2, FAO (Fischer et al., 2008)
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Table S2. Overview over all plant trait variables included in data analyses.

Explanatory variable	Code	Definition	Units	Source
Plant Shannon diversity	PlantShannonDiversity	Calculated for each site using the function <i>diversity</i> from package ‘vegan’ in R (R Core Team, 2021)	Shannon index	Vegetation surveys 2021
Plant family	Family	If the species belongs to the legume family (Fabaceae), aster family (Asteraceae), or other family (Other).	3 categories (Fabaceae, Asteraceae, Other)	Norwegian flora (Lid, 1952)
Plant life form (longevity)	cLongevity	Plant life history type (longevity) was divided in three categories: annuals, biennials, and perennials. Plants with longevity = 1 (Tyler et al., 2021) was classified as annuals , plants with longevity = 2 (Tyler et al., 2021) was classified as biennials , plants with longevity = 3 and 4 (Tyler et al., 2021) was classified as perennials .	3 categories (annual, biennial, perennial)	Trait overview: supplementary from Tyler et al. (2021)
Ellenberg Nitrogen (N) Indicator Value	EllenbergNitrogen	Plant trait on a continuous scale, were species with score 1 are non-nitrophilous (i.e., nitrophobous), and species with score 9 are highly nitrophilous.	2 categories (nitrophilous, non-nitrophilous)	
Grazing/mowing criteria	Mowing	Plant trait on a continuous scale, were species with score 1 does not endure any mowing, and species with score 8 needs continuous mowing.	Numeric, 1-8	
Plant CWM [Longevity]	PlantLongevityCWM	I first calculated trait value * frequency for each species in the community	Numeric	Equation of CWM retrieved from (Garnier

Plant CWM: [Ellenberg N]	PlantNitrogenCWM	(x was the trait value for each plant species, and r the frequency of a plant species at each study site).		et al., 2004; Ricotta & Moretti, 2011)
Plant CWM [Mowing]	PlantMowingCWM	I then added all the values together to get the community weighted mean (see equation given in methods section).		

Table S3. Overview over all bee trait variables included in data analyses.

Explanatory variable	Code	Definition	Units	Source
Functional group relating to sociality and tongue length	GroupTL	<p>SolitaryLT (Megachilidae and Apidae)</p> <p>SolitaryST (solitary species belonging to other families)</p> <p>BombusLT: Bombus species with tongue length ≥ 7.9 mm</p> <p>BombusST: Bombus species with tongue-length < 7.9 mm</p>	4 categories	Bombus data on tongue lengths (Wood et al., 2021)
Registered visitor of legumes (Fabaceae)	RegFabaceaeVisitor	<p>If the bee species is a registered visitor of Fabaceae plants (1) or not (0)</p> <p>Variable “RegFabaceaeVisitor” based on (Rasmussen et al., 2021), specifying whether the bee species is a documented visitor of legumes (1) or not (0).</p>	Binomial (1, 0)	Data from: (Rasmussen et al., 2021), except: <i>Bombus wurflenii</i> foraging plants from Wood et al. (2021) <i>Ceratina cyanea</i> foraging plants from Bees Wasps & Ants Recording Society (BWARS) (2022d)
Floral preference niche score	DCA1	<p>Information about foraging plant preference for each bee species retrieved from a dataset of all known forage plants of bees in Denmark (Rasmussen et al., 2021).</p> <p>Then, the niche score for each species was calculated by detrended correspondence analysis</p>	<p>The niche scores are on a continuous scale, where: 1.8 (exclusively Fabaceae-specialists), 1.6</p>	<p>Data on plant-pollinator network from (Rasmussen et al., 2021)</p> <p>DCA1 calculated using package</p>

			(DCA) using the function <i>decorana</i> from package “vegan” in R (Oksanen et al., 2007). For the complex <i>Bombus sensu strictu</i> , the value of <i>Bombus terrestris</i> was used.	(specialists on flowers with longer corolla, e.g., Fabaceae and Lamiaceae), to generalists (0-1), and specialists on flowers with short corolla (e.g., pollinators of Asteraceae and Apiaceae) scoring from 0 to -2.	‘vegan’ (Oksanen et al., 2007).
Bee CWM [floral preference]	CWM	CWM	Before calculation of CWM, the orchid specialist and <i>Apis mellifera</i> was removed from Rasmussen et al. dataset. Community weighted mean based on niche score of bees, The niche score was calculated with DCA, where the scale separating legume specialists from generalists and non-legume pollinators (DCA1. See Fig. S1).	Continuous scale from (-2) - 2	(Garnier et al., 2004; Ricotta & Moretti, 2011)

B. SPECIES INFORMATION

Table S4. Overview over the plant (angiosperm) species registered at the sites in Norway and Denmark in 2021. The count (n) is the number of occurrences (i.e., presence in 1 m² plot). Some species were only determined to genus (e.g., *Hieracium spp.*).

Plant species	Family	n	Plant species	Family	n
<i>Achillea millefolium</i>	Asteraceae	316	<i>Artemisia campestris</i>	Asteraceae	8
<i>Vicia cracca</i>	Fabaceae	195	<i>Erigeron acris</i>	Asteraceae	8
<i>Ranunculus acris</i>	Ranunculaceae	186	<i>Bellis perennis</i>	Asteraceae	7
<i>Trifolium pratense</i>	Fabaceae	155	<i>Viola palustris</i>	Violaceae	7
<i>Lotus corniculatus</i>	Fabaceae	143	<i>Allium scorodoprasum</i>	Amaryllidaceae	6
<i>Anthriscus sylvestris</i>	Apiaceae	141	<i>Cerastium arvense</i>	Caryophyllaceae	6
<i>Rumex acetosa</i>	Polygonaceae	140	<i>Geranium robertianum</i>	Geraniaceae	6
<i>Plantago lanceolata</i>	Plantaginaceae	132	<i>Geranium spp.</i>	Geraniaceae	6
<i>Leucanthemum vulgare</i>	Asteraceae	121	<i>Myosotis ramosissima</i>	Boraginaceae	6

<i>Stellaria graminea</i>	Caryophyllaceae	121	<i>Noccaea caerulescens</i>	Brassicaceae	6
<i>Cirsium arvense</i>	Asteraceae	118	<i>Agrimonia eupatoria</i>	Rosaceae	5
<i>Cerastium fontanum</i>	Caryophyllaceae	115	<i>Galium boreale</i>	Rubiaceae	5
<i>Trifolium repens</i>	Fabaceae	110	<i>Geranium molle</i>	Geraniaceae	5
<i>Veronica chamaedrys</i>	Plantaginaceae	81	<i>Jasione montana</i>	Campanulaceae	5
<i>Hieracium spp.</i>	Asteraceae	79	<i>Ononis repens</i>	Fabaceae	5
<i>Knautia arvensis</i>	Caprifoliaceae	78	<i>Potentilla argentea</i>	Rosaceae	5
<i>Rumex acetosella</i>	Polygonaceae	74	<i>Potentilla recta</i>	Rosaceae	5
<i>Galium album</i>	Rubiaceae	63	<i>Potentilla thuringiaca</i>	Rosaceae	5
<i>Trifolium campestre</i>	Fabaceae	63	<i>Salix aurita</i>	Saliceae	5
<i>Viola riviniana</i>	Violaceae	62	<i>Vaccinium vitis-idaea</i>	Ericaceae	5
<i>Lathyrus pratensis</i>	Fabaceae	59	<i>Circaea lutetiana</i>	Onagraceae	4
<i>Filipendula ulmaria</i>	Rosaceae	56	<i>Galeopsis bifida</i>	Lamiaceae	4
<i>Scorzoneroidea autumnalis</i>	Asteraceae	56	<i>Hylotelephium maximum</i>	Crassulaceae	4
<i>Tussilago farfara</i>	Asteraceae	56	<i>Melampyrum pratense</i>	Orobanchaceae	4
<i>Vicia hirsuta</i>	Fabaceae	56	<i>Rhinanthus spp.</i>	Orobanchaceae	4
<i>Hypochaeris radicata</i>	Asteraceae	55	<i>Rosa canina</i>	Rosaceae	4
<i>Tanacetum vulgare</i>	Asteraceae	51	<i>Rubus saxatilis</i>	Rosaceae	4
<i>Achillea ptarmica</i>	Asteraceae	49	<i>Ajuga reptans</i>	Lamiaceae	3
<i>Artemisia vulgaris</i>	Asteraceae	48	<i>Barbarea vulgaris</i>	Brassicaceae	3
<i>Potentilla erecta</i>	Rosaceae	46	<i>Centaurea jacea</i>	Asteraceae	3
<i>Salix caprea</i>	Saliceae	44	<i>Jacobaea vulgaris</i>	Asteraceae	3
<i>Hypericum maculatum</i>	Hypericaceae	43	<i>Maianthemum bifolium</i>	Asparagaceae	3
<i>Linaria vulgaris</i>	Plantaginaceae	42	<i>Pastinaca sativa</i>	Apiaceae	3
<i>Angelica sylvestris</i>	Apiaceae	41	<i>Prunus spinosa</i>	Rosaceae	3
<i>Trifolium medium</i>	Fabaceae	40	<i>Sorbus aucuparia</i>	Rosaceae	3
<i>Rubus idaeus</i>	Rosaceae	39	<i>Stachys sylvatica</i>	Lamiaceae	3
<i>Fragaria vesca</i>	Rosaceae	37	<i>Succisa pratensis</i>	Caprifoliaceae	3
<i>Ranunculus repens</i>	Ranunculaceae	37	<i>Acer campestre</i>	Sapindaceae	2
<i>Plantago major</i>	Plantaginaceae	35	<i>Acer pseudoplatanus</i>	Sapindaceae	2
<i>Trifolium hybridum</i>	Fabaceae	35	<i>Ajuga pyramidalis</i>	Lamiaceae	2
<i>Urtica dioica</i>	Urticaceae	32	<i>Anthyllis vulneraria</i>	Fabaceae	2
<i>Galium aparine</i>	Rubiaceae	31	<i>Caltha palustris</i>	Ranunculaceae	2
<i>Galium verum</i>	Rubiaceae	30	<i>Carum carvi</i>	Apiaceae	2
<i>Pimpinella saxifraga</i>	Apiaceae	28	<i>Chenopodium album</i>	Amaranthaceae	2
<i>Anemone nemorosa</i>	Ranunculaceae	27	<i>Cota tinctoria</i>	Asteraceae	2
<i>Crepis capillaris</i>	Asteraceae	27	<i>Dianthus deltoides</i>	Caryophyllaceae	2
<i>Vicia sepium</i>	Fabaceae	27	<i>Filago vulgaris</i>	Asteraceae	2
<i>Calluna vulgaris</i>	Ericaceae	23	<i>Fraxinus excelsior</i>	Oleaceae	2
<i>Epilobium spp.</i>	Onagraceae	23	<i>Geranium pyrenaicum</i>	Geraniaceae	2
<i>Tragopogon pratensis</i>	Asteraceae	23	<i>Heracleum sphondylium</i>	Apiaceae	2
<i>Campanula rotundifolia</i>	Campanulaceae	22	<i>Lepidotheca suaveolens</i>	Asteraceae	2
<i>Lathyrus linifolius</i>	Fabaceae	22	<i>Lonicera periclymenum</i>	Caprifoliaceae	2
<i>Potentilla reptans</i>	Rosaceae	22	<i>Rumex spp.</i>	Polygonaceae	2

<i>Trifolium arvense</i>	Fabaceae	22	<i>Salix repens</i>	Saliceae	2
<i>Cirsium palustre</i>	Asteraceae	21	<i>Senecio spp.</i>	Asteraceae	2
<i>Hypericum perforatum</i>	Hypericaceae	21	<i>Silene latifolia</i>	Caryophyllaceae	2
<i>Alchemilla spp.</i>	Rosaceae	20	<i>Silene nutans</i>	Caryophyllaceae	2
<i>Chamaenerion angustifolium</i>	Onagraceae	20	<i>Sonchus asper</i>	Asteraceae	2
<i>Equisetum arvense</i>	Equisetaceae	20	<i>Viola canina</i>	Violaceae	2
<i>Cirsium vulgare</i>	Asteraceae	19	<i>Viola tricolor</i>	Violaceae	2
<i>Daucus carota</i>	Apiaceae	19	<i>Viscaria vulgaris</i>	Caryophyllaceae	2
<i>Rubus plicatus</i>	Rosaceae	19	<i>Cardamine amara</i>	Brassicaceae	1
<i>Sonchus arvensis</i>	Asteraceae	19	<i>Cichorium intybus</i>	Asteraceae	1
<i>Glechoma hederacea</i>	Lamiaceae	18	<i>Clinopodium vulgare</i>	Lamiaceae	1
<i>Myosotis arvensis</i>	Boraginaceae	18	<i>Convallaria majalis</i>	Asparagaceae	1
<i>Prunella vulgaris</i>	Lamiaceae	18	<i>Conyza canadensis</i>	Asteraceae	1
<i>Senecio jacobaea</i>	Asteraceae	17	<i>Crataegus spp.</i>	Rosaceae	1
<i>Geranium sylvaticum</i>	Geraniaceae	16	<i>Digitalis purpurea</i>	Plantaginaceae	1
<i>Rhinanthus minor</i>	Orobanchaceae	16	<i>Echium vulgare</i>	Boraginaceae	1
<i>Vicia sativa</i>	Fabaceae	16	<i>Equisetum sylvaticum</i>	Equisetaceae	1
<i>Galium mollugo</i>	Rubiaceae	15	<i>Galium odoratum</i>	Rubiaceae	1
<i>Rumex crispus</i>	Polygonaceae	15	<i>Geranium pusillum</i>	Geraniaceae	1
<i>Aegopodium podagraria</i>	Apiaceae	14	<i>Gnaphalium uliginosum</i>	Asteraceae	1
<i>Convolvulus arvensis</i>	Convolvulaceae	14	<i>Hypericum spp.</i>	Hypericaceae	1
<i>Lupinus polyphyllus</i>	Fabaceae	14	<i>Lysimachia europaea</i>	Primulaceae	1
<i>Veronica officinalis</i>	Plantaginaceae	14	<i>Lysimachia vulgaris</i>	Primulaceae	1
<i>Anchusa officinalis</i>	Boraginaceae	13	<i>Medicago lupulina</i>	Fabaceae	1
<i>Pilosella officinarum</i>	Asteraceae	13	<i>Oxalis acetosella</i>	Oxalidaceae	1
<i>Sagina procumbens</i>	Caryophyllaceae	13	<i>Persicaria maculosa</i>	Polygonaceae	1
<i>Trifolium dubium</i>	Fabaceae	13	<i>Pilosella aurantiaca</i>	Asteraceae	1
<i>Geum urbanum</i>	Rosoideae	12	<i>Polygala vulgaris</i>	Polygonaceae	1
<i>Solidago virgaurea</i>	Asteraceae	12	<i>Primula veris</i>	Primulaceae	1
<i>Lychnis flos-cuculi</i>	Caryophyllaceae	11	<i>Rosa mollis</i>	Rosaceae	1
<i>Melilotus albus</i>	Fabaceae	11	<i>Rosa rugosa</i>	Rosaceae	1
<i>Rumex longifolius</i>	Polygonaceae	11	<i>Rosa spp.</i>	Rosaceae	1
<i>Cirsium heterophyllum</i>	Asteraceae	10	<i>Sedum acre</i>	Crassulaceae	1
<i>Galeopsis tetrahit</i>	Lamiaceae	10	<i>Sisymbrium officinale</i>	Brassicaceae	1
<i>Galium elongatum</i>	Rubiaceae	10	<i>Stellaria holostea</i>	Caryophyllaceae	1
<i>Geranium dissectum</i>	Geraniaceae	10	<i>Stellaria nemorum</i>	Caryophyllaceae	1
<i>Geum rivale</i>	Rosoideae	10	<i>Trifolium striatum</i>	Fabaceae	1
<i>Melampyrum sylvaticum</i>	Orobanchaceae	10	<i>Vaccinium myrtillus</i>	Ericaceae	1
<i>Silene vulgaris</i>	Caryophyllaceae	10	<i>Vaccinium uliginosum</i>	Ericaceae	1
<i>Tripleurospermum inodorum</i>	Asteraceae	10	<i>Valeriana sambucifolia</i>	Caprifoliaceae	1
<i>Bistorta vivipara</i>	Polygonaceae	9	<i>Vicia spp.</i>	Fabaceae	1
<i>Lapsana communis</i>	Asteraceae	9	<i>Viola spp.</i>	Violaceae	1
<i>Senecio vulgaris</i>	Asteraceae	9			

Table S5. Overview over the bee species collected in May, June, and July 2021, from all sites. The count (n) is number of occurrences (i.e., presence at a site). The DCA1 value is their floral preference niche score. Blue color indicates preference towards zygomorphic flowers (e.g., legumes), and red color indicates preference towards actinomorphic flowers (e.g., asters). All kleptoparasites were omitted from the dataset. The most abundant social bee was *Bombus pascuorum* (n = 58). The solitary bee with highest occurrence was *Halictus tumulorum* (n = 25).

	Bee species	n	DCA1
Bombus-LT	<i>Bombus pascuorum</i>	58	0.565
	<i>Bombus hortorum</i>	30	0.786
	<i>Bombus sylvarum</i>	19	0.954
	<i>Bombus humilis</i>	14	0.91
	<i>Bombus ruderarius</i>	7	1.107
	<i>Bombus distinguendus</i>	3	0.544
	<i>Bombus subterraneus</i>	4	1.034
	SUM(n)	135	
Bombus-ST	Bee species	n	DCA1
	<i>Bombus lapidarius</i>	38	0.464
	<i>Bombus pratorum</i>	30	0.203
	<i>Bombus sensu strictu</i>	24	0.401
	<i>Bombus soroeensis</i>	19	0.817
	<i>Bombus hypnorum</i>	16	-0.026
	<i>Bombus wurflenii</i>	4	1.429
SUM(n)	131		
Solitary-LT	Bee species	n	DCA1
	<i>Eucera longicornis</i>	12	1.872
	<i>Megachile willughbiella</i>	11	1.085
	<i>Megachile circumcincta</i>	3	1.485
	<i>Megachile alpicola</i>	5	0.767
	<i>Anthidium punctatum</i>	2	1.52
	<i>Chelostoma florissomne</i>	3	-0.161
	<i>Hoplitis claviventris</i>	3	1.078
	<i>Osmia leaiana</i>	2	-0.085
	<i>Anthidium manicatum</i>	1	1.534
	<i>Ceratina cyanea</i>	1	0.74
	<i>Heriades truncorum</i>	1	-0.354
	<i>Megachile nigriventris</i>	1	1.882
	<i>Megachile versicolor</i>	1	0.494
<i>Osmia uncinata</i>	1	0.879	

	<i>Trachusa byssina</i>	1	1.986
	SUM(n)	48	
Solitary-ST	Bee species	n	DCA1
	<i>Colletes daviesanus</i>	14	0.257
	<i>Halictus tumulorum</i>	25	-0.354
	<i>Andrena subopaca</i>	18	-0.424
	<i>Andrena denticulata</i>	14	-0.257
	<i>Halictus rubicundus</i>	22	-0.304
	<i>Andrena haemorrhoa</i>	13	-0.796
	<i>Lasioglossum leucopus</i>	17	-0.27
	<i>Lasioglossum albipes</i>	13	-0.479
	<i>Lasioglossum calceatum</i>	6	-0.354
	<i>Lasioglossum villosulum</i>	7	-0.212
	<i>Hylaeus communis</i>	5	-0.014
	<i>Lasioglossum fratellum</i>	8	0.078
	<i>Hylaeus confusus</i>	13	0.257
	<i>Andrena chrysoceles</i>	6	-0.942
	<i>Andrena nigroaenea</i>	8	-0.525
	<i>Lasioglossum quadrinotatum</i>	8	-0.075
	<i>Dasypoda hirtipes</i>	6	-0.257
	<i>Lasioglossum leucozonium</i>	6	-0.14
	<i>Lasioglossum zonulum</i>	7	-0.102
	<i>Andrena wilkella</i>	8	1.709
	<i>Hylaeus brevicornis</i>	3	-0.419
	<i>Panurgus calcaratus</i>	5	-0.257
	<i>Lasioglossum rufitarse</i>	6	-0.289
	<i>Andrena semilaevis</i>	5	-0.953
	<i>Colletes similis</i>	4	-0.257
	<i>Melitta haemorrhoidalis</i>	3	-0.023
	<i>Andrena hattorfiana</i>	4	0.184
	<i>Andrena lathyri</i>	4	1.986
	<i>Hylaeus rinki</i>	4	-1.009
	<i>Macropis europaea</i>	3	0.471
	<i>Andrena bicolor</i>	2	-0.273
<i>Andrena cineraria</i>	3	-0.502	
<i>Colletes fodiens</i>	3	-0.257	
<i>Hylaeus dilatatus</i>	1	-0.245	
<i>Lasioglossum lativentre</i>	3	0.515	
<i>Andrena fucata</i>	2	-0.707	
<i>Andrena helvola</i>	3	-0.63	

<i>Andrena labiata</i>	1	-0.456
<i>Andrena nigriceps</i>	2	0.114
<i>Dufourea dentiventris</i>	2	0.157
<i>Hylaeus hyalinatus</i>	2	-0.614
<i>Andrena fulva</i>	1	-0.815
<i>Andrena fulvida</i>	1	-0.408
<i>Andrena humilis</i>	1	-0.257
<i>Andrena tarsata</i>	1	-0.376
<i>Colletes cunicularius</i>	1	-0.812
<i>Hylaeus pectoralis</i>	1	-0.049
<i>Lasioglossum fulvicorne</i>	1	-0.203
<i>Lasioglossum morio</i>	1	-0.281
<i>Lasioglossum punctatissimum</i>	1	0.184
<i>Lasioglossum sexstrigatum</i>	1	-0.218
SUM(n)	296	
TOTAL SUM(4n)	610	

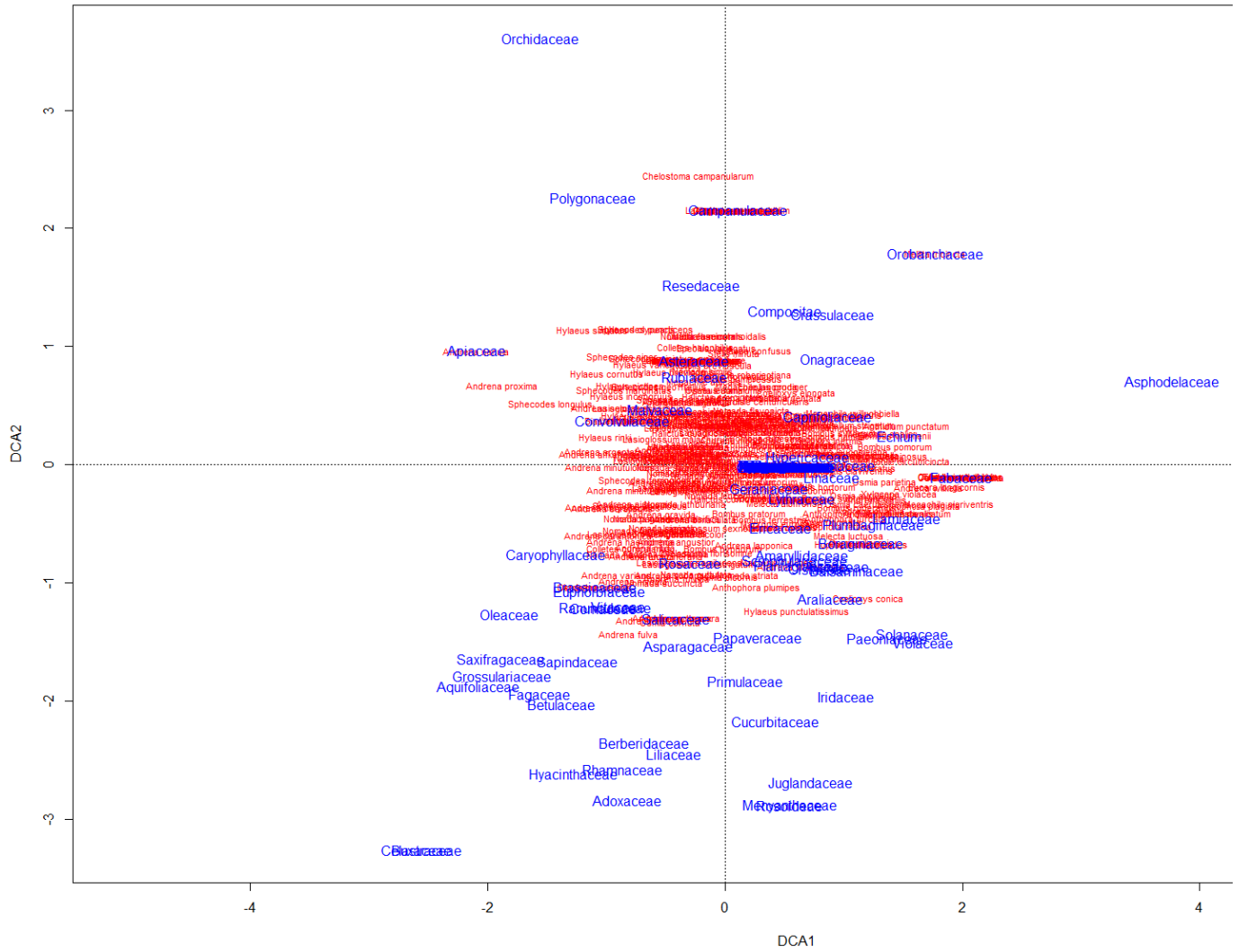


Figure S1. Ordination plot of the DCA analysis of floral preferences. The DCA1 score is the niche score for each bee species (in red). Bee species that exclusively pollinate plants of family Fabaceae (e.g., Fabaceae specialists) get the niche score 1.9 (DCA1 = 1.9). Pollinators of flowers with deeper corolla (Fabaceae and Lamiaceae) scores around 1.7. *Apis* was deleted from the dataset before the DCA, and some of the plant families in this plot are only pollinated by *Apis*.

C. CORRELATIONS BETWEEN ENVIRONMENTAL VARIABLES

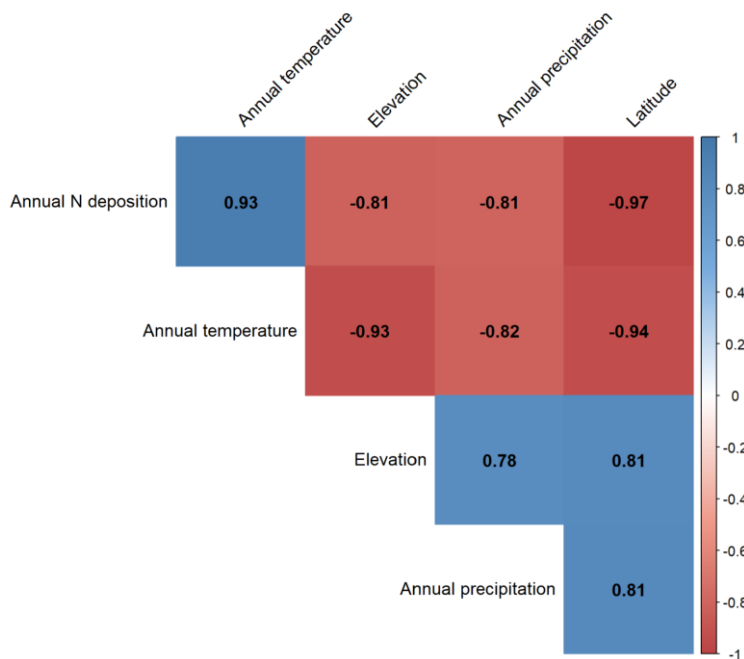


Figure S2. Pearsons' correlations of environmental variables from Norway and Denmark (70 sites). The variables correlate strongly with N deposition, thus the issue of multicollinearity. Therefore, temperature, precipitation, elevation, and latitude were all excluded from the final models from all sites (model 1 and 3).

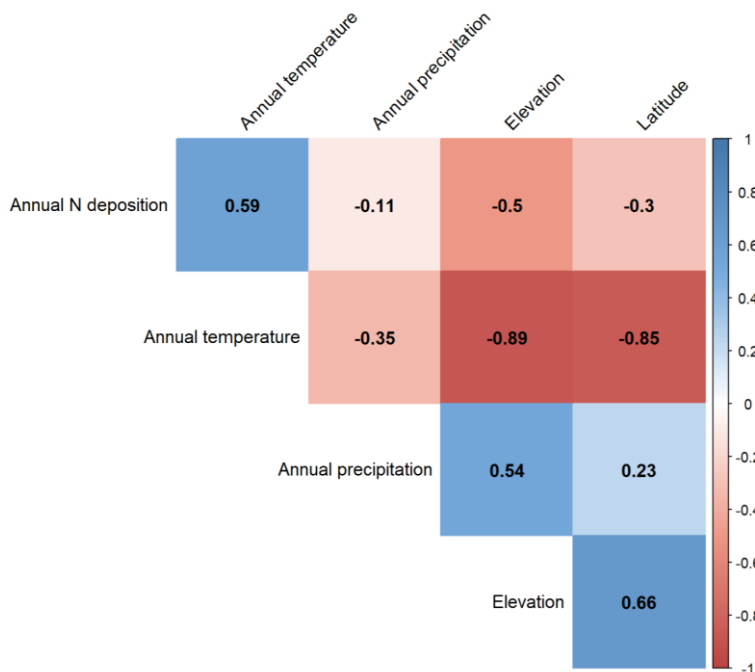


Figure S3. Pearsons' correlations between environmental variables in Norway (41 sites). There was very weak negative correlation between N deposition and precipitation, and precipitation was therefore included in model 2 and 4.

Table S6. Output of *anova* test between model 1A (with N deposition as fixed effect) and model 1B (with mean annual temperature as fixed effect). Model1B is the exact same model as Model1A, but with bio1 instead of annual N deposition. There was no significant difference between the two models since they explain the same variation (see Figure S3).

	<i>npar</i>	<i>AIC</i>	<i>BIC</i>	<i>logLik</i>	<i>deviance</i>	<i>Chisq</i>	<i>Df</i>	<i>Pr(>Chisq)</i>
Model1A Nitrogen	16	30848	31005	-15408	30816			
Model1B Temperature	16	30825	30982	-15396	30793	22.5	0	



Figure S4. Linear combinations of environmental variables were created using function *prcomp* in R. The two first loadings (PCA1 and PCA2) explained 91.1% of the total variation. There is an issue with multicollinearity: Total N deposition and temperature (bio1) explains the same variation (Pearson correlation > 0.9) and is almost perfectly negatively correlated with precipitation (bio12), latitude and elevation. In the biplot, each point is a site. Since temperature (bio12) and N deposition explain the same variation, their effect cannot be separated.

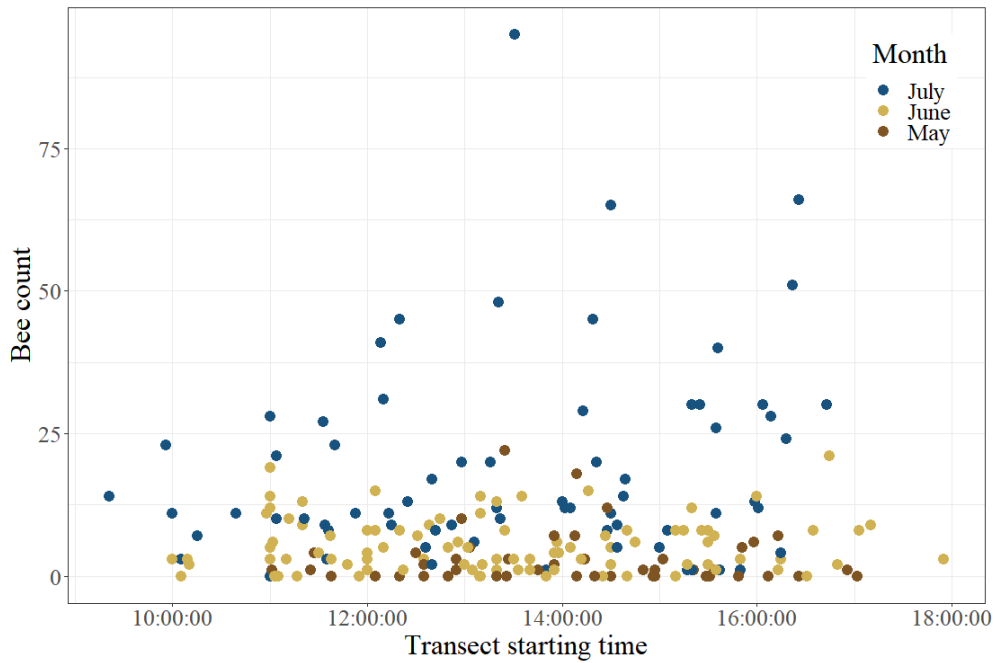


Figure S5. Number of individuals collected versus time of the day of capture. In July, there was higher activity between 12:00 and 17:00. This can possibly influence the response variable ‘bee species occurrence’ since bees were captured at different times during the day with variations in traffic intensity.

D. ODDS RATIOS

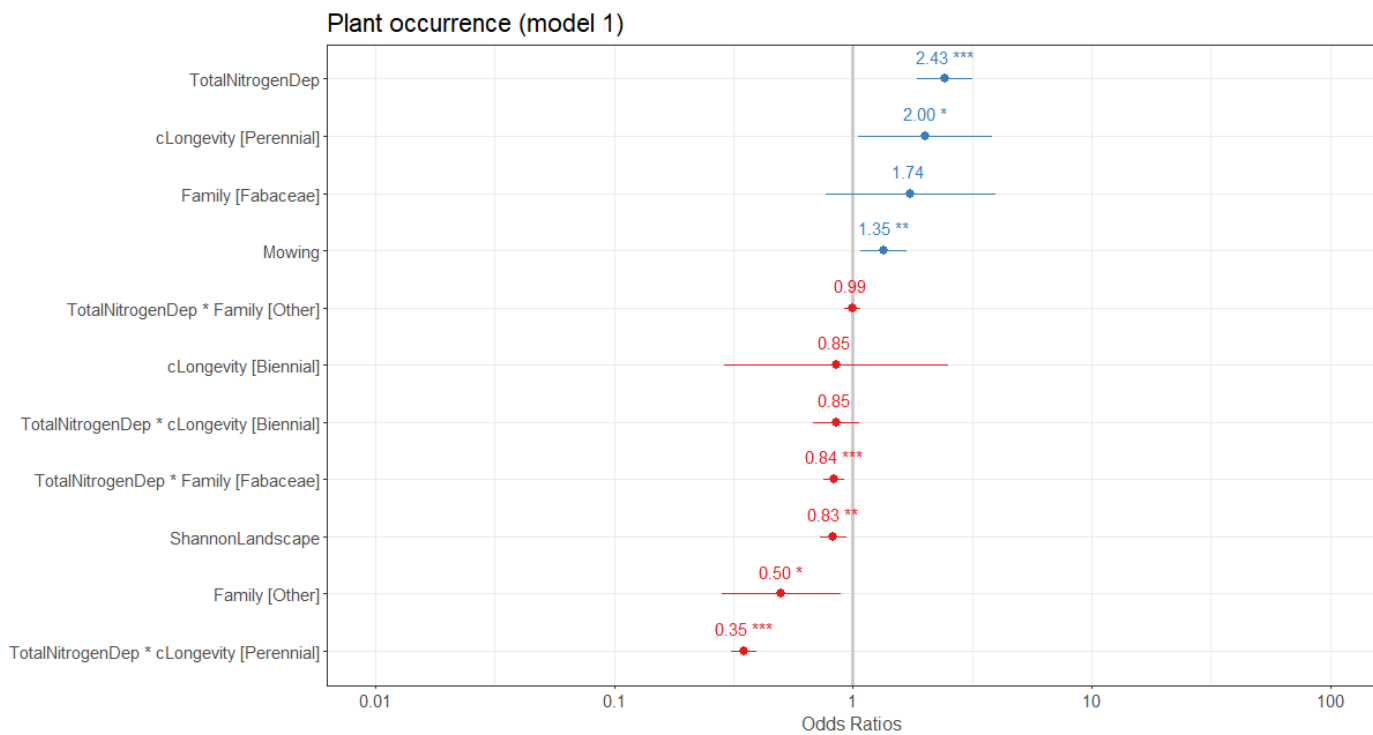


Figure S6. Odds Ratios from Model 1 (plant occurrence in Norway and Denmark).

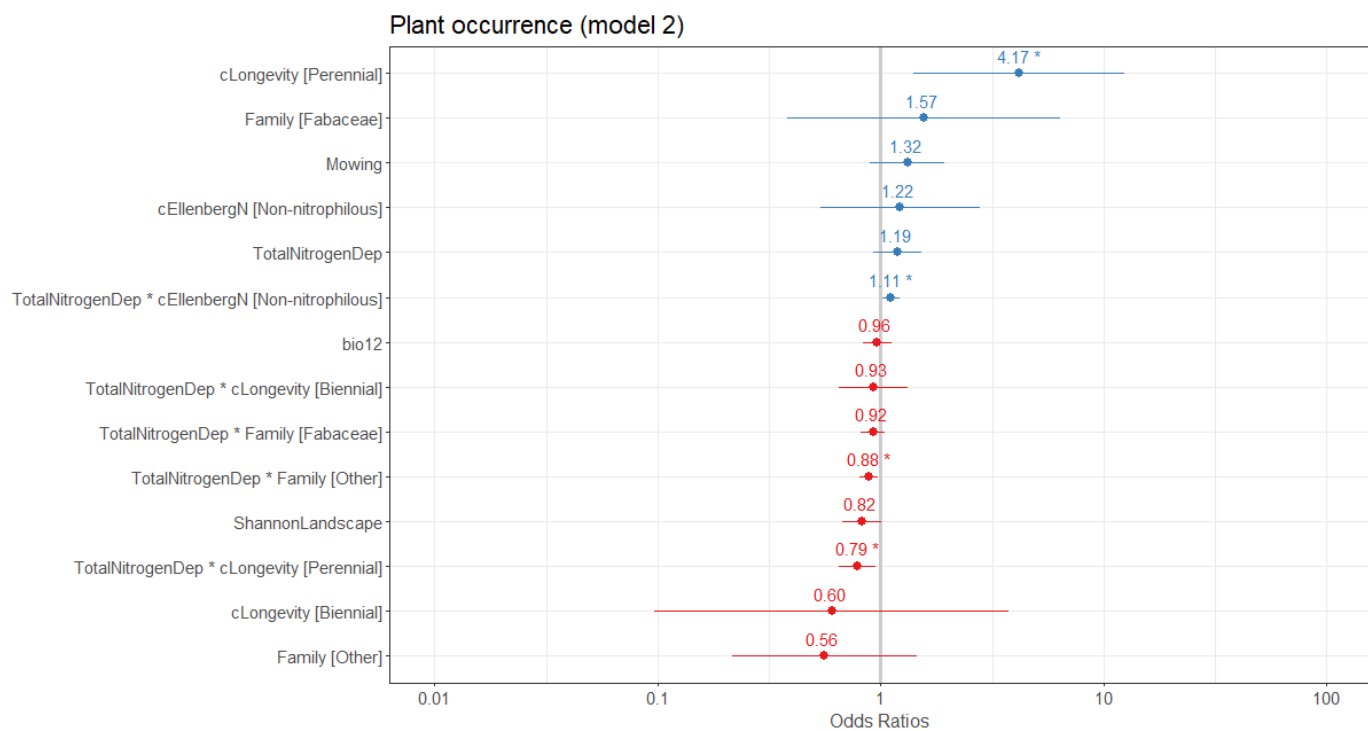


Figure S7. Odds Ratios from Model 2 (plant occurrence in Norway).

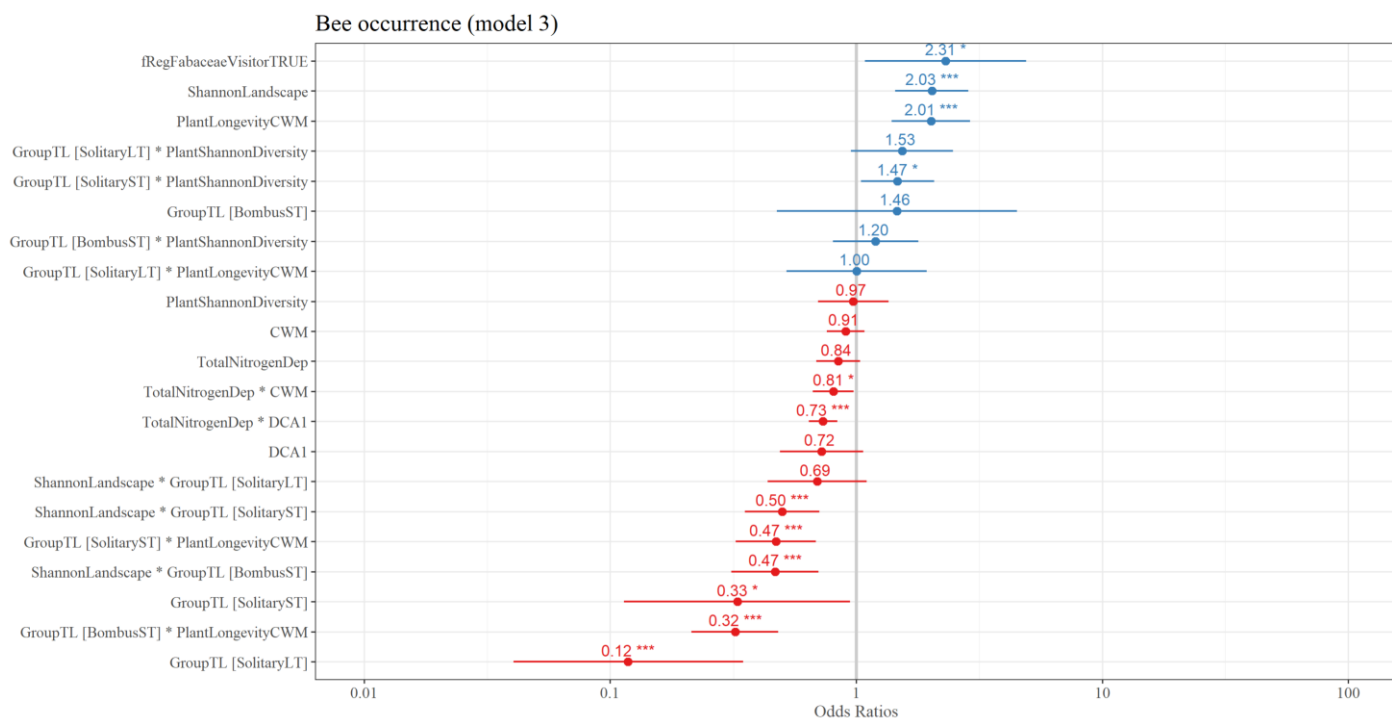


Figure S8. Odds Ratios from Model 3 (bee occurrence in Norway and Denmark).

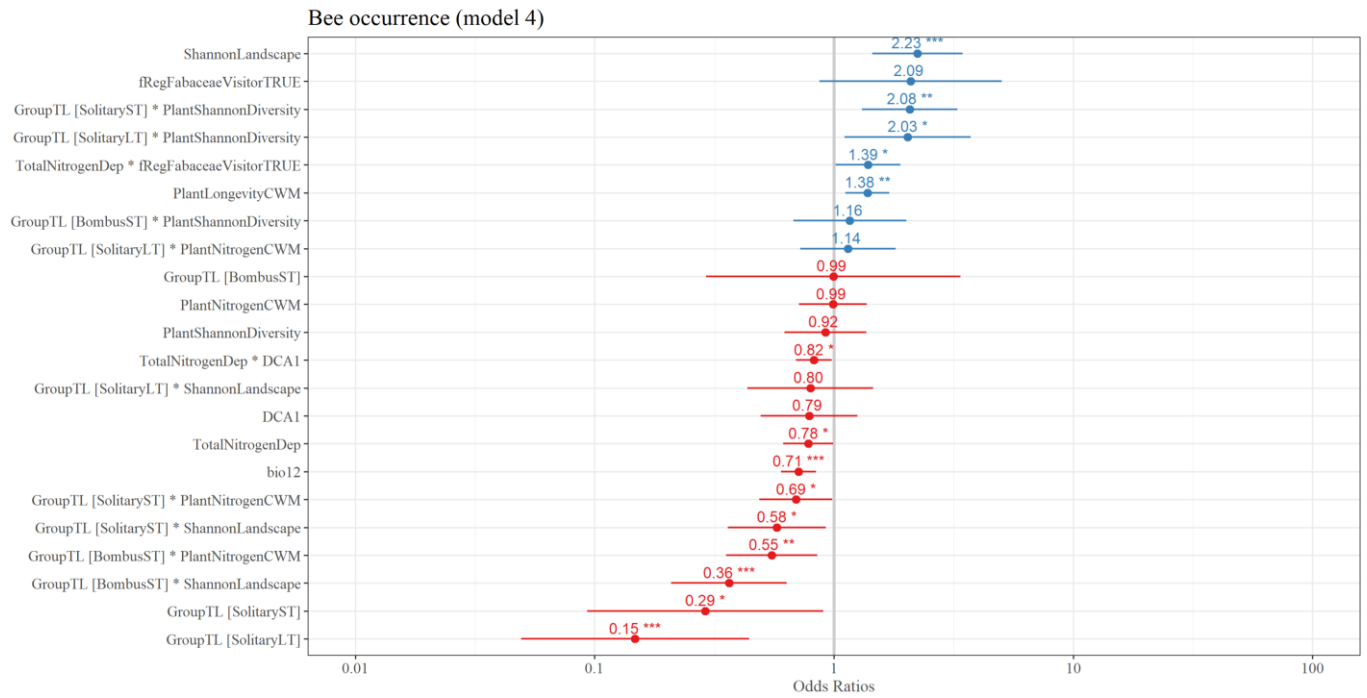


Figure S9. Odds Ratios from Model 4 (bee occurrence in Norway).

E. TABLE OVERVIEW OF MODELS (GLMMs)

Table S7. Results from generalized linear mixed effect model (GLMM) with plant occurrence as response variable (whole region; Model 1). Soil quality and Ellenberg N was removed during stepwise backward model selection procedure. For random effects, see Table 1.

Model 1. Probability of plant occurrence				
Predictors	Estimate	Std. error	z value	p
(Intercept)	-4.814056	0.369727	13.021	< 2e-16 ***
scale(TotalNitrogenDep)	0.888525	0.138274	6.426	1.31e-10 ***
Family[Fabaceae]	0.555665	0.406132	1.368	0.171253
Family[Other]	-0.690298	0.287952	2.397	0.016518 *
cLongevity [Biennial]	-0.161524	0.535490	0.302	0.762929
cLongevity [Perennial]	0.694650	0.325819	2.132	0.033006 *
scale(Mowing)	0.302660	0.113819	2.659	0.007834 **
scale(ShannonLandscape)	-0.188898	0.065102	2.902	0.003713 **
scale(TotalNitrogenDep):FamilyFabaceae	-0.179797	0.050952	3.529	0.000418 ***
scale(TotalNitrogenDep):FamilyOther	-0.005535	0.040547	0.137	0.891422

scale(TotalNitrogenDep):cLongevityBiennial	-0.163994	0.113683	1.443	0.149147
scale(TotalNitrogenDep):cLongevityPerennial	-1.048138	0.063390	16.535	< 2e-16 ***
Observations	135 800			
Marginal R2 / Conditional R2	0.067/0.677			

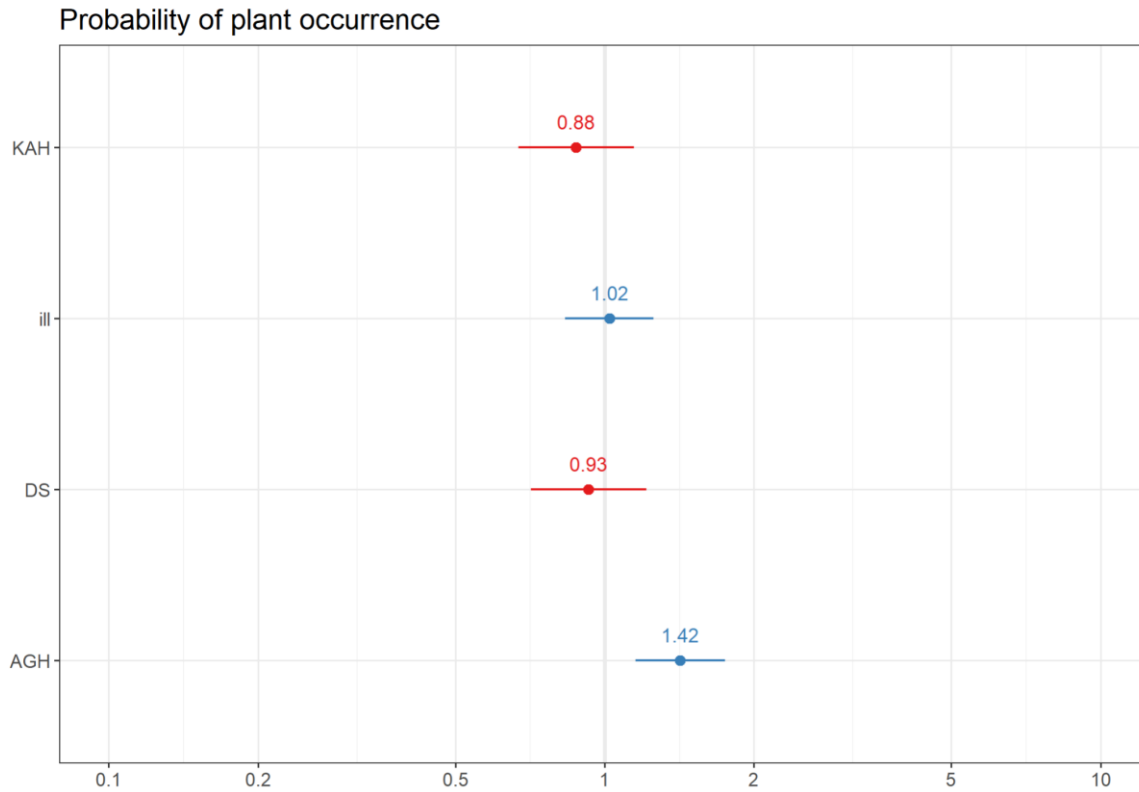


Figure S10. The probability of plant occurrence was dependent on collector (y-axis), and collector was therefore included as a random effect in models 1 and 2.

Table S8. Results from generalized linear mixed effect model (GLMM) with plant occurrence as response variable (Norway; Model 2). For random effects, see Table 1.

Model 2. Probability of plant occurrence				
Predictors	Estimate	Std. error	z value	p
(Intercept)	6.53017	0.64076	10.191	<2e-16 ***
scale(TotalNitrogenDep)	0.17750	0.12610	1.408	0.1593
Family[Fabaceae]	0.45094	0.71542	0.630	0.5285
Family[Other]	-0.57781	0.48897	1.182	0.2373
cLongevity [Biennial]	-0.50547	0.91911	0.550	0.5823
cLongevity [Perennial]	1.42779	0.55283	2.583	0.0098 **
cEllenbergN [Non-nitrophilous]	0.20076	0.41908	0.479	0.6319

scale(Mowing)	0.27643	0.19426	1.423	0.1547
scale(ShannonLandscape)	-0.19626	0.10346	1.897	0.0578 .
bio12	-0.03632	0.07614	0.477	0.6333
scale(TotalNitrogenDep):FamilyFabaceae	-0.07855	0.06159	1.275	0.2022
scale(TotalNitrogenDep):FamilyOther	-0.12365	0.04964	2.491	0.0127 *
scale(TotalNitrogenDep):cLongevityBiennial	-0.07228	0.17979	0.402	0.6877
scale(TotalNitrogenDep):cLongevityPerennial	-0.24092	0.09611	2.507	0.0122 *
scale(TotalNitrogenDep):cEllenbergNNon-nitrophilous	0.10807	0.04667	2.315	0.0206 *
Observations	135 800			
Marginal R2 / Conditional R2	0.087/0.476			

Table S9. Results from generalized linear mixed effect model (GLMM) with probability of bee occurrence as response variable (whole region; Model 3). PlantNitrogenCWM and PlantMowingCWM were removed during stepwise backward model selection procedure. For random effects, see Table 2.

Model 3. Probability of bee occurrence			
Predictors	Odds Ratios	CI	p
(Intercept)	0.11	0.04 - 0.33	< 0.001
ShannonLandscape	2.03	1.44 – 2.86	< 0.001
GroupTL [BombusST]	1.46	0.48 – 4.50	0.508
GroupTL [SolitaryLT]	0.12	0.04 – 0.35	< 0.001
GroupTL [SolitaryST]	0.33	0.11 – 0.94	0.038
PlantShannonDiversity	0.97	0.70 – 1.35	0.865
TotalNitrogenDep	0.84	0.69 – 1.06	0.100
DCA1	0.72	0.49 – 1.06	0.100
CWM	0.91	0.76 – 1.08	0.267
fRegFabaceaeVisitorTRUE	2.31	1.08 – 4.91	0.030
PlantLongevityCWM	2.01	1.39 – 2.91	< 0.001
ShannonLandscape * GroupTL[BombusST]	0.47	1.31 – 0.70	< 0.001
ShannonLandscape * GroupTL[SolitaryLT]	0.69	0.44 – 1.10	0.121
ShannonLandscape * GroupTL[SolitaryST]	0.50	0.35 – 0.71	< 0.001
PlantShannonDiversity * GroupTL[BombusST]	1.20	0.08 – 1.79	0.376
PlantShannonDiversity * GroupTL[SolitaryLT]	1.53	0.95 – 2.48	0.079
PlantShannonDiversity * GroupTL[SolitaryST]	1.47	1.04 – 2.07	0.027
TotalNitrogenDep * DCA1	0.73	0.64 – 0.84	< 0.001
TotalNitrogenDep * CWM	0.81	0.67 – 0.98	0.027
PlantLongevityCWM * GroupTL[BombusST]	0.32	0.21 – 0.48	< 0.001

PlantLongevityCWM * GroupTL[SolitaryLT]	1.00	0.52 – 1.94	0.991
PlantLongevityCWM * GroupTL[SolitaryST]	0.47	0.32 – 0.68	<0.001
Observations	5600		
Marginal R ² /Conditional R ²	0.213 / 0.418		

Table S10. Results from generalized linear mixed effect model (GLMM) with probability of bee occurrence as response variable (Norway; Model 4). PlantNitrogenCWM and PlantMowingCWM were removed during stepwise backward model selection procedure. For random effects, see Table 2.

Model 4. Probability of bee occurrence			
Predictors	Odds Ratios	CI	p
(Intercept)	0.24	0.08 – 0.74	0.013
TotalNitrogenDep	0.78	0.61 – 0.99	0.043
DCA1	0.79	0.49 – 1.25	0.311
fRegFabaceaeVisitorTRUE	2.09	0.87 – 5.02	0.099
PlantLongevityCWM	1.38	1.11 – 1.70	0.003
GroupTL [BombusST]	0.99	0.29 – 3.38	0.991
GroupTL [SolitaryLT]	0.15	0.05 – 0.44	<0.001
GroupTL [SolitaryST]	0.29	0.09 – 0.90	0.032
PlantNitrogenCWM	0.99	0.71 – 1.37	0.951
ShannonLandscape	2.23	1.44 – 3.44	<0.001
PlantShannonDiversity	0.92	0.62 – 1.37	0.681
bio12	0.71	0.60 – 0.84	<0.001
TotalNitrogenDep * DCA1	0.82	0.69 – 0.98	0.026
TotalNitrogenDep * RegFabaceaeVisitorTRUE	1.39	1.01 – 1.90	0.040
PlantNitrogenCWM * GroupTL [BombusST]	0.55	0.35 – 0.85	0.007
PlantNitrogenCWM * GroupTL [SolitaryLT]	1.14	0.72 – 1.81	0.572
PlantNitrogenCWM * GroupTL [SolitaryST]	0.69	0.49 – 0.98	0.040
ShannonLandscape * GroupTL [BombusST]	0.36	0.21 – 0.63	<0.001
ShannonLandscape * GroupTL [SolitaryLT]	0.80	0.43 – 1.46	0.459
ShannonLandscape * GroupTL [SolitaryST]	0.58	0.36 – 0.92	0.022
PlantShannonDiversity * GroupTL [BombusST]	1.16	0.68 – 2.00	0.584
PlantShannonDiversity * GroupTL [SolitaryLT]	2.03	1.11 – 3.73	0.022
PlantShannonDiversity * GroupTL [SolitaryST]	2.08	1.31 – 3.29	0.002
Observations	2337		
Marginal R ² /Conditional R ²	0.217 / 0.416		



Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway