NORWEGIAN BIODIVERSITY INFORMATION CENTRE

The state of knowledge about insect pollination in Norway

– THE IMPORTANCE OF THE COMPLEX INTERACTION BETWEEN PLANTS AND INSECTS

NORWEGIAN BIODIVERSITY INFORMATION CENTRE

The state of knowledge about insect pollination in Norway

– THE IMPORTANCE OF THE COMPLEX INTERACTION BETWEEN PLANTS AND INSECTS

Editor	Ørjan Totland, Norwegian University of Life Sciences
Co-authors	Knut Anders Hovstad, Bioforsk Frode Ødegaard, Norwegian institute for nature research Jens Åström, Norwegian institute for nature research
Publisher	Norwegian Biodiversity Information Centre
Layout	Mona Ødegården, Åshild Stolsmo Viken
Illustrations	Åshild Stolsmo Viken, Ivar Herfindal, NTNU (fig. 1)
English translation	Richard Binns, RB Translations
Recommended citation	Totland, Ø., Hovstad, K. A., Ødegaard, F., Åström, J. 2013. State of knowledge regarding insect pollination in Norway – the importance of the complex interaction between plants and insects. Norwegian Biodiversity Information Centre, Norway
Distributed by	Norwegian Biodiversity Information Centre, N-7491 Trondheim Tlf. + 47 73 59 21 45 E-mail: postmottak@artsdatabanken.no
Copies	150
Print	Skipnes Kommunikasjon ISBN (pdf): 978-82-92838-36-5
Cover	A bumblebee (*Bombus* sp.) on a field scabious (*Knautia arvensis*). Photo: Arnstein Staverløkk.

Svanemerket trykksak fra Skipnes Kommunikasjon Lisensnr. 241 731

Preface

The Norwegian Biodiversity Information Centre is a national bank of information about nature diversity. Its principal task is to disseminate up-to-date, easily available information on species and habitat types. Information about interactions in nature is an important part of this task, but the complexity of such interactions makes them hard to investigate and describe. Insects which visit plants to find pollen and nectar, and plants which are dependent upon insect visitations to seed, are part of such an interaction. It is easy to understand the importance of this interaction, but we know little about it.

A group of experts from the Norwegian University of Life Sciences, Bioforsk and the Norwegian Institute for Nature Research was commissioned by the Norwegian Biodiversity Information Centre to prepare this report, which describes the essential aspects of what we know about insect pollination in Norway today. The report identifies important gaps in our knowledge and priorities for acquiring information in the future. The Norwegian Biodiversity Information Centre hopes that the report will be a valuable instrument for management agencies, producers of knowledge and others who want to know more about this topic when strategies for acquiring information and managing the species are to be drawn up.

This is the first time such an overview of the state of knowledge on pollination ecology has been prepared in Norway. Good cooperation between groups of scientists in Norway and the Norwegian Biodiversity Information Centre has been essential for this work. The Norwegian Biodiversity Information Centre wishes to thank the authors of the report and the participating institutions.

Trondheim 16 May 2013

Ivar Myklebust
Director, Norwegian Biodiversity Information Centre

Contents

Summary

This report summarizes the state of knowledge in Norway concerning insect pollination. It explains what pollination is and the significance it has for plants and insects. It goes on to examine pollination as an ecosystem service and the consequences human pressures have on this complex interaction. The report identifies gaps in our knowledge about insect pollination in Norway and proposes measures to remedy them.

Little is known in Norway about the importance of pollination as an ecosystem process.

Insect pollination is a process whereby insects transport pollen grains from stamens to stigmas on either the same or different flowers, thus perhaps initiating seed production in the receptive flower. Insect pollination is an important interaction between plants and animals. The reproduction of many species of plants depends upon insect pollination, and many groups of insects get their nourishment from the pollen and nectar they find in flowers. Habitat loss, climate change, alien species and other changes in the environment threaten the species richness of both the pollinating insects and the plants from which they obtain their food. This may have far-reaching consequences for the integrity, stability and composition of the ecosystems and a global pollination crisis may threaten world food supplies. Little is known in Norway about the importance of pollination as an ecosystem process.

Management of ecosystems must be based on knowledge, and knowledge about pollination is important for the management of individual species and ecosystems. Lack of knowledge about the pollination ecology of individual species of insects and plants may therefore lead to detrimental management measures. In

international circles, there is an increasing understanding of the need to manage interactions (predation, parasitism and mutualism), rather than the actual individual species, and to do so it is important to have detailed knowledge about the actual interactions.

To improve the understanding of the importance of pollination ecology in Norwegian nature management circles, the committee behind this report believes that a fundamental platform for knowledge on pollination ecology must be formed. This will form the basis for generating more knowledge and collecting data on more specific problems in pollination ecology that are relevant for the management of ecosystems in Norway. In particular, the committee believes that the effort ahead should be directed at 1) mapping pollinators and which species of plants they visit, 2) the availability of pollinators for rare species of plants, 3) the importance of pollen limitation for seed production and population growth in rare species of plants, 4) Norwegian contributions to global knowledge on pollination, and 5) the education of competent pollination ecologists.

Interaction between plants and pollinators

A white-tailed bumblebee (Bombus s. str.) *feeding on nectar in a sunflower.*
Photo: Arnstein Staverløkk.

Studies of pollination have a long history that stretches all the way back to the Greek philosopher, Theophrastus (around 320 BC), who, among other things, described the complex pollination mechanism in the fig. In more recent times, the contributions by Charles Darwin on pollination in orchids (Darwin 1862) and reproduction in plants (Darwin 1876) perhaps formed the starting point for present-day scientific studies on pollination.

The interaction between flowering plants and pollinating insects is a mutualism where the plants have their reproductive gametes (pollen grains) dispersed by insects which visit their flowers, and the insects are "rewarded" for their visit, mainly in the form of nectar and pollen (see Willmer 2011 for the most up-to-date textbook on this topic). This interaction is called pollination, and its study pollination ecology or pollination biology. The seed production of probably nearly 80 % of wild plant species in Norway is favoured by insects visiting their flowers, and the insects are the only pollinators in northerly ecosystems. In tropical ecosystems, birds (e.g. hummingbirds), bats and a few other mammals (e.g. lemurs) are also important pollinators. A flower visitor which effectively transports pollen from stamens to stigmas is called a pollinator. All flower-visiting creatures are, however, not pollinators. Some, for example, are too small to come into contact with the reproductive organs of the flower (anthers with pollen and stigmas). Consequently, they do not transport pollen, but rather function like parasites on the mutualism between flowering plants and their real pollinators. Other insects, such as *Bombus wurflenii*, a bumblebee, bite holes in the nectary spur in flowers and steal the nectar from it without performing pollination.

The seed production of probably nearly 80 % of wild plant species in Norway is favoured by insects visiting their flowers.

Animals are not the only vector for pollen transport between stamens and stigmas. Many plants, like grass, pine and spruce, are wind pollinated and a few have their pollen grains transported in or on the surface of water (e.g. eelgrass *Zostera* and pondweed *Potamogeton*).

The first terrestrial plants to develop the ability to attract animals to transport pollen grains are thought to have evolved 250-200 million years ago when the first fossil gymnosperms show evidence of animal pollination (probably flies and beetles). Pollination is thus an interaction with a long evolutionary history, and there are many examples of co-evolutionary characteristics between flowering plants and pollinators which have made some plant-pollinator interactions very specialized (Darwin's orchid *Anagraecum sesquipedale* and the African hawk moth *Xanthophan morganii praedicta*, the fig and fig wasps, yucca and "yucca moths"). In addition to these obvious examples of exceptionally specialized plant-pollinator co-evolution, the majority of plant-pollinator interactions have passed through a more diffuse co-evolution. The enormous diversity in the colour, shape, size and scent of flowering seed plants has been forced by selection pressure based on the preferences of pollinators for different variants of flowers within the same species. This demonstrates what stupendous process the interaction between flowering plants and animals is, and the huge evolutionary potential that lies in this interaction.

Interactions where a plant species is pollinated by just one animal species, at the same time as it visits only this particular plant species are rare. In Norway, there are just a few examples of such highly specialized interactions. One is the globeflower (*Trollius europaeus*), which is pollinated by flies in the *Chiastocheta* genus (Diptera, Anthomyiidae), the females of which lay eggs in the ovaries of the flower. Another is the northern wolf's-bane (*Aconitum lycoctonum*), which is pollinated by a single bumblebee (*Bombus consobrinus*), and a third is the fly orchid (*Ophrys insectifera*), which is pollinated by a digger wasp in the *Argogorytes* genus (the fly orchid resembles a female wasp and attracts sexually motivated males). Such cases of extreme specialization are very rare. By far the majority of flowering plants are visited and pollinated by many more than one species of animal, and the vast majority of flower-visiting creatures visit more than one species of plant. Hence, by far the majority of plant-pollinator interactions are generalized and can be described in an interaction network which links together species of flowering plants and flower-visiting animals. Even though most plant-pollinator interactions involve many species, it is still possible to identify groups within such networks. For instance, there is a group of plants with long nectary spurs (many species in the orchid, legume (pea) and figwort families) which are for the most part dependent upon bumblebees with long tongues (e.g. the garden bumblebee (*Bombus hortorum*) and *Bombus consobrinus*) for successful pollination, and these bumblebees chiefly visit these plant species. Consequently, these species

The fly orchid (Ophrys insectifera)*, which is pollinated by digger wasps in the* Argogorytes *genus. The fly orchid resembles a female wasp attracting sexually motivated males. In addition, its scent mimics the sexual pheromone of the female wasp. Photo: Bernd Haynold (CC-BY-SA 3.0).*

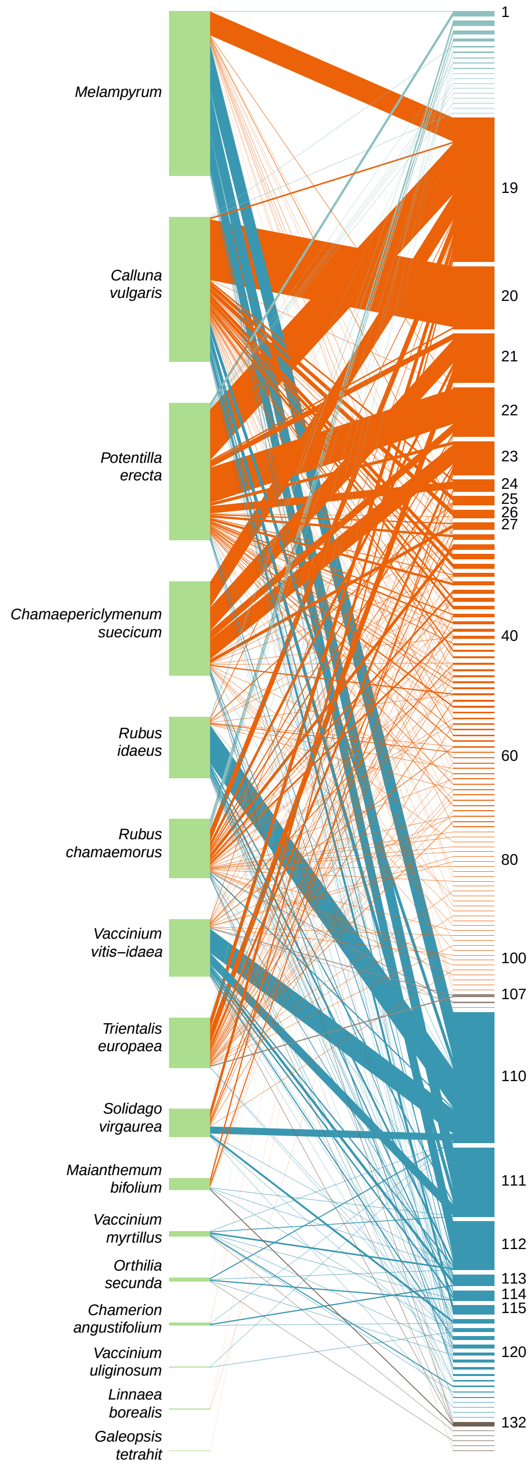


Figure 1: Quantitative pollination webs of pollinator visitation frequency in boreal forest in Norway. Plant species are shown as rectangles on the left and visitor species are shown on the right. The height of the rectangles reflects the relative abundance of flower visitors and plants. Links represent interactions between species, and the width of the lines indicates the relative quantitative visitation rate between an interacting pair of species. Green refers to plant species, and the other colours represent different orders of insects, light blue: Coleoptera, orange: Diptera, light grey: Hemiptera, blue: Hymenoptera, dark grey: Lepidoptera. Animal species codes are only given for pollinators with a visitation frequency of ≥ 15. For scientific names and common names of plant species, see Appendix I. For a list of all pollinator species codes, see Appendix II. The figure is based on Nielsen (2007).

Bombus consobrinus*, a bumblebee, uses its long tongue to reach the nectar deep down in the flowers of the northern wolf's-bane* (Aconitum lycoctonum). *Photo: Arnstein Staverløkk.*

of plants and bumblebees probably constitute a co-evolved group which is evolutionarily specialized to each other. In other cases, plants and pollinators are ecologically specialized, which means that the indigenous range of pollinators (or plants) is so limited that few pollinator species can potentially visit a flower of a plant species (or few plant species can be visited), as in arctic and high-alpine habitats.

Flowers are, thus, not pollinated by a random selection of pollinators. Some properties in flowers mean that some groups of pollinators visit and pollinate them more than others. Hence, flowers can be characterized as being mainly (but certainly not always) pollinated by bees, flies, butterflies and moths, etc., because of the properties of the flowers. Open, radially symmetrical, yellow flowers with comparatively large amounts of pollen and nectar readily available are, for example, mainly visited (and pollinated) by flies, because flies have properties that make them capable of visiting such flowers and obtaining a reward from them. On the other hand, zygomorphic (bi-symmetrical), violet flowers with a relatively long nectary tube are mainly visited (and pollinated) by bumblebees. Such categories of flowers are called pollination syndromes (Fægri and van der Pijl 1979), but this is a controversial term among some pollination ecologists (see Waser and Ollerton 2006). Table 1 presents the most important pollination syndromes found in Norway.

Table 1. Properties of flowers in various pollination syndromes present in Norway. Modified after Willmer (2011).

Syndrome	Pollinator	Blooming time	Most important flower colour	Presence of nectar guides	Flower scent	Flower shape	Location of nectar	Nectar quantity (Q) and concentration (C)	Pollen quantity	Pollen deposition on pollinator
Cantharophily	Beetles	Day or night	Cream, green, usually pale colour	No	Strong; fruity, or similar to decaying organic material	Radially symmetrical; flattened or bowl shaped	Exposed	Q: small C: medium	Medium-large	Face, legs, lower side of body
Myophily	Flies	Day	White, yellow, greenish	No	Usually mild, not sweet	Radially symmetrical; flattened, or flat inflorescence	Usually quite exposed	Q: small C: medium-high	Small-medium	Legs, face, thorax
Psychophily	Butterflies	Day	Pink, orange, yellow, lavender	In some cases	Moderately sweet	Often small flowers with a long nectar tube. Flowers often aggregated in compact inflorescences	Hidden	Q: small C: low	Small	Face, tongue, (legs)
Phalaenophily	Most moths	Dusk, night	Creamy, yellow, greenish	No	Quite strong, sweet	Usually radially symmetrical; moderate nectar tube	Hidden	Q: small-medium C: low	Small	Face, tongue
Sphingophily	Hawk moths	Dusk, night	White, creamy, pale green	No	Strong and sweet	Usually radially symmetrical; long nectar tube	Hidden	Q: medium C: low	Small	Face, tongue
Melittophily	Bees	Dawn, day	Pink, lilac, blue, white, yellow	Yes	Moderate, usually sweet	Bilateral or radially symmetrical; short to medium-long nectar tube	Exposed or hidden	Q: medium C: medium	Medium	Head, body

Importance for plants

Connection between pollination and seed production

As mentioned above, the seed production of most flowering plants is favoured by pollinators visiting their flowers. The actual seed production takes place in four phases: 1) pollination, when pollen is transferred from the anther to the stigma), 2) germination of a pollen tube (from the pollen grain), which contains two male gametes, down the style into the ovary, 3) fertilization of eggs and nuclei in ovules, and 4) development of embryos and then fertile seeds.

Pollination is thus the introductory process leading to the production of offspring in flowering plants. By far the majority of plants (exceptions are apomictic species which can initiate embryo development without fertilization by male gametes (e.g. dandelions and hawkweeds)) must be pollinated to produce seeds.

The reproductive system of plants is intricate (see Richards 1997 for a detailed survey). Individuals of about half of all plant species are totally dependent on receiving pollen from another individual for the pollen tube to be able to germinate; they are said to be self-incompatible. Other species are self-compatible, and the individuals can fertilize their egg with their own pollen (self-fertilization). Some of these potentially self-fertilizing species are, nevertheless, dependent on a pollinator visiting the flower to move the pollen grain from the anther to the stigma, either within the same flower (if it is hermaphroditic) or between different flowers on the same plant. However, in some self-compatible species, such self-pollination can take place without an insect visit (autogamy). These species are thus not entirely dependent upon a pollinator visiting their flowers to enable them to produce seeds. Most of them will, nevertheless, achieve higher seed production and viability if they are cross-pollinated. An important reason why cross-pollination (that is, transport of pollen between individuals) is advantageous is that self-pollination can lead to abortion of the seed development at an early stage. Thus, basically, cross-pollination is most favourable for the reproductive success of plants because inbreeding depression is avoided. Plants have two main mechanisms which help to reduce the chance of self-pollination in a flower. In flowers of some species, the distance between the anther and the stigma is so long that self-pollination within the same flower is unlikely (herkogamy). In other species, the timing of pollen dispersal and stigma maturing is so different that the chance of self-pollination is slight (dichogamy). There may be considerable variation in the degrees of herkogamy and dichogamy within a single species (Vos et al. 2012). An evolutionary breakdown of these mechanisms, which basically prevent self-pollination, linked with loss of self-incompatibility (that is, acquisition of self-compatibility), is all that is required for a population to no longer need pollinator visits to produce seeds. Many populations or species in areas with chronically poor access to pollinators (e.g. the

Arctic) have rid themselves of all obstacles for self-pollination and self-fertilization through evolution, and use this as a strategy to ensure their seed production (Eckert et al. 2010).

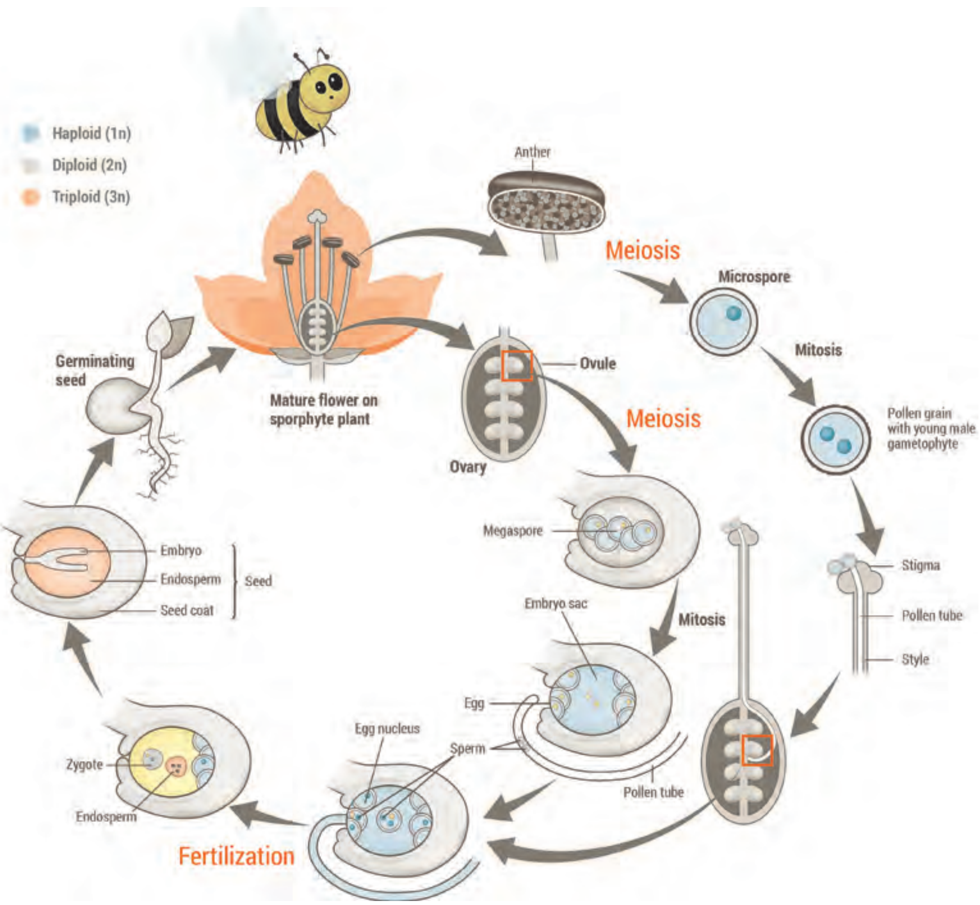


Figure 2: An example of a plant life cycle where flowers form on the dominant sporophyte plant. They consist of highly specialized male and female reproductive organs. Flowers produce spores that develop into gametophytes. Male gametophytes consist of just a few cells within a pollen grain and produce sperm. Female gametophytes produce eggs inside the ovaries of the flowers. Flowers also attract animal pollinators. If pollination and fertilization occur, a diploid zygote forms within an ovule in the ovary. The zygote develops into an embryo inside a seed which forms from the ovule and also contains food to nourish the embryo. The ovary surrounding the seed may develop into a fruit. Fruits attract animals that may disperse the seeds they contain. If a seed germinates, it may grow into a mature sporophyte plant and repeat the cycle.

Pollen and resource limitations on seed production

Many experimental studies show that the seed production of most plant species, particularly those that are self-incompatible, is limited by access to pollen (Knight et al. 2005). This means that if the plants in a population had had more pollen grains deposited on their stigmas they would have produced more seeds. Because pollen deposition on stigmas is mainly a result of visits by pollinators, the term pollinator limitation is often used about the seed production of plants. Visits to plants by pollinators influence the number of pollen grains deposited on stigmas, mainly through the number of visits and their efficiency (the number of species-specific pollen grains deposited per visit). The pollen grains placed on a stigma are usually a mixture of species-specific (their own) pollen, pollen from other individuals of the same species and pollen grains from other species, and this mixture of pollen is, among other things, influenced by the degree of specialization and the behaviour of the pollinators. The more pollen grains from other individuals of the same species, the better potential the plant has to have all its ovules fertilized and then develop them all into mature seeds. This means that the species composition of the pollinator community and the density of the various pollinator species, as well as the presence of other plant species, greatly influence the introductory (and decisive) phase of seed production in plants.

Obviously, not only pollination influences the seed production of plants. In most species, seed production is also limited by abiotic factors such as availability of light, nutrients in the soil, access to water and temperature conditions. Such limitations, together with pollen (or pollinators), influence the seed production (Burd 1994). For instance, a plant

The musk beetle (Aromia moschata) *develops in sallow wood, but the adults are keen flower visitors and prefer members of the carrot family, such as the moon carrot* (Seseli libanotis). *Photo: Frode Ødegaard.*

can receive more than enough of the correct pollen on its stigmas, but still not develop all its fertilized ovules to mature seeds, for example because access to water or nutrients is so limiting for the seed production that it cannot be increased even though the pollination is optimal. Production of seeds and fruits represents a major resource cost for a plant, which may reduce its survivability and future reproduction. Hence, even though a plant is optimally pollinated, it is not certain that it ”should” take the chance of producing a maximum amount of seed or fruit.

The recent decline in the species richness and density of pollinators has probably resulted in an increase in the pollen limitation on the seed production of many species of plants (Potts et al. 2010). Because the reduction in pollen availability has taken place so rapidly, it is unlikely that the reproduction strategies of the plants have had time to adapt by evolution to such a new situation with chronic pollen limitation on their seed production. If such a situation lasts, the population density of a number of plant species that depend upon pollinators can be reduced in the longer term, and some species will probably die out.

Geographical variation in pollination adaptations

The ability of a plant population to recruit individuals and, through the process, survive in the long run, depends upon many factors, only one of which is pollination, even though that is essential. Some plant populations are adapted to a chronically poor availability of pollinators. Geographical variation in both the physical environment and the availability of pollinators for plants may lead to the development of geographical variation in the reproductive system within a plant species (Busch and Delph 2012). In an environment where the plants experience unstable access to pollination services, selection may, over time, lead to the development of self-compatible reproductive systems and mechanisms for transferring pollen within the same flower or plant. Geographical variation in pollination systems is often important for evolving new species and subspecies through evolutionary processes over a long time, and the development of self-compatible populations or species has been proposed as an example of an evolutionary response to a lack of pollinators or other individuals with which to exchange pollen. In environments with stable access to pollinators, systems can also be expected to be seen where the likelihood of self-pollination increases in late-opening flowers on a plant because the chance of successful cross-pollination declines. Such adaptations take place over long evolutionary time and cannot be expected to be a solution for plants experiencing the ongoing reduction in pollinator availability.

The variation in pollination systems in the gradient from lowland to highland or northwards towards the Arctic is particularly relevant in Norway. Several groups of insects which are important pollinators in lowland areas, especially bumblebees and bees, are less numerous in alpine and arctic environments (where flies are frequently the most abundant pollinators) and this can result in the access of plants to efficient pollinators being lower in the mountains than in the lowlands. A short growing season and frequently shifting weather conditions in alpine and arctic ecosystems also help to make pollination by insects more unreliable. Pollen limitation is often cited as a reason why self-pollination and asexual reproduction are more widespread in alpine and arctic environments than in the lowlands and further south (Körner 2003). It is, nevertheless, not the case that plants in alpine and arctic environments are necessarily more pollen limiting than those of the same species further south or in the lowlands (Garcia-Camacho and Totland 2009). For plants in the mountains, it is often temperature and other factors that are more limiting for seed setting than the availability of pollen. To compensate for poor access to pollinators, many alpine plants bloom longer and are receptive to pollen over a longer period than lowland plants (Bingham and Orthner 1998, Lundemo and Totland 2007). The time a flower is receptive to pollen declines with rising temperature and the amount of pollination.

In addition to variations in pollination systems from the lowlands to the mountains, we can also expect variations between large populations and small, isolated populations and between the central parts and the margins of the range of a species. So far, little is known about these kinds of pattern, but several studies suggest that self-incompatible species may evolve self-compatible populations in areas where the species are invasive (Petanidou et al. 2012). The populations will, thus, become less dependent upon pollinators and can invade areas where their original pollinators do not occur.

Red clover (Trifolium pratense) *nectar is much sought-after, but it may be difficult for bumblebees that lack a very long tongue to reach it. This red clover is being visited by a shrill carder-bee* (Bombus sylvarum), *which has a short to medium long tongue.*
Photo: Arnstein Staverløkk.

Importance for insects

In contrast to plants, it is not in the immediate interest of insects that pollination is successful. A flower is, moreover, not just a source of pollen and nectar for insects. For some species, the flower is where the larvae live and develop in the corollas, for others it is the meeting place for predator and prey or parasite and host, and for yet others it is simply a hiding place. In some of these cases, the insect visits may also have a negative effect on the pollination success.

The reward received by the pollinating insects for their interaction with the plant is first and foremost nectar and/or pollen. In a longer perspective, successful pollination is obviously advantageous to the insects, too, since it influences the size of the plant population and its survival, which, in turn, increases the future availability of food for the insects. However, evolution does not look forward in such long-term perspectives and the behaviour of insects is controlled by what maximizes their reproduction to the next generation. This means that the actual pollination may entail a cost for the insects, for instance, because they must expend more energy to fly with a pollen load, or they have to negotiate difficult entrances to the nectar source, and so on.

As the importance of the pollination interaction varies significantly between groups of flower-visiting insects, the various groups are described separately below.

In contrast to plants, it is not in the immediate interest of insects that pollination is successful.

Bees, bumblebees, wasps and ants (Hymenoptera)

The pollen and nectar producing plants are essential for many species of insects and entire groups of insects are completely dependent on collecting such resources. For bees and bumblebees, which are the most important groups of pollinators in this part of the world, pollen is their only significant source of protein and is absolutely essential for the production of new individuals. Nectar is, moreover, their most important source of energy. Pollen is collected by the females (including workers in bumblebees and semi-domesticated bees) to rear their larvae, while the nectar is used as a source of energy for adults of both genders. Nearly all bees and bumblebees are directly dependent on plants since they derive their energy from pollen and nectar. Parasitic bees and cuckoo bumblebees (*Psithyrus* sp.) (25 % of all bees in Norway) also get their nectar from plants, but they cannot collect pollen. They parasitize other bees or bumblebees by eating their larvae and pollen stores.

A distinction is drawn between solitary bees, which do not form communities, but live as separate, independent individuals, and social bees, which form larger or smaller communities and in most cases behave in a way that best serves their community as a whole. Bumblebees (*Bombus* genus) and honey bees make up the social species in Norway. There are 34 species of bumblebees in Norway, 28 of which are social. The European honey bee (*Apis mellifera*) has occurred naturally in Western Europe, but it is uncertain whether there were natural occurrences in Norway before the species began to be domesticated in the 18th century. All honey bees in Norway therefore come from a semi-domesticated stock.

Bees and bumblebees form communities that are active throughout the summer. This is because the queen, who produces eggs, normally remains in the nest after the production of workers begins. She is therefore less prone to dangers in the surroundings (e.g. predation). How many offspring each queen has is decided by how large and how long-lived the community gets. For bumblebees, which are annual, climate and nutrient availability play decisive roles for the size of the community, but this varies between species. Bumblebee communities rarely number more than 500 individuals, whereas a honey bee community, which is perennial, often consists of 50-60 000 workers. By far the majority of social species of bees require continuous access to flowering plants from which they

It is not only the bees among the Aculeata that are keen flower visitors, but also digger wasps, cuckoo wasps and spider wasps. This is a digger wasp on rosebay willowherb (Chamerion angustifolium).
Photo: Åslaug Viken.

fetch nectar and pollen to enable the colony to survive. The need for energy also rises with the size of the bee community. This means that the quality of their habitat is determined by the size of the area and the species richness of the plant community through the season.

Solitary bees lack the worker caste, so the females collect pollen and nectar. The female constructs a concealed brooding chamber in suitable substrate, and the larvae develop there. The number of offspring a solitary bee can feed is not particularly large (often between 5 and 20 larvae), but since the females frequently gather in colonies, local populations may be quite large. A distinction is generally drawn between species which nest in the ground and those which nest in other substrates. The species which make holes in the ground generally use sun-facing, sandy slopes that provide extra warmth for the development of the larvae. The most important groups of ground-living bees are sweat bees (Halictidae), mining bees (*Andrena*) and plasterer bees (*Colletes*). Bees which make use of other substrates are the Megachilidae and *Hylaeus* sp. They generally nest in dead branches that face the sun and have old insect exits, beneath stones or in old plant stalks. Many also exploit constructions built by people, such as sun-heated timber walls, roofs, or crevices and holes in walls. A total of 205 species of bees (including social species) have been recognized in Norway.

The solitary bees are often more specialized to specific species of flowering plants than the social bees and synchronize their flight period with the blooming of the plants. Many

Of the insects in the Lepidoptera order, it is generally butterflies we think of as flower visitors, but many species in several other families also regularly visit flowers, including this mother-of-pearl moth (Pleuroptya ruralis). *Photo: Åslaug Viken.*

species are therefore very vulnerable to changes in the landscape because they rarely fly more than a few hundred metres from their nesting site to collect pollen and nectar. Because the species are fastidious as regards both their nesting site and their source of pollen, the total resource requirement will be limiting for the occurrences. Solitary bees often live for a shorter period as adults than a bumblebee community, which survives the entire growing season and is therefore less vulnerable to lack of continuity in plant diversity through the season, but more dependent on specific resources and when these are available.

The Hymenoptera is the largest order of insects in Norway, and includes subgroups which can function as pollinators, particularly the Aculeata which, in addition to the bees, includes ants, stinging wasps, digger wasps, spider wasps, mason wasps, *Tiphia* wasps and cuckoo wasps. Many species in these groups regularly occur in flowers. These groups are primarily predators or parasites, and chiefly visit flowers to obtain food (nectar) rapidly.

Among the ants, it is common for wood ants (*Formica* sp.), *Lasius* sp. and *Myrmica* sp. to be found in large numbers in various species of flowers. The queens of stinging wasps (Vespinae) usually fetch food from sallow flowers, for example, in spring before they begin to build their nests. In late summer, male stinging wasps are the typical flower visitors, plants of the parsley family and thistles being particularly popular. As regards wasps, many species of sawflies (Symphyta) and various groups of parasitic wasps (Parasitica) occur more or less regularly in flowers. Plants of the parsley family are particularly often visited by pollen-feeding sawflies. Parasitic wasps are perhaps most frequently found in large corollas of, for instance, plants of the daisy family where they are seeking host insects which inhabit the corollas (e.g. Pteromalidae and Torymidae), but a few species of gall wasps (Cynipoidea), which form galls, are also found in corollas. There are, however, large gaps in our knowledge about the importance of flowers for other Hymenoptera than bees and bumblebees, and to what extent some may be important pollinators.

Butterflies and moths (Lepidoptera)

Unlike bees, butterflies and moths have their primary source of protein in the vegetative parts of the plants, which their larvae eat. Pollen therefore plays a more minor role, but nectar as a source of energy may be very important for adults of many different species of butterflies and moths. It is assumed that they are, in many cases, poorer pollinators than bees since they are less directly linked to the plants and do not collect pollen. The development of a long proboscis may, for example, result in less contact with the reproductive parts of plants. Some Lepidoptera have mandibles which are reduced in size, and they do not feed as adults. There are, nevertheless, many groups of butterflies and moths, mostly the former, which are regular pollinators, and some are also extremely specialized (e.g. the pine hawk-moth on the lesser butterfly-orchid). The few species of plants in Norway that are pollinated at dusk or during the night are probably all pollinated by hawk moths.

True flies (Diptera)

Many groups of true flies feed on nectar or pollen from flowers and a few species, like the large bee fly *Bombylius major* (Bombyliidae) with its long tongue, are entirely dependent upon flowers to survive. The most important pollinators among the flies belong, however, to the species-rich groups with many common species like house flies (Muscidae), Anthomyiidae, tachina flies (Tachinidae), Empididae and hoverflies (Syrphidae). Probably more than 1000 species in these groups can pollinate.

As in the case of the Lepidoptera, many families of flies are phytophagous (plant eating) and will occasionally be found in the flowers, more or less fortuitously, and depending upon how they exploit the plants. Important groups here are gall midges (Cecidomyiidae), leaf-miner flies (Agromyzidae) and tephritid fruit flies (Tephritidae). Particularly the last-mentioned group is common on certain flowers because the species are often quite host specific and develop in the corollas. Parasitic flies, like the thick-headed flies (Conopidae) and the bee flies (Bombyliidae), also often sit inside flowers, either to eat or to wait for their host bee.

In general, flies are regarded as rather inefficient pollinators because most lack the dense hairy coat that makes bumblebees and bees good pollen transporters. However, there are

Rose chafer (Cetonia aurata) *beetles on moon carrot* (Seseli libanotis). *A crab spider is also sitting on a flower, waiting for a suitable prey.*
Photo: Frode Ødegaard.

exceptions, such as a few genera of hoverflies and bee flies, which are exceedingly hairy. The behaviour of most flies when they visit flowers is, however, less “targeted” than in the case of bumblebees and bees. In some habitats, such as alpine areas, flies may be important pollinators due to their abundance and the lack of other pollinators.

Beetles (Coleoptera)

Some groups of beetles can be characterized as important pollinators because they are covered with dense hairs and mainly feed on pollen (and nectar) and thus regularly visit flowers with a specific aim in mind. These groups include the large Lepturinae, a subfamily of the longhorn beetles, and flower chafers (Cetoniinae). A number of groups of smaller beetles regularly visit flowers and often occur in large numbers. These are the rove beetles in the *Eusphalerum* genus, *Anaspis* sp., the Mordellidae, Phalacridae, false blister beetles (Oedemeridae), *Meligethes* sp., soft-wing flower beetles (Dasytidae) and Malachiinae. They particularly visit flowers with a simple flower structure with small, often white, flowers arranged in clusters. Many of these beetles probably lack special properties which make them good pollinators, but they can, nevertheless, probably contribute as pollinators precisely because they may occur in extremely large numbers.

There are, furthermore, a large number of species among the phytophagous beetles (i.e. Phytophaga, leaf beetles, bean weevils, longhorn beetles and true weevils) which can be compared with the butterflies and moths in that it is mostly the vegetative parts that are exploited as food by the larvae, although the adults can sometimes be observed in flowers.

Lepturinae beetles, a subfamily of longhorn beetles, regularly visit flowers. This species, Anastrangalia reyi*, sitting on a tansy* (Tanacetum vulgare)*, generally develops in pine wood and is mostly found on flowers in woodland edges and on mires where there is a considerable amount of dead wood. Photo: Åslaug Viken.*

A six-spot burnet moth (Zygaena filipendulae) *on a field scabious* (Knautia arvensis). *Burnet moths (Zygaenidae) are obligatory flower visitors and locally occur in large numbers in late summer.*
Photo: Frode Ødegaard.

Some of these may be called regular flower visitors, including the true weevils in the *Anthonomus* and *Larinus* genera, which develop in flower buds, true weevils in the *Miarus* genus, which often eat the petals of various plants, the pine flower weevils (Nemonychidae) in pine flowers and the bean weevils which develop in the seeds of legumes.

Finally, ground beetles in the *Amara, Harpalus* and *Lebia* genera can also be found in flowers; the first two eat seeds, and the third is a parasite on leaf beetle pupae. Jewel beetles in the *Anthaxia* genus regularly visit yellow flowers, while carpet beetles in the *Anthrenus* genus, a few species in the sap beetle genus *Epuraea*, the silken fungus beetles in the *Cryptophagus* and *Antherophagus* genera and click beetles (Elateridae) have a few representatives which may be locally common in flowers. It is also not unusual to find active predators like soldier beetles (Cantharidae) in flowers.

Some 100 species of beetles in Norway regularly occur in flowers, but perhaps twice that number can be found there occasionally. Most beetles which visit flowers are probably quite inefficient pollinators, often because they are so small that they do not make contact with the reproductive organs of the flower and because they mostly visit very few flowers in the course of their life.

Other groups of arthropods

Several other groups of insects and other arthropods may have representatives which are more or less regularly found in flowers. One important group is thrips (Thysanoptera), which has several obligatory flower visitors. However, it is uncertain whether they are particularly efficient pollinators. Furthermore, a number of true bugs (Hemiptera), including Heteroptera, cicadas (Auchenorrhyncha) and aphids (Aphidae), often visit flowers. These species mainly suck sap and therefore largely exploit the green parts of the plant. A special case is stylops (*Stylops melittae* of the twisted-wing parasites, Strepsiptera) whose larvae are strewn in flowers where they wait to be picked up by bees which they parasitize. Other insects which may visit flowers are earwigs, booklice and net-winged insects. A few species of crab spiders can sit in flowers and camouflage themselves while hunting other flower visitors. Mites and ticks, springtails, woodlice, snails and slugs, and annelids may all occur in flowers. Some use the flowers as hiding places, whereas others find food there. These groups will, however, always be insignificant in the context of pollination.

An interaction with great variation

The strength in the interaction between plants and pollinators is greatly influenced by the density of the species. On the whole, pollinators have more variable populations than the plants they pollinate. Considerable differences in the size of populations from one year to another are not unusual and there are several potential reasons for this. Insects are generally characterized by a short generation time and high potential reproductive ability, making them capable of rapidly responding to favourable environmental conditions. In addition, density-dependent pressure factors (e.g. competition, facilitation and mutualism) and displacements as a function of time in the occurrence of plant and pollinator species may influence the interaction. All pollinating insects in our latitudes are annual, and can therefore not overwinter in seasons with poor conditions, in contrast to plants with a seed bank in the soil which is ready to germinate when conditions are favourable. Poor years may therefore reduce the density of pollinators, despite their relatively high reproductive ability, and these factors result in the population density of pollinating insects varying much more over time than the density of the plant species they pollinate. A large diversity of pollinators may therefore be especially important, because it may increase what is referred to as the "response diversity", which results in a greater likelihood that at least one species can tackle the shifting weather conditions.

The occurrence and distribution of plants which depend upon pollination and of their pollinators are determined by a combination of several factors and will thus vary considerably over time and geographically, precisely because the pressure factors also vary in strength in time and space. A distinction is often drawn between the fundamental or potential niche of an organism and its realized niche. The fundamental niche describes which environmental prerequisites the organism needs to survive, and spans larger geographical areas than the realized niche, which is also limited by interactions with other organisms, and chance. This means that both plants and their pollinators should potentially be able to live in more areas than they do today, but their distribution is partly limited by the habitat demands of their respective partners. For instance, it is possible

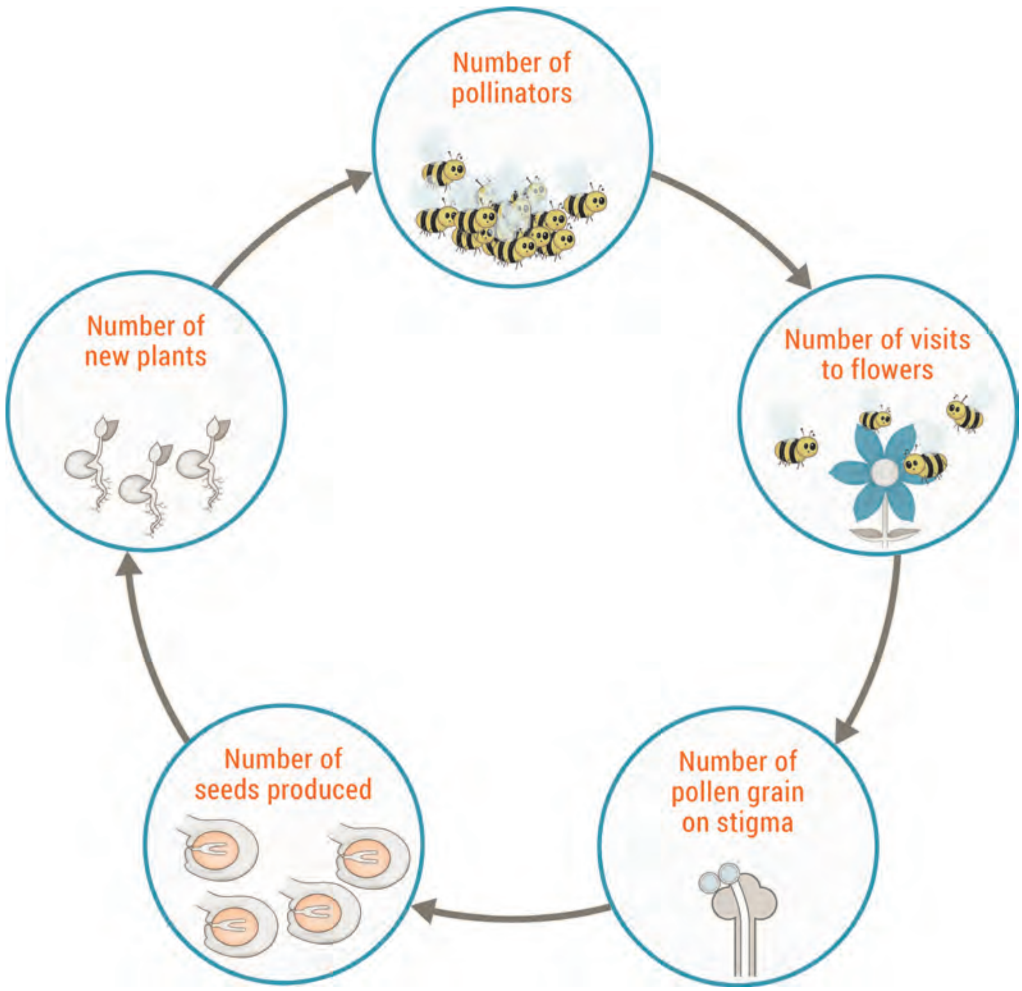


Figure 3: The connections between the numbers of pollinator that are available to a population and its recruitment potential. The correlations are positive, that is, an increase in one factor leads to an increase in the next factor in the chain.

that some flowering plants would manage to grow in regions with a colder, more unstable climate than they do today, but their distribution is limited by the lack of ability of their pollinating insects to survive such conditions. For example, the distributions of the specialized and mutually dependent pair of species, northern wolf's-bane and the bumblebee, *Bombus consobrinus*, largely overlap, maybe suggesting that their availability limits each one's distribution.

In theory, there is a cause and effect line from pollinator visitation to the density fluctuations of a plant population over time, or variation in density between populations: the more efficient pollinators there are, the more correct pollen grains are deposited on stigmas, the more seeds are produced, the more seedlings germinate, and the more individuals are recruited to the population. However, whole of this cause and effect line has been studied for fewer than 20 species globally, and some of these studies suggest that the line can be broken by limitations arising from many other factors, such as access to resources, competition from other plant species, herbivory or unfavourable climatic conditions. Obviously, and perhaps of greater relevance, the cause and effect line may be negative: the fewer insects, the less pollen on stigmas, the less seed, etc.

The effect of spatial or temporal fluctuations in the density of pollinator species is probably greater for the reproduction of specialist plant species than for generalists. For instance, it has been suggested that a reduction in Great Britain in the abundance of bumblebee species with long tongues and of their density has resulted in a decline in the density of populations of plant species with long nectar tubes (Carvell et al. 2006). Generalist plants, species which can be pollinated by many different species and groups of pollinators, are probably less sensitive to a decline in the density of a single pollinator species than more specialized species. Thus, generalization may function as a buffer for fluctuations in population density in pollinators in both time and space. Even though the populations of some species of insects may vary considerably from year to year, other species will often be able to take over if one pollinator should fall out. The pollinating success of such generalist plants may therefore be quite stable over time and between populations, even though the species composition of their pollinators may vary considerably. However, pressure factors which act equally on large groups of pollinators may have an obvious effect on pollination. For instance, many pollinators are sun loving, and many solitary bees are highly thermophilous and normally have their main distribution in more southerly latitudes. Poor summer weather over short periods, and large-scale, long-term climate change (especially higher precipitation) will therefore have a considerable effect on the pollinating success of plants which primarily depend upon bee pollination. This will also be the case with other large-scale impacts which either change the availability of habitats for the insects (e.g. lack of nesting sites) or have other kinds of negative effects on entire groups of insects. For many self-compatible species of plants, it has also been shown that autogamous self-pollination may function as an insurance mechanism in periods or habitats where few pollinators are available.

Because most plant-pollinator interactions are generalized, and population densities of plants, and especially insects, vary greatly, pollinating interactions are extremely variable in time and space. This means, for example, that the pollinator fauna of a plant species may change considerably across short distances simply because the species composition in a pollinator community changes. Likewise, the plant species a specific pollinator species visits will also vary considerably over both short and long distances, because the species composition of its plant community varies. A plant population may also experience dramatic changes in the species composition of its pollinator fauna over time, from one season to the next. Such temporal changes may lead to fluctuations in the reproductive ability of plant populations.

The state of knowledge about pollination in Norway

Surveying is important to enhance our knowledge of pollinating insects. Bumblebees are an extremely important group of insects in Norway, and most species can be identified in the field. Photo: Arnstein Staverløkk.

Recent decades have seen less activity in pollination ecology in Norway than other Scandinavian countries. Most emphasis here has been placed on studying how natural selection shapes the properties of flowers (e.g. Totland 2001, Sletvold et al. 2012a), pollination ecology in alpine plants (e.g. Totland 1993), effects of pollen limitation on reproduction (e.g. Hegland and Totland 2007), pollination interaction on the community level (e.g. Lazaro et al. 2010), effects of introduced species on pollination in native species (Bjerknes et al. 2007) and effects of climate warming on pollination interactions (Hegland et al. 2009).

Viewed from an entomological perspective, studies of pollinators in Norway are now limited in extent. However, several major projects have been taking place recently to map the distribution of insects, and pollinating species like bumblebees and solitary bees have figured centrally here, for instance as parts of the National Programme for Mapping Biological Diversity through the ARKO Project (Ødegaard et al. 2010) and the Norwegian Biodiversity Information Centre's efforts to enhance knowledge of species diversity through its Species Project and INVENT-ART Project. The primary aims of these projects have been to record observations of poorly known species and obtain rough overviews of the distribution of species.

Recent decades have seen less activity in pollination ecology in Norway than other Scandinavian countries.

In connection with the preparation of a Nature Index for Norway, annual observations of the distribution of bumblebees and butterflies and moths began in parts of Norway in 2009, and six counties are now being covered. The principal aim of this project is to follow trends in the populations of common and moderately common species. The project makes use of voluntary observers who note the occurrences in random, but geographically representative, marked transects which give a correct picture of the distribution of habitat types in lowland Norway.

Bioforsk has carried out some studies of pollination in a farming context, but otherwise there have been no national studies of the effects of habitat loss and fragmentation in the agricultural landscape like those performed in Sweden, England, the Netherlands and Germany (Steffan-Dewenter et al. 2002, Kohler et al. 2007, Öckinger and Smith 2007), for instance.

A simple analysis of scientific publications dealing with pollination shows significant differences between Norway and neighbouring countries. The Reference database, ISI Web of Science, was used to locate scientific articles with the keywords *"pollination"* or *"pollinator"* (or their plural forms). This database contains articles published from 1975 onwards, and covers a large number of reputable scientific journals. In addition to those keywords, statistics were obtained on the number of publications listed in the database under "*ecology*". This gives an impression of the relationship between articles dealing with pollination and with ecology more generally.

From 1975 to 2012 inclusive, 178 scientific articles mentioning pollination were published in Norway. By comparison, in the same period, 630 articles in which pollination was a keyword were published in Sweden and nearly 1400 in Great Britain. Here, it should be stressed that statistics of this kind do not necessarily give an entirely correct picture of the research activity. Various countries did not put equal emphasis on publishing in international scientific journals if we go back some decades. In Norway, the great majority of scientific articles on pollination have been published from 1995 onwards. Changes in the organization and funding of research have helped to raise the number of scientific publications in most disciplines since the 1980s. The figures imply that the increase in the number of publications came somewhat later for pollination compared with ecology more generally. In Norway, scientific articles on pollination comprise less than 4 % of the total number of articles published on ecology in the past three years (2010-2012). This is a lower proportion than in the majority of countries with which it is natural to compare.

Professor Knut Fægri, through his collaboration with Leendert van der Pijl, made what was then the most important contribution to our knowledge of pollination in Norway by way of their internationally classic textbook on pollination biology: "The principles of pollination ecology" (Fægri and van der Pijl 1979). Its first edition came in 1966 and the 3rd and last in 1979. This work is a fundamental and detailed introduction to pollination and plant reproduction, and is perhaps the most complete compilation of theories about pollination syndromes. Even though the book does not specifically deal with conditions surrounding pollination ecology in Norway, Professor Fægri was a pioneer in this subject. In the same period (1973), Astrid Løken, a head curator of zoology at Bergen Museum, published her valuable work, "Studies of Scandinavian bumblebees (Hymenoptera,

Flies, mainly in the Muscidae and Syrphidae families, on an inflorescence of garden angelica (Angelica archangelica archangelica) *at Finse.*
Photo: Ørjan Totland.

Apidae)", in the Norwegian Journal of Entomology (Løken 1973). This has been a fundamental source of information about the distribution and ecology of Scandinavian species of bumblebees. Løken (1949) also performed important studies on the pollination of northern wolf's-bane by the bumblebee, *Bombus consobrinus*.

Peculiarities in Norwegian conditions

In common with all other European countries (with the possible exception of lizards in the Mediterranean region), insects are the only pollinators in Norway. In tropical regions, the pollinator fauna also includes birds (e.g. hummingbirds in America) and mammals (bats and lemurs). The number of species of pollinating insects is, moreover, lower in Norway than in many other countries. On a global scale, the Norwegian pollinator fauna (like that of many other northerly countries) can therefore be characterized as comparatively species-poor. To the extent that the pollinator fauna functions as a filter for which species of plants can reproduce in a given area, it is therefore possible that the relatively impoverished pollinator fauna and the absence of specific groups of pollinators over evolutionary time have resulted in species in the Norwegian flora lacking some pollination-related properties which can be found in other floras. For instance, Norway lacks species with distinctly red flowers and a long nectar tube, probably because of the absence of hummingbirds, which are important pollinators for species with such flowers. Such conclusions, based on the theory of pollination syndromes (which are controversial, see Ollerton et al. 1996), can be drawn for many other flower properties not found in species in the Norwegian flora.

Norway has a comparatively large number of species and density of bumblebees compared with areas further south in Europe and in the tropics (where bumblebees are absent). Furthermore, the species richness and density of solitary bees is relatively low in Norway compared with further south, and solitary bees seem to be largely replaced by various families of flies in Norway and other northern countries. Compared with other areas where insects alone comprise the pollinator fauna, we can therefore conclude that the pollinator fauna in Norway and other northerly areas probably mainly comprises bumblebees and true flies (hoverflies, house flies and Empididae), whereas other groups of pollinating insects, like beetles, butterflies and moths, and solitary bees, probably play a smaller role as pollinators in Norway compared with areas further south. Because there are big differences in the composition of the pollinator community between the lowlands and the mountains, and southern and northern parts of Norway, it is difficult to draw unambiguous conclusions concerning differences in the pollinator fauna between Norway and other countries.

Broadly speaking, the entomophilous species in the Norwegian flora can be split into three groups: 1) those pollinated almost exclusively by bumblebees (e.g. many species of clover), 2) those pollinated by other insects in addition to bumblebees (e.g. many species in the daisy family), and 3) those pollinated by other species than bumblebees (mainly flies and, to some extent, solitary bees; e.g. meadow buttercup).

The composition of the pollinator community may have consequences for the pollination and reproductive ecology of the plant species. Bumblebees are comparatively efficient pollinators because they deposit many pollen grains at each visitation and are quite faithful in their choice of species when seeking pollen and/or nectar. On the other hand, since bumblebees often occur in comparatively low densities, the number of visits is low. This may mean that seed production in many species of plants in Norway that are mainly specialized to be pollinated by bumblebees is on the whole limited by the availability of pollen. Flies are comparatively inefficient pollinators (they deposit few pollen grains on each visit) and often pay little regard to which species they visit. On the other hand, flies can be rather abundant. This means that the seed production of Norwegian plant species that are chiefly visited by flies (and to some extent solitary bees, which are more efficient than flies) may be pollen limited when the density of flies is low, and not pollen limited when it is high (the density of flies varies considerably in time and space). Furthermore, it is possible to predict that the production of plant species visited by both bumblebees and other pollinators (flies, solitary bees, beetles and butterflies and moths) is probably less pollen limited. These ”super-generalists” take good advantage of the efficiency of bumblebees and the abundance of flies and to a lesser degree other groups of pollinators.

Ipomopsis aggregata*, an American species mainly pollinated by hummingbirds. Photo: Walter Siegmund, CC-BY-SA 3.0).*

On the global scale, it is estimated that 85 % of plant species have their seed production increased (to a greater or lesser degree) by pollinators visiting their flowers. We do not know whether this estimate is representative for the Norwegian flora. However, the figure is likely to be lower here because the proportion of species in an area that depend upon pollinator visits is known to sink with increasing latitude and altitude above sea level, and Norway is located far north and has comparatively large areas above the tree line. In that case, this will first and foremost mean that many species of plants in Norway, perhaps percentage-wise more than further south, will be self-compatible, that is, they will be able to produce seeds by self-pollination. Furthermore, a higher percentage of these self-compatible species will perhaps also be autogamous, that is, the self-pollination can take place without insects visiting the flower, thus making them independent upon a pollinator visit to produce seeds. This lack of dependence is interpreted as reproductive insurance against poor pollination conditions and may also function as a buffer if the density and presence of pollinator species sinks due to human pressure. Far more research into the distribution and frequency of pollen limitation and its importance for seed production and the evolution of reproductive strategies in species in the Norwegian flora is required before the above suppositions can be verified. Such knowledge will also make us better equipped to predict how changes in the pollinator fauna may affect the reproductive ability of the plant.

These "super-generalists" take advantage of the efficiency of bumblebees and the abundance of flies.

The great majority of species in the Norwegian flora are generalists and are visited by more than two groups, most of them by many groups of pollinators. However, there are two groups of specialist plant species in Norway. One group is pollinated by a small array of bumblebees with long tongues (e.g. the garden bumblebee and *Bombus consobrinus*) and far less by butterflies and hawk moths. These plants are characterized by having a zygomorphic (bisymmetric) flower with a long nectar tube. An example of such a species is the early purple orchid. The other group can be characterized as super-specialists, that is, they are only pollinated by a single species of insect, or in a few cases two closely related species. Known examples of such super-specialists are the globeflower, which is pollinated by a few species in the fly genus *Chiastocheta* (Diptera, Anthomyiidae), whose females lay eggs in the flower ovaries, and the fly orchid (*Ophrys insectifera*), which is pollinated by digger wasps in the *Argogorytes* genus (the fly orchid resembles a female wasp, thus attracting sexually motivated males). Another orchid, red helleborine, is pollinated by the wood-dwelling bees, *Chelostoma rapunculi* and *C. campanularum*, which normally fetch pollen and nectar from harebells, but are tricked into visiting red helleborines, which resemble harebells and thus achieve pollination even though they lack nectar (Nilsson 1983). Because of the relative paucity of species of pollinators in Norway, added to a low span in pollinator behaviour and morphology, the Norwegian flora probably consists of a smaller proportion of super-specialists than the flora in countries further south.

The topography of Norway, with steep valley sides and extensive mountainous tracts, also limits the living conditions and dispersal paths of the pollinators in quite a different way than in most of the rest of Europe. This takes place purely physically, with high mountain chains limiting dispersal routes, and also because the topography creates sharp climatic gradients. At the same time, the south- and southwest-facing valley sides create living conditions for many thermophilous species that are otherwise not found so far north. These conditions probably lead to more isolated populations, which therefore to a lesser degree react to changes beyond their immediate vicinity. In this way, the populations become more dependent upon the local conditions, because all their resource requirements (access to places to live and an adequate diversity and number of flowering plants) must be satisfied locally. At the same time, isolated populations take advantage of being

The early-purple orchid (Orchis mascula) *is a specialist with a long nectar tube and is therefore pollinated by long-tongued bumblebees and hawk moths. Photo: Saarland, (CC-BY-SA 3.0.).*

shielded from some harmful pressures, like being infected by diseases. However, it is not known what effect diseases have on the Norwegian pollinator fauna and how vulnerable populations of pollinators are in Norway.

Norway shares her flora and pollinator fauna with large parts of the Nordic countries, and information on the connections which Norwegian plants and pollinators have with each other can to some degree be transferred from other countries where these species have already been studied. The specialist (oligolectic) pollinators probably have the same demands on the presence of specific flowering plants in Norway as in other countries since their interactions are a result of evolutionary adaptations over a long period. Among the generalist (polylectic) species, great differences can be expected between which plants they visit in other countries and in Norway, even though these interactions probably largely correspond to those in Sweden, for example. It should, however, be noted that no systematic mapping has taken place of which plants pollinating insects visit in Norway, and conversely from which insects pollination-dependent plants receive visits.

The pollination ecology of some species in the Norwegian flora has been studied in other countries and valuable, relevant information can be obtained from these studies. Owing to the considerable spatial variation in the composition of the pollinator fauna and the density of pollinator species, it is, however, hazardous to draw conclusions for Norwegian conditions based on results from other areas, with the possible exceptions of Sweden and Finland which, relatively speaking, are fairly similar to Norway as regards climate and geography. Hence, when studies show that the seed production of a plant species is not limited by the availability of pollinators in, for example, the Netherlands, it cannot be concluded that the same is the case for Norwegian populations of the species, primarily because the Norwegian plants experience different climatic conditions which affect the composition and density of the pollinator fauna and also influence other factors which may directly affect the ability of the plants to produce seed (e.g. temperature, length of season and access to food), and which thus work together with pollen limitation. Large parts of Norway are characterized by a climate that is periodically harsh and not least variable. This may greatly affect short-lived species like solitary bees and also, for instance, bumblebees which live longer. There is no doubt that weather conditions can limit the number of pollinators, but their real effect on the number of species and the size of pollinator populations in Norway is not known.

Pollination as an ecosystem service

The greater knapweed (Centaurea scabiosa) *is a super-generalist which is pollinated by many different groups of insects, in this case two species of Tachinid flies. It is also a key species for several endangered species of solitary bees like* Megachile lagopoda *and* Halictus eurygnathus*, both of which were listed as Critically Endangered (CR) in the 2010 Norwegian Red List for Species. Photo: Ørjan Totland.*

In many contexts, pollination is regarded as an essential ecosystem service (Millennium Ecosystem Assessment 2005, TEEB 2010, Cardinale et al. 2012), primarily based on the interaction leading to the production of fruit, which is an important constituent of the diet of people in the industrialized world and, not least, in developing countries. There are still no thoroughly prepared estimates of the economic significance of pollination in Norway. Moreover, pollination and the resulting production of wild berries (e.g. cloudberries, bilberries, cowberries, raspberries and wild strawberries) are also valuable in a recreational context in connection with berry picking. To the extent that pollination helps to maintain the species diversity of flowering plants and flower-visiting creatures, the pollination interaction also undoubtedly represents an important ecosystem service. Nonetheless, no studies from Norway can document that a species has died out, locally or nationally, because the interaction has collapsed. It may be imagined that if all bumblebees, for some reason or other, die out locally it would have great negative consequences for the survival of populations of a number of plant species which depend upon bumblebee visits for their seed production in the area affected. Thus, theoretically, local changes in the density of pollinators generally, or some groups of pollinators particularly, might have considerable effects on species richness and the composition of the plant community which will then have consequences for the function of the ecosystem (for instance, nitrogen fixation in species of the pea family, many of which depend upon bumblebee pollination). Moreover, such local changes, if they continue and increase in scale, will have considerable effects on a larger, national scale. In the same way, a major reduction in the density of plants which offer nectar and pollen will have substantial negative consequences for the population density and species composition of flower-visiting insects in the ecosystems.

In Norway, there has been no systematic mapping of which plants pollinating insects visit, or from which insects pollination-dependent plants receive visits.

Pollination is an ecosystem service that has great importance for agriculture throughout the world. According to Gallai et al. (2009), this ecosystem process contributes an economic value of 153 billion Euros annually on a global basis, which was 9.5 % of the total value of global agricultural production in 2005. The value of pollination for farming in the EU is 22 billion Euros per year (Gallai et al. 2009). Valuable farm products like wheat, rice and maize are wind pollinated, but some 70 % of the crops that are used directly as human food are dependent upon pollination by, in the main, insects, but also some vertebrates (Klein et al. 2007, but see Ghazoul 2005).

Large parts of the Western world report an ongoing decline in the number of species and individuals of bumblebees and butterflies in the past 50 years, for instance in England and the Netherlands (Biesmeijer et al. 2006). A recent pan-European compilation of national observation data reports a 50 % decline since the 1990s in the butterflies that were investigated (Van Swaay et al. 2012). In Sweden, a substantial change has been documented in the community structure of bumblebees in the agricultural landscape during the past 70 years, with a reduction in the number of species and an increase in the dominance of generalists with a short tongue (Bommarco et al. 2012a). Beekeepers are also experiencing increasing problems with losses of colonies in winter and the spreading of parasites and a number of viral diseases. Reports from the USA of Colony Collapse Disorder (CCD) have been particularly frequent in recent years, and the causes are still not fully understood. These trends have resulted in scientists speaking of a global pollination crisis.

It is well documented that insects living in (semi-)natural habitats may significantly influence the pollination of mass-flowering crops (Klein et al. 2007), but there is little specific information about this from the Nordic countries. In the Nordic countries, the production of fruit, berries, oilseed crops, and the seeds of clover and other species in the pea family, in particular, may experience a decline in their yield and quality if the availability of pollinating insects is reduced. The production of red clover seed in Sweden has declined in yield and stability since the 1930s, and this change coincides with considerable changes in the bumblebee fauna in the same area (Bommarco et al. 2012a).

Rape cultivation trials in Sweden have shown that insect pollination can raise the yield by 18 % compared with a system of cultivation based on wind pollination (Bommarco et al. 2012b). Pollinating insects also help to enhance the quality of the rape yield, and it has been well documented that both honey bees and native insects are valuable for pollination (Jauker et al. 2012). The availability of mass-flowering plants may also to some extent

Honey bees can be used to increase the yield of several mass-flowering crops.
Photo: Arnstein Staverløkk.

influence the number of pollinators in the surrounding area (Westphal et al. 2009, Persson and Smith 2013). Norwegian buyers of red clover seed report that producers can only meet half the demand, resulting in difficulty in obtaining enough red clover for organic agricultural production. Reduced pollination is the main explanation for this reduction in red clover seed production. As a consequence, semi-domesticated bees are sometimes released and commercially produced bumblebee nests are even occasionally deployed to replace the pollinator fauna which used to carry out the work without charge. However, it is uncertain to what extent the occurrence of wild plants has been limited by a lack of pollination due to the decline in the pollinator fauna in recent decades.

Even though the importance of pollination as an ecosystem service and for the function of ecosystems is *apparently* obvious, except for the importance of honey bees for commercial fruit production very little is really known about these aspects and what we believe to be true is based on assumptions that are poorly quality assured. A major international meta-analysis, however, recently concluded that the contribution of the wild pollinators to pollination of mass-flowering plants is considerable and cannot be fully replaced by honey bees (Garibaldi et al. 2013).

Consequences of human pressure

The use of pesticides on fields of mass-flowering crops has a negative impact on pollinators. Moreover, the frequent use of herbicides and the decreasing number of field margins result in an agricultural landscape that is almost devoid of foraging plants for pollinators. Photo: Arnstein Staverløkk.

Since the main causes of the decline in pollinators are well known, large-scale reversion to former agricultural practices and land use could, in the long term, restore the populations to their former levels. However, it is obviously not practical to revert to agriculture practices that dominated 50 to 100 years ago. Since it is unrealistic in the short term to be able to increase the availability of all the resources pollinating insects require, it is important to understand their relative significance. Which measures should we concentrate upon? To implement measures that have the greatest possible effect, it is necessary to have detailed knowledge of the pollination ecology of plants and the habitat demands of the pollinators. Many different factors limit the population size and distribution of pollinators. To be able to manage the pollinators, it is therefore important to know which pressures limit the size of their populations. Wintering, fertile, bumblebee queens require, for example, early-flowering sources of nectar and pollen when they end their winter hibernation to meet their need for energy and to produce the first workers. They also need enough available nesting sites. Both these factors limit how many wintering queens are successful in forming functional colonies. Then, in late spring and early summer, they need continuous access to nectar and pollen if the colony is to grow large. Hence, the total availability of flowers and distribution of resources through the season determines how large the surviving colonies will be and ultimately how many males and new queens will be produced.

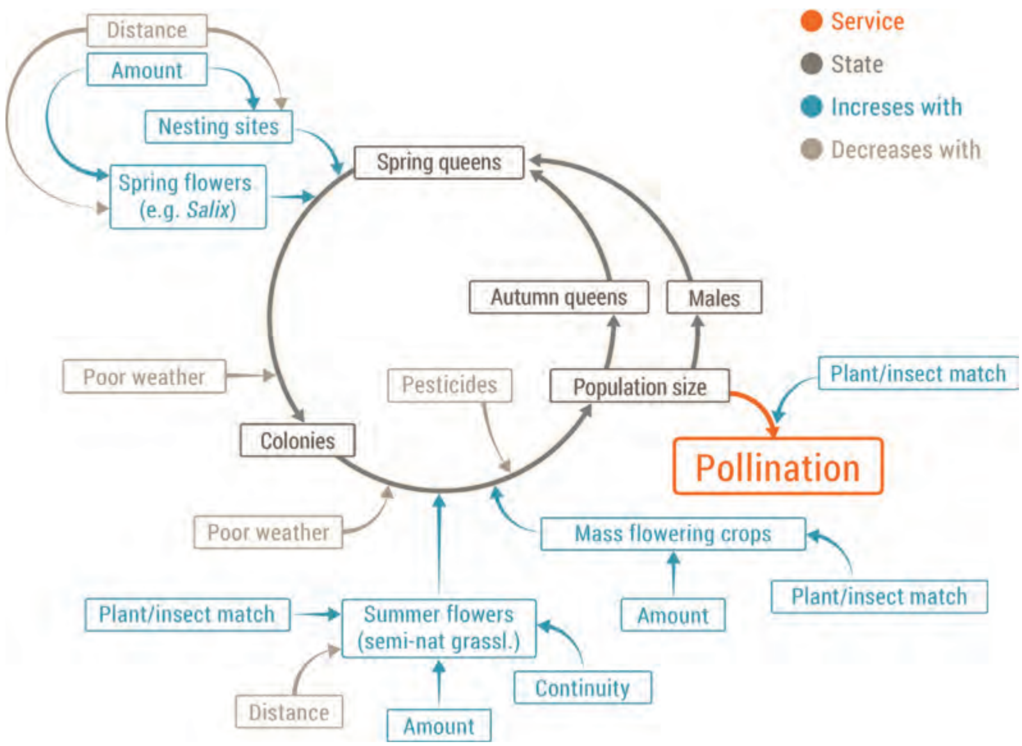


Figure 4: An example of a schematic population model for bumblebees. The long-term survival of the bumblebees is influenced by a number of different factors throughout their active season. Even though the population size is large enough to give adequate pollination, there must also be sufficient resources late in the season to satisfy their own reproduction. Analyses of the relative importance of each pressure factor are difficult and population studies on wild pollinators are therefore largely lacking today.

In general, several impact factors may limit population size and presence simultaneously, or one factor at a time can be limiting. In the first case, management actions can be implemented against several of these factors (e.g. as regards bumblebees: early pollen-producing species, nesting sites, amount of flowering plants through the summer, blooming continuity, and presence of late-blooming species). Some measures may be more efficient than others, but all have a positive effect on the pollinator community. In the other case, it is important to identify which factor is limiting for a certain species in a specific area. It may be difficult to decide whether the pollinators really are limited by just a single factor or by several simultaneously, and which factor is most cost effective to implement measures against. As the correct measures will probably differ in different areas, they must be differentiated.

Butterflies have been relatively well investigated in many countries for a long time, because they are comparatively easy to study and identify, and they have been collected in Western countries for very many years. Despite this, detailed population studies have been performed in the Nordic countries for only a few species, and generally only because they are used as model organisms for general ecological theories, like metapopulation research. A similar lack of population studies is also the case for bees and all the other important groups of pollinators in Norway. For the great majority of pollinator species in the Nordic countries, it is therefore only possible to roughly reason out the causes of changes in population development. This is unfortunate since such information is valuable for our understanding of how the species diversity of plants and their pollinators influences each other and how other factors affect it.

Changes in species diversity

Changes in species diversity are a result of changes in the density and presence (determined by dying out and immigration) of individual species. It is not known to what extent factors directly linked with pollination can explain why some plant and pollinator species are, or become, rare or endangered, and not others, and what significance pollination factors have compared with other factors (like habitat loss, fragmentation and introduced species) in processes that lead to plants and pollinators becoming rare or dying out. It is not only the density and presence of the rare species that can be affected by pollination factors. As pollination interaction is mostly generalized, a reduction in the population density of an important generalist pollinator can have major significance for many species of plants. Likewise, a decline in the density of a common plant species may have a great effect on the food available to many pollinator species. For instance, it is well known that the field scabious is an important food resource for several groups of pollinators (Franzén and Nilsson 2008). It is reasonable to assume that its occurrence has declined due to changes in farming practices since about the Second World War, but we have no specific basis today to account for the change in its occurrence. So far, there is no documented information from Norway about such aspects, although pollination factors are claimed to be important drivers for the increasing rarity and extinction of both plant and pollinator species in other areas. Studies of the connection between pollinator availability and recruitment success in populations of rare plant species may help to enhance our knowledge in this field. Likewise, studies of the connection between the availability of flower resources (nectar and/or pollen) in habitats and the population density of rare or endangered pollinator species may provide valuable information that will be important for our understanding of the significance of pollination factors for species diversity.

Because flowers of most species in the Norwegian flora are visited by individuals of many species of insects, this may act as a buffer against changes in the pollinator fauna (species diversity, densities and species composition) due to human impact. Many studies, however, have shown that only a few species of insects perform the majority of the pollination for most generalist plant species. This means that the sensitivity of a plant species to changed densities and species compositions in the pollinator community is probably considerably influenced by which insects suffer a change in density or die out from the habitat. Little is known about how the function of an insect species as an efficient pollinator for a certain plant species can be replaced by other existing pollinator species. The importance of a pollinator species for a given plant species is determined by 1) how frequently it visits the plant and 2) the number of species-specific pollen grains it deposits on stigmas per visit (visitation efficiency). This means that an ineffective pollinator may be important if it visits flowers sufficiently often and, the opposite, a rare visitor may be important if it deposits many pollen grains per visit.

An ineffective pollinator may be important if it visits flowers sufficiently often, while a rare visitor may be important if it deposits many pollen grains per visit.

For many plant species, it is important to have a high diversity of pollinators to achieve efficient pollination, precisely because the efficiency (or importance) of pollinators varies between plant species. An insect species which is very important as a pollinator for one plant species may be insignificant for another. For instance, the length of the tongues of bumblebees and butterflies determines how well they function as pollinators for various species of plants. A long tongue is required for the efficient pollination of flowers with a long nectar tube and conversely it is an energetic cost for species with a long tongue to balance and obtain nectar from flowers with a short nectar tube. Several plants also require that the insects have a certain weight or are sufficiently strong to move petals covering the entrance to the reproductive organs of their flowers. Others (for instance, species in the wintergreen family) depend upon the powerful whirring of bumblebee wings to ensure that the pollen is released from their anthers. A species-rich plant community therefore requires a species-rich pollinator community so that as many as possible of the plant species will achieve efficient pollination. The efficiency of a pollinator to pollinate a particular plant also depends upon the phenology of the pollinator and the plant (flight period of the pollinator, blooming period of the plant) matching or at least overlapping. A sufficiently large number of pollinators must be active when the plants bloom to achieve adequate pollination.

The insects vary not only in how they interact with the plants and the surroundings, they also react differently to disturbances like weather conditions, changes in the amount and structure of habitats, and changes in management regimes. This means that high pollinator diversity can function as insurance against the effects of, for instance, changed management or climate. If the pollinators react differently to a change in, for instance, the weather, a decline in the density of one species may, in theory, be compensated for by an increase in another. Because of a reduction in the total number of species in recent years and an increasing homogenization of habitat structures it is, however, unlikely that a random decline in one species can be compensated for by an increase in another species (Bengtsson et al. 2003). This is a possible explanation for the increasing variation from year to year in the size of pollinator-dependent mass-flowering crops in recent years.

A chronically low availability of pollinators will have negative consequences for the survival of populations of the great majority of plant species which depend upon pollinator visitation for reproduction, and consequently also for the species diversity of plants in areas with a reduced availability of pollinators. It is impossible to draw up a specific list of the most vulnerable species in the event of a decline of pollinators in Norway, but it is possible to suggest which properties the most vulnerable species probably will have. The population density in species with short-lived individuals (annual, biennial and perennial species) and short survival in the seed bank are vulnerable to a reduction in the number of seeds supplied to the seed bank. These species with short-lived individuals probably include some that are specialized with respect to pollination (visited by a few species of pollinators) at the same time as they are incapable of self-pollination (or are self-incompatible), and these will be especially at risk if their pollinator is reduced in density or dies out. In addition, there are indications that particularly early-flowering species may come out of step with their pollinators in the event of a warmer climate. Red helleborine is an example of a species which may be threatened by failing pollination. Its pollinators (the bee family *Chelostoma*) nest in dead, sun-facing tree trunks which may be in short supply near to where the plant grows. The bees must, moreover, have harebells available in the vicinity (they cannot survive by allowing themselves to be tricked by red helleborines, which lack nectar). The harebell is their most important food plant. Red helleborines lack nectar and are pollinated by the bees ”in error”.

Most pollinators visit more than one plant species (i.e. they are polylectic), and most pollination-dependent plants are visited by more than one species of pollinator (i.e. they are generalists). Such species have a larger buffer against a decline in the populations of their respective partners since another species (either a plant or a pollinator) can take over and perform the service. Oligolectic pollinators, on the other hand, are limited to one or just a few host plants for their collecting of nectar and pollen, thus making them vulnerable to changes in the occurrence and population size of the plants. Because of the fragmentation of their flower resources, in both time and geographically, oligolectic bees are especially hard hit by the changes in farming. In addition, most species of wild bees have rather special requirements concerning nesting sites, which must be in the immediate vi-

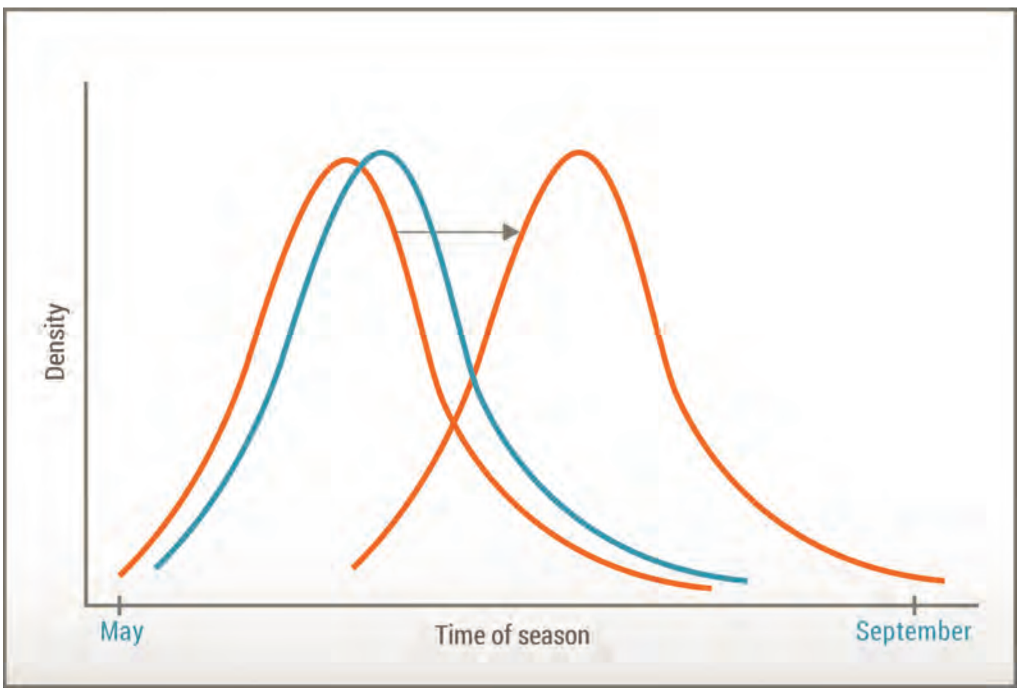


Figure 5: Explanation of how phenological mismatch may take place. A species (e.g. a pollinator) delays its period of activity until later in the season, whereas its plant species (blue) is unaffected by climate change.

cinity of the pollen source. Few bee species are willing to fly more than 500-1000 m from their nest to fetch food. This is reflected in the Red List for Species (Kålås et al. 2010), which showed that 1/3 of the bee species in Norway are Red Listed, making them one of the groups of species with the highest proportion of endangered species. An example of a group of species that may be in decline because of deteriorating pollination conditions is the Lepturinae (a subfamily of longhorn beetles). They are absolutely dependent upon flowers when they are adults. Of 20 species that are known to have lived in Norway, 4 are thought to be extinct and several are critically endangered. A disproportionate number of Lepturinae have thus declined. It is not clear whether this is due to stringent demands on their habitat linked with the development of their larvae in dead wood, a reduction in flowering in woodland habitats, or other factors.

Very few studies have been carried out on population dynamics in pollinating insects, at any rate in northern Europe. This makes it difficult to assess the relative significance of these conceivable, dynamic-creating mechanisms. The potential for variation from year to year places higher demands on observations of pollinators than their associated plants. To enable us to better understand the mechanisms that control the interaction between the host plants and the pollinators we need good population studies based on monitoring of both insects and plants. Such studies will also enhance our understanding of how the species diversity of plants and their pollinating insects is mutually influenced.

The red helleborine (Cephalanthera rubra) *is an example of a species that may be threatened by failing pollination. Its pollinators (the bee family Chelostoma) nest in dead, sun-facing tree trunks, which may be in short supply near to where the plant grows. Red helleborines lack nectar and trick the bees into pollinating them in error. The bees are therefore dependent upon harebells* (Campanula rotundifolia) *as their most important foraging plant. Photo: L. B. Tettenborn, (CC-BY-SA 3.0).*

Pressure factors

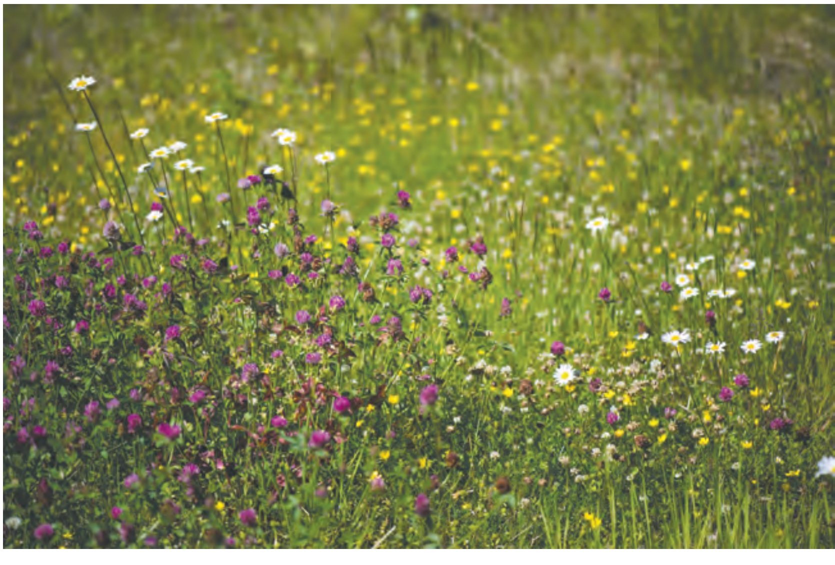
Most processes in nature are affected by human activity to a greater or lesser degree, and this is also true of pollination interactions. It is virtually impossible to find an answer to how the interaction between plants and pollinators would have taken place and how they would have mutually influenced one another in a situation where one or both partners remained unaffected by people. An understanding of human influence on processes in nature, like pollination, is therefore absolutely essential for correct nature management. We have recently become increasingly aware of the positive significance this interaction has for people through the ecosystem service it represents. The most important human-induced factors affecting the interaction between pollinators and plants are described below.

Changes in landscape structure and land use

Changes in land use, especially in farming since about 1950, have great consequences for the availability of habitats with a high quality for many pollinators and plants. Semi-natural habitat types with a high diversity of plants and insects have substantially declined. The 2011 Norwegian Red List for Ecosystems and Nature Types (Norderhaug and Johansen 2011) assessed species-rich hay meadows, for instance, as being a critically endangered habitat type. For hundreds of years, large areas of little productive land have been used as grazing or non-fertilized hay-making land (Fjeldstad et al. 2010). This unbroken form of management has prevented the landscape from becoming overgrown and meant that herbs are outcompeted by more rapidly growing grass and strongly competitive rosette plants. The acreage of hay-making land and extensive grazing in Norway and the rest of the Nordic area has declined greatly during the past hundred years (Norderhaug and Johansen 2011). This may have led to a decline in the amount of habitats for pollinating insects and increasing fragmentation of the remaining resources. For the longer-living bumblebees, these changes also mean that their flower resources also become fragmented if a lack of flowering plants periodically arises during the growing season. Since these changes lead to less diversity in flowering plants, they subsequently result in a reduction in the diversity of insect species that rely upon these flower resources, at any rate locally.

The changes in land use have also had consequences for the edge zones and how they function as habitats for plants and pollinating insects. In landscapes with intensive farming, the field margins are particularly valuable as refuges, but the species composition and ecological processes in these margins depend upon how the adjacent land is used (Marshall and Moonen 2002). It has been estimated that 40 % of the field margins in areas with intensive farming in the Oslofjord district were removed during the period from 1945 to 1995 (Fry et al. 1998). A similar trend has been recorded for Trøndelag, too (Hovd 2006). Several groups of pollinating insects have edge zones between fields, meadows and woodland as an important part of their habitat (Kells et al. 2001, Bäckman and Tiainen 2002, Sydenham 2012). The density of host plants helps to determine the quality of an area for seeking food (Saville et al. 1997, Dramstad at al. 2003, Sydenham 2012), and for bumblebees and solitary bees it has been shown that the density of important host plants has a positive effect on both the number of individuals and the richness of species (Rundlöf et al. 2008, Sydenham 2012). The connections here are, nevertheless, complex since the insects often need food throughout the summer and generally different biotopes for different parts of their life cycle. For instance, stone walls, meadows in an early stage of becoming overgrown and other areas that are not regularly mowed or grazed, but are, nevertheless, relatively open, have proved to be valuable nesting areas for bumblebees (Svensson et al. 2000). For some groups of pollinating insects, including many butterflies, transition zones between woodland and open habitats are especially valuable because the trees offer shelter from the wind, and such edge zones may have good, sunny conditions and be a habitat for species of plants that are important nectar and/or pollen resources. Kuussari et al. (2007) showed that uncultivated woodland margins and small patches of meadow adjacent to woodlands offering shelter from the wind, but still providing much sunshine, are valuable habitats for many butterflies in Finland.

Habitat fragmentation is probably an important explanation for the local and regional loss of pollinators. Twelve species of bees appear to have disappeared from Norway in the past hundred years, and the decline seems to have taken place broadly in neighbouring countries, too. Many of these species still seem to have patches of optimum habitat, but they are probably too small and too widely spaced for the isolated populations to be able to survive. Several of our most threatened species of bees have disappeared from some



Species-rich flowering meadows attract many specialist bumblebees and bees.
Photo: Arnstein Staverløkk.

localities where there are plenty of host plants and potential living sites. One example is a species of mining bees (*Andrena hattorfiana*). Its essential host plant, field scabious, is still very common in Norway, but present-day occurrences are probably too small and unstable, and too scattered to be able to maintain continuous populations of *Andrena hattorfiana* (Ødegaard 2012), which is now only found in three localities in Norway.

If access to pollinators is poor for a long period, it may lead to evolutionary changes in the reproductive strategy of the plant population.

Landscape fragmentation may affect populations of pollinators and plants in various ways. Changes in the interaction between pollinators and plants may, in turn, have consequences for populations of both. For the plants, a reduction in the availability of pollinator services may influence seeding and seed quality through pollen limitation. Reduced access to pollinators may also lead to a larger proportion of the seeds being a result of self-pollination (Aizen and Harder 2007). For species that reproduce vegetatively, the relationship between sexual and vegetative reproduction may be displaced towards the latter, thus gradually reducing the genetic diversity (Vandepitte et al. 2010). If access to pollinators is poor for a long period, it may lead to evolutionary changes in the reproductive strategy of the plant population (Eckert et al. 2010). For instance, some studies have shown that mechanisms which are supposed to prevent self-pollination become weaker in isolated populations with poor access to pollinators (Brys and Jacquemyn 2011). However, comparatively little research has so far been performed on the consequences of fragmentation on pollination success in plants.

Poor access to pollinators may also lead to less gene flow between fragments in the landscape where the plant is found. Exchange of pollen between neighbouring plants will then often form a major proportion of the pollen exchange in the population. The result is often inbreeding due to cross-pollination between closely related individuals, termed biparental inbreeding.

Relatively few studies have been performed in Norway on how landscape fragmentation affects pollination, gene flow in the landscape and genetic diversity in plant populations, but Sletvold et al. (2012b) have studied inbreeding in small populations of fragrant orchids (*Gymnadenia conopsea*). They found that it had significant negative effects on seeding and germination, and its effect on small, often isolated populations may contribute to a further decline of this orchid. The specialized fragrant orchid is chiefly pollinated by butterflies (Meekers et al. 2012). Poor access to pollinators has been shown to have a direct negative effect on seeding in some populations (Sletvold and Ågren 2010). Such knowledge forms an important basis for the management of nature and land use. As several species-rich types of habitat now mainly survive as isolated patches in the landscape, processes that can create gene flow between such habitats will become more important.

Alien species

Two important pollinators, the honey bee (*Apis mellifera*) and the buff-tailed bumblebee (*Bombus terrestris*), have been introduced into Norway (or parts of Norway) and may affect the interaction between native plants and pollinators. In addition to these two insects, many of the introduced plant species may influence the pollinating success of native plants and the population densities of pollinators.

The honey bee (*Apis mellifera*) is an important pollinator of many mass-flowering crops in Norway. The extent to which the honey bee is an introduced species is debatable. A subspecies, the European dark bee (*Apis mellifera mellifera*), is native to Western Europe and was probably widely distributed before being semi-domesticated. It probably lived in climatically favourable places in southern Norway in warm periods after the last Ice Age. However, all honey bees now found in Norway have been introduced, even though swarms can become established in the wild for short periods. Some studies in areas with dense populations of honey bees have shown that competition takes place with native pollinators for access to nectar or the large number of honey bees simply stresses other pollinators. Such competition may be particularly unfortunate for endangered species of wild bees which often visit the same plant species as the honey bee. A possible example from Norway is *Andrena hattorfiana*, which fetches pollen exclusively from field scabious, which is also a very attractive plant for honey bees.

The buff-tailed bumblebee (*Bombus terrestris*) is widely used in greenhouses to pollinate tomatoes as it is an effective pollinator for this plant and is comparatively easy to breed. It only used to occur in southernmost Norway, but its commercial use in greenhouses is suspected to be one reason why it is now spreading northwards. It competes for resources with other bumblebees and may thus lead to a decline in their populations. Commercial breeding of buff-tailed bumblebees based on Norwegian individuals is well established, but due to price competition from further south in Europe, by far the majority used in Norway now are imported. This threatens native pollinators because the genes of the imported bumblebees may spread to local populations of buff-tailed bumblebees by hybridization and pass on diseases to native bumblebees. Strong, negative effects of imported foreign pollinators, including buff-tailed bumblebees, have been found elsewhere, including the USA, Japan and Argentina (Gjershaug and Ødegaard 2012). The importation of buff-tailed bumblebees is controversial in Norway. The Norwegian Food Safety Authority recently banned their import on the scientific advice of Norwegian and foreign biologists, but subsequently lifted the ban following protests from market gardeners.

Alien and invasive plant species may affect interaction between native pollinators and plants, and thus lead to changes in the diversity of both plants and insects. The Norwegian Biodiversity Information Centre publishes a list of alien species which reproduce in the wild in Norway and performs assessments of the ecological hazard they may exert on the native nature diversity. The most recent review (Gederaas et al. 2013) judged that 71 vascular plants constituted a very high risk. Many of these, such as amelanchier or juneberry (*Amelanchier*), cotoneasters (*Cotoneaster* sp.), Indian balsam (*Impatiens glandulifera*), laburnum (*Laburnum*), lupin (*Lupinus*), Japanese rose (*Rosa rugosa*) and Canadian goldenrod (*Solidago canadensis*), are very attractive to many groups of pollinators. Several of these species have established large populations in Norway, especially in semi-natural habitats, and thus affect the interaction between native plants and their pollinators. Alien species may negatively affect the pollinating success of native species by attracting individual pollinators, which would otherwise visit the native species, and by transporting pollen grains from the alien species to stigmas in native species, thus perhaps blocking the stigmas for correct pollen. Many studies have shown that this competition may have negative effects on the reproductive success of native plants (Bjerknes et al. 2007).

Alien species may also have positive effects on native plants by attracting pollinators which thereafter visit native plants. Furthermore, alien species conceivably help to maintain populations of pollinators through the large nectar and/or pollen resources they offer (Bjerknes et al. 2007). Studies from the Continent have shown that the establishment of Indian balsam can sometimes lead to reduced pollination in native species, but the overall effect of Indian balsam is, nevertheless, complex since this species may also attract pollinators which increase the pollination of native species locally in the area where Indian balsam grows (Vilà et al. 2009). We still know little about how Indian balsam and other alien plants affect the density of pollinators on a larger scale. In Norway, Indian balsam is particularly attractive to the long-tongued garden bumblebee (*Bombus hortorum*). The effect of alien plant species on the pollination of native species probably greatly depends upon the extent of the overlap in the pollinator community between alien and native species (Thijs et al. 2011, Hegland and Totland 2012). Alien species may also be sources of nectar to replace other plants that have declined due to changes in farming practices, for example. Particularly important here are species which flower early or late in the growing season and thus offer nectar and/or pollen when many other species have not begun to flower, or have finished flowering.

A problem relating to alien species is the effect of mass-flowering crops on pollination in other species. Such crops may lead to increased competition between the plants for pollinating insects, as well as increasing the pollination of wild plants through positive effects on the population of pollinators in the area (Blitzer et al. 2012). On the other hand, mass-flowering crops may favour some groups of pollinating insects, such as honey bees, thus resulting in enhanced competition for other groups of pollinators (Steffan-Dewenter and Tscharntke 2000). The result may be less pollination of wild plants (Steffan-Dewenter and Westphal 2008, Holzschuh et al. 2011). In Norway, it is likely that oilseed rape, red clover, fruit trees, strawberries and raspberries can potentially influence the pollination of plants outside tilled land.

We need to learn more about how the establishment of alien species and mass-flowering crops affects natural pollination networks and the success of pollination and reproduction in native plant species.

Pesticides

The use of pesticides is a significant part of modern, conventional farming. According to figures from Norway Statistics, 94 % of all tilled land in Norway in 2011, except grazing and meadows, was treated with some kind of pesticide (Aarstad and Bjørlo 2012). Weed-killers (herbicides) are by far the most used group of pesticides, followed by fungicides and vermin killers. Herbicides reduce the occurrence of flowering herbs which the farmer does not want to have in his fields, but they simultaneously reduce the availability of pollen and nectar for pollinators. As 90-99 % of the area used for most varieties of corn and

Indian balsam (Impatiens glandulifera) *is very attractive to long-tongued bumblebees like the garden bumblebee* (Bombus hortorum). *Many successful alien plants are very attractive to insect pollinators, which helps to explain their rapid expansion by good seeding. The spreading of such alien plants may out-compete native plants and displace the balance in the relationship between native plants and their pollinators. Photo: Ørjan Totland.*

vegetables is treated with herbicides several times in the course of a growing season, the availability of food for pollinators is obviously greatly limited in the modern agricultural landscape.

Even though herbicides are most used, vermin killers probably have the greatest effect on pollinators in the agricultural landscape. Although pollinating insects are seldom or never investigated, the measures are often effective on a broad range of insects and therefore also affect pollinating insects. The question is not whether the pesticides are toxic to pollinators, which most are, but whether they are harmful in the concentrations used in the field. The most commonly used group of vermin killers is pyrethroids, which are acutely toxic to bees. Many, however, also have an effect which discourages bees, thus perhaps reducing the actual harmful effect on pollinators. A good piece of general advice is therefore not to spray when the pollinators are active, but instead to wait until the evening. It is particularly rape, apples, strawberries and to some extent potatoes which are treated with pyrethroids. These species are attractive to many wild pollinators. No study has been performed to learn how their potentially toxic nectar and pollen may affect individuals and populations of pollinators in Norway.

Neonicotinoids are a class of insecticide that is relatively new to Norway. These are systemic substances that are taken up by the plant and dispersed throughout the plant, including its nectar and pollen (Eggen and Odenmarck 2012). They have the potential to act as a nerve toxin on insects. One neonicotinoid that is in use, imidacloprid, is approximately 7 000 times more toxic to insects than DDT. Extremely small doses of these substances are therefore applied.

Glandular globe-thistle (Echinops sphaerocephalus) *is an alien species that is very attractive to pollinators. Chemicals are currently being used to try to eradicate it from Hovedøya, an island in Oslo. Photo: Frode Ødegaard.*

Many studies show that neonicotinoids have sub-lethal effects on pollinators, like changing their behaviour, reducing their ability to navigate and reducing population growth in honey bees and bumblebees, even in legal doses (Blacquiere et al. 2012, Henry et al. 2012, Whitehorn et al. 2012). The effect of neonicotinoids on wild pollinators and hon-ey bees is still strongly debated, and legislation controlling their use varies from country to country. Norway has banned the use of imidacloprid on oilseed rape since 2012, partly based on a risk assessment issued by the European Food Safety Authority (EFSA 2012), although the substance is still permitted in the EU. However, in Norway, imidacloprid is still approved for use in greenhouses and to treat seed potatoes. Another

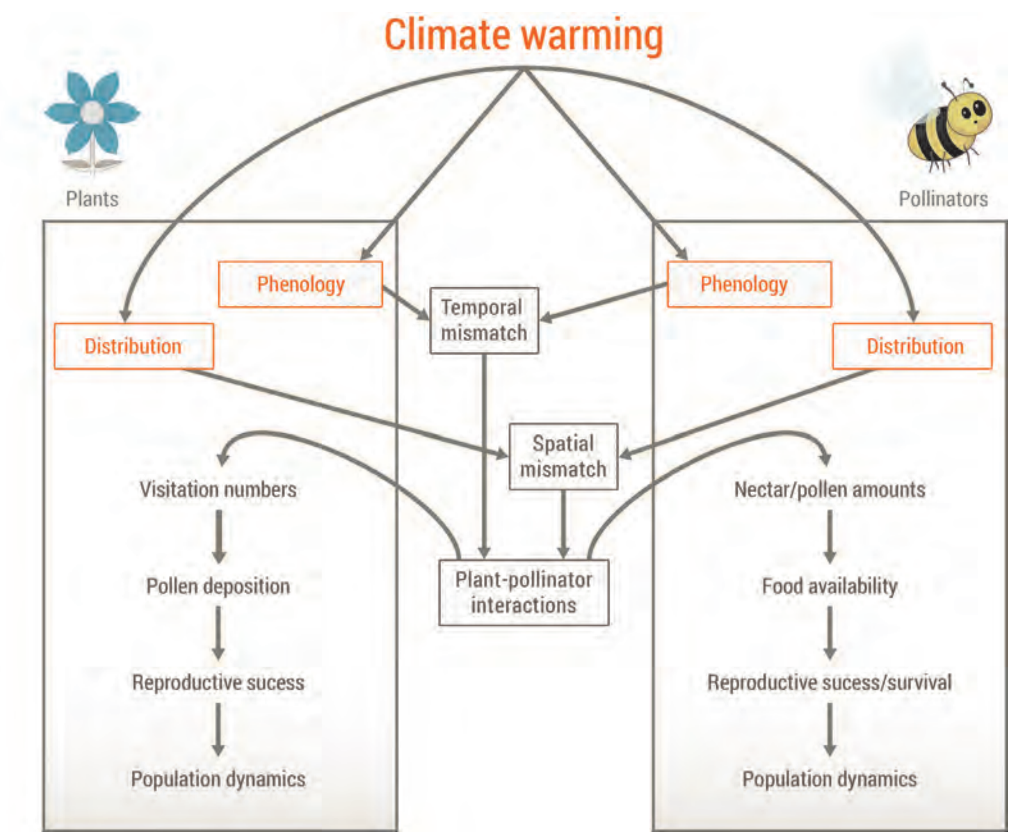


Figure 6: Illustration of how climate warming may affect the phenology and distribution of plants (left panel) and pollinators (right panel), thereby creating temporal and spatial mismatches in plant-pollinator interactions. The lower half of the panels shows how and by which key factors the demography of the mutualistic partners is likely to be affected. The pathway leading to the mismatches is largely known, whereas the mismatches and the subsequent effects are still mostly unknown and require additional research. Figure redrawn from Hegland et al. (2009).

neonicotinoid, tiacloprid, is sprayed on rape, apples and strawberries, for example. Studies of the effects of these substances on pollinators in the field are difficult, but should be given priority due to the potentially great negative effects on wild and domesticated pollinators.

Climate change

Climatic conditions generally control the distribution and density of species, including flowering plants and pollinators. Moreover, many studies show that phenological events (e.g. the onset of flowering or flying) are strongly controlled by climatic conditions. Climate change may therefore influence the interaction between plants and pollinators through changes in population densities and species composition, as well as phenological or spatial mismatches (Hegland et al. 2009).

Many flower-visiting insects are thermophilous and require sunshine to be active. Many therefore have a southerly distribution and are only found in the climatically most favourable places in Norway. Climate change which entails more cloudy weather in summer will therefore have a negative effect on many of these species, even if the average temperature rises.
It is quite certain that climate change, like any other environmental change (e.g. loss of habitat, fragmentation and alien species) will have the greatest effect on specialized species, whether plants or pollinators. Still more specifically, climate change will probably have the greatest effect on specialized, early-active species because they have few alternative interaction partners and may experience being active (flowering or flying) outside the activity period of their specific partners. A change in climate that leads to a change in the density of a specialized mutualistic partner may have an immediate indirect effect on the success of the other partner, even if that itself is not affected by the climate change.

A specialized species of plant which loses pollinator visits because its pollinator is reduced in density due to climate change may thus experience reduced seed production through pollinator limitation without being directly influenced by the climate change. Phenological mismatches have the same effect even though they do not necessarily lead to changes in density. A pollinator species which begins to fly earlier due to a rise in temperature may experience ”losing” its plant if that does not also advance its flowering period in response to the rise in temperature. Some studies seem to suggest that insects in general are more phenologically affected than plants and phenological mismatches may become common in the future. As mentioned above, the consequences of such mismatches vary between specialists and generalists. A generalist that has its phenology changed can simply get new interaction partners without special negative consequences, because an alternative partner will always be available.

On the whole, our knowledge of the effects of climate change on species and communities is quite good. However, effects on the plant-pollinator interaction are little known, particularly because this is a problematical field of research in which realistic experiments are difficult to perform. Thus we know little about the relative importance of climate change and other environmental changes on plants, pollinators and their interactions. Nevertheless, many populations of pollinators in Norway are likely to be especially vulnerable to climate change because they are in the marginal zone of the total range of the species, where the effects of environmental changes in general are often strongest.

The most obvious way to improve knowledge in this area would be to study plant-pollinator interactions and their consequences along natural climatic gradients.

Recommendations for acquiring more knowledge on pollination ecology

Andrena hattorfiana*, a species of mining bee, is completely dependent upon collecting pollen from field scabious* (Knautia arvensis). *It used to be seen in the agricultural landscape across most of southern Norway, but is now restricted to three sites. Photo: Frode Ødegaard.*

Owing to the comparatively modest research activity on pollination ecology in Norway, our current knowledge is, on the whole, slight and fragmentary. Moreover, our opportunity to extrapolate knowledge from studies in other countries to Norwegian conditions is, as mentioned above, limited due to Norway's special climatic and geographical conditions. Nature management bodies in Norway therefore have a limited basis for implementing aspects of pollination in their management activities and strategies. In particular, too little is known about how dependent plant species in Norway are on pollination for their seed production, the distribution and density of important groups of pollinators and which species of plants they are dependent upon and which they pollinate, and how the population development of rare species of plants and pollinators is affected by pollination interactions. Furthermore, we know too little about how pollinator communities have changed over time, and which pressure factors underlie any changes.

Because of the poor state of knowledge, it is difficult to give clear recommendations for how the gaps in knowledge can best be filled. In reality, it is more a question of how we can most effectively acquire a platform of knowledge that can function as a starting point to generate hypotheses and gather data on more specific problems within pollination ecology that are relevant for managing ecosystems in Norway.

The committee views the following as being most important for our understanding of pollination and the further generation of knowledge in this sphere.

Mapping pollinators and which plant species they visit

The general paucity of knowledge on the diversity of species in Norway applies to pollinators, too. It can therefore be assumed that we have still not recognized several species of pollinators in Norway. This applies particularly in the most poorly mapped groups, like some families of true flies (Diptera; e.g. Anthomyiidae, which regularly visit flowers). A few undiscovered flower visitors can also be expected among most of the other groups of insects. However, the number depends upon the current status of the ongoing mapping, which differs greatly from one insect group to another. In the case of solitary bees, for example, it is probably still possible to discover 5-10 species that are new to Norway, whereas we now know a great deal about bumblebees. The pollinator fauna is also continually changing. For instance, the latest Red List for Species (Kålås et al. 2010) shows that 12 bee species have disappeared from Norway, while new flower-visiting insects are constantly arriving and become established here.

Acquiring information on which pollinator species are important for plants and the most important plants for pollinators is a typical mapping task, but it also calls for considerable research. The ongoing mapping is focusing upon identifying the species in some flower-visiting groups of insects and determining their distribution. However, which species of flowers the various insects visit is not being mapped, so it is not possible to demonstrate the specific pollination interaction in which these insects participate. This work therefore needs to be extended by initiating long-term mapping of which species of insects visit flowers and which plants they visit, and this task must take place in a systematic and scientifically rigid manner. It should also aim to document the spatial and temporal variations in the composition of pollinators visiting different species of plants and the extent to which the choice of plant varies geographically. A major challenge for this mapping is linked with expertise in insect taxonomy and the number of people having such expertise. There is good taxonomic expertise in Norway for some of the most important groups of pollinators (especially hoverflies, solitary bees, bumblebees, and butterflies and moths), but since few people have this expertise it will be difficult to have the collected specimens identified at the species level in an efficient and good manner. Moreover, it will be time consuming to collect data on the insect fauna of all the more than 1000 native insect-pollinated species of plants in Norway (we probably have detailed knowledge about no more than 50 of them). This work should be coordinated by a group of experts in Norway, and a national committee of experts should be appointed to determine how the mapping should be carried out and how much it will cost.

It is important that the ongoing mapping of the wild bee specialists continues and is supplemented, especially in view of the decline of many of their populations and their significance as pollinators. Compilations of knowledge about bees and which species of plants they visit and *vice versa* exist for Sweden (Pettersson et al. 2004). These lists largely agree with conditions in Norway and can be used as an indication of possible pollination links here. However, there are many regional differences which should be mapped, for instance that some plants are visited by few species of insects in one region and more in others. It is important to uncover such regional differences and then study them in relation to their effect for pollination, precisely because pollinators differ greatly in their efficiency.

We therefore need to know which species should be regarded as pollinators in Norway. The next steps will be to study which plants they visit and, ultimately, how far the various species contribute to pollination. There are large gaps in knowledge here.

Ongoing mapping projects that help to enhance our knowledge of the occurrence of various groups of pollinators should be extended and new groups of pollinators should be included (especially flies and flower-visiting beetles). The mapping should take place on national, regional (counties) and local levels, depending upon the distribution pattern of the groups being investigated. Furthermore, the mapping of specialist plants and pollinators (which are particularly vulnerable to changes in the availability of partners) will be a valuable tool in the vulnerability analysis and preservation of such species.

In connection with the ongoing mapping and the data that will be gathered in the future, work has started to build up a database at the Norwegian Biodiversity Information Centre to assimilate information on pollination for species of insects and plants in Norway. The challenge now will be to fill the database with specific data linking plants to pollinators (and *vice versa*). Few documented data exist today. It will be important to feed in those that already exist and start systematic data collection to fill the database with valuable information. The committee recommends that data collection be organized in accordance with taxonomic groups and rare species.

A general challenge in pollination ecology is that flower-visiting species vary a great deal in their efficiency as pollinators. Some are pure parasites on the mutualism between the really efficient pollinators and the plants, while others are very efficient pollinators for some species of plants, but not for others. This is a relevant challenge for the mapping which aims to link flower-visiting insects to plant species. Some flower visitors are simply not pollinators, partly because they are too small, just visit a flower, or are incapable of transporting pollen grains. We therefore need to know which species should be regarded as pollinators in Norway. The next steps will be to study which plants they visit and, ultimately, how far the various species contribute to pollination. There are large gaps in knowledge here.

Surveying the occurrence of pollinating insects is time consuming. Catching them with the help of a malaise trap like this is an important way of obtaining information about the pollinator fauna in a particular area. Photo: Oddvar Hanssen, NINA.

Availability of pollinators for rare plant species

Quantifying the frequency of pollinator visits to flowers is time consuming. The usual procedure is to observe the flowers of a plant species repeatedly through the flowering period of the population and count the number of visits made by various groups of pollinators. For a given species of plant, there should be sufficient observation periods to be able to obtain a representative estimate of the frequency of visits and their variation over time (24 hours and season) and between populations. As it is important that such measurements give comparable results, it is necessary to put in a coordinated effort. It is most unlikely that such measurements can be performed for all flowering plants in the Norwegian flora. Such work should therefore initially concentrate on mapping the frequency of visits to the most vulnerable plants in the Norwegian flora. Such information can form a good basis for any management actions aimed at these species.

Pollen limitation on seed production and population dynamics in rare species

An effort should be made to understand the importance of pollen limitation in relation to other limiting factors for seed production in as many rare, insect-pollinated species as possible. It will also be important to include species which can be characterized as pollination specialists, such as many orchids and other species with long nectar tubes. At the same time, it will also be useful to know more about how dependent rare species in the Norwegian flora are of pollinator visits for their seed production. In this context, it will also be very relevant to understand how pollen limitation can affect population dynamics and survival through its influence on seed production. These are challenging research tasks which will call for considerable fieldwork and data collection over many years and will probably only be able to be carried out for a few relevant species. Such studies must be able to quantify the degree of pollinator limitation on the seed production of the plants through experiments which saturate the stigmas of the plants with pollen and compare their seed production with plants which only receive natural pollination intensity from the insects present in the habitat. Population matrix studies must also be performed to quantify the degree to which reproduction is important for recruitment to the population and its long-term dynamics. The management of threatened species is dependent upon such information to be able to take the correct actions. If access to pollinators is an important reason why a species is threatened, action must be taken to tackle this problem, for instance through active management of the insect populations which pollinate the species. There is little point in managing a plant whose seed production is severely pollen limited (e.g. many orchids), if the pollinator fauna of the plant is not taken into account, too. Likewise, the management of specialist bees will probably have little success if considerable awareness is not also directed at the plant species on which they depend for their pollen and nectar.

The management of rare plant species will be further improved if we know their compatibility system and the degree to which they depend upon pollinator visits to be able to produce seeds. The compatibility system of many species has been investigated and is known, but because compatibility may vary geographically, it is important to undertake investigations in Norwegian populations of species that have already been studied in another country. Species which are self-compatible may potentially produce seeds by self-pollination. However, as self-compatible species show wide variation in the ability to self-pollinate, it is important to investigate each species in detail.

Norwegian contributions to international knowledge on pollination

Geographical and climatic conditions give Norway a special position in Europe. Moreover, the geographical conditions offer possibilities to study ecological problems along sharp environmental gradients (e.g. temperature, precipitation, length of season, degree of fragmentation and human encroachment) over short distances. Norwegian scientists thus have good opportunities to occupy leading positions in pollination ecology, especially directed at how pollination ecological factors vary with other environmental factors in their effect on the reproduction and population density of plants and pollinating insects. Furthermore, Norwegian scientists are particularly well equipped to study and provide important contributions to global knowledge of how climate change may impact on plant-pollinator interactions and their effects on plant reproduction and insect density.

Education

Norwegian universities currently have no regular offer of education specifically directed at pollination ecology. Owing to the funding system used for Norwegian universities and because relatively few students are likely to take advantage of such a specialized offer at each university, it is recommended that Norwegian universities cooperate to set up courses on pollination ecology at the Master and PhD levels. These courses should also be available to Master and PhD students from other Nordic countries who wish to take part. A possible way of organizing this might be to set up a Norwegian or Nordic research school or network in pollination ecology. Norwegian pollination ecology scientists are valuable contributors to the Scandinavian Association for Pollination Ecologists (SCAPE), in part by organizing the SCAPE Conference every 4th year. This is a platform that can function as a network building and information exchange forum for Norwegian Master and PhD students and other specialists in pollination ecology and related subjects.

Experts on pollination ecology in Norway should cooperate more on joint research projects which, in particular, help to train Master and PhD students.

References

Aizen, M. A., Harder, L. D. 2007. Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. Ecology, 88: 271-281.

Bäckman, J. -P. C., Tiainen, J. 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). Agriculture, Ecosystems & Environment, 89: 53-68.

Bengtsson, J., Angelstam, P., Elmqvist T., Emanuelsson, U., Folke, C., Ihsec, M., Moberg, F., Nyström, M. 2003. Reserves, resilience and dynamic landscapes. Ambio, 32: 389-396.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R,. Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R,. Thomas, C. D., Settele, J., Kunin, W. E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science, 313: 351-354.

Bingham, R. A., Orthner, A. R. 1998. Efficient pollination of alpine plants. Nature, 391: 238-239.

Bjerknes, A. L., Totland, Ø., Hegland, S. J., Nielsen, A. 2007. Do alien plant invasions really affect pollination success in native plant species? Biological Conservation, 138: 1-12.

Blacquiere, T., Smagghe, G. van Gestel, C. A., Mommaerts V. 2012. Neonicotinoids in bees: a review on concentrations, side-effects and risk assessment. Ecotoxicology, 21: 973-992.

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A. -M., Rand, T. A., Tscharntke, T. 2012. Spillover of functionally important organisms between managed and natural habitats. Agriculture, Ecosystems & Environment, 146: 34-43.

Bommarco, R., Lundin, O., Smith, H. G., Rundlöf, M. 2012a. Drastic historic shifts in bumble-bee community composition in Sweden. Proceedings of the Royal Society, Biological Sciences, 279: 309-315.

Bommarco, R., Marini, L., Vaissière, B. E. 2012b. Insect pollination enhances seed yield, quality, and market value in oilseed rape. Oecologia, 169: 1025-1032.

Brys, R., Jacquemyn, H. 2011. Variation in the functioning of autonomous self-pollination, pollinator services and floral traits in three Centaurium species. Annals of Botany, 107: 917-925.

Burd, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation on fruit and seed set. Botanical Review, 60: 83-139.

Busch, J. W., Delph, L. F. 2012. The relative importance of reproductive assurance and automatic selection as hypotheses for the evolution of self-fertilization. Annals of Botany, 109: 553-562.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., Naeem, S. 2012. Biodiversity loss and its impact on humanity. Nature, 486: 59-67.
Carvell, C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D., Goulson, D. 2006. Declines in forage availability of bumblebees at a national scale. Biological Conservation, 132: 481-489.
Darwin, C. R. 1862. On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. John Murray, London, UK.
Darwin, C. R. 1876. The effects of cross and self fertilisation in the vegetable kingdom. John Murray, London, UK.
Dramstad, W. E., Fry, G. L. A., Schaffer, M. J. 2003. Bumblebee foraging — is closer really better? Agriculture, Ecosystems and Environment, 95: 349-357.
Eckert, C. G., Kalisz, S., Geber, M. A., Sargent, R., Elle, E., Cheptou, P.-O., Goodwillie, C., Johnston, M. O., Kelly, J. K., Moeller, D. A., Porcher, E., Ree, R. H., Vallejo-Marin, M., Winn, A. A. 2010. Plant mating systems in a changing world. Trends in Ecology and Evolution, 25: 35-43.
European Food Safety Authority. 2012. Statement on the findings in recent studies investigating sub-lethal effects in bees of some neonicotinoids in consideration of the uses currently authorised in Europe. EFSA Journal. 10(6):2752. doi:10.2903/j.efsa.2012.2752.
Eggen, T., Odenmarck, S. R. 2012. Opptak og translokering av insektmidlet imidakloprid i kulturplanter - eksponering av bier. Bioforsk Report Vol. 7, No. 169.
Franzén, M., Nilsson, S.G. 2008. How can we preserve and restore species richness of pollinating insects on agricultural land? Ecography, 31: 698-708.
Fry, G., Ims, R. A., Lid, I. B. 1998. Naturen i et hav av åker. In: Framstad, E., Lid, I. B. (eds.). Jordbrukets kulturlandskap. Forvaltning av miljøverdier. University Press, Oslo, 100-105 pp.
Fægri, K., van der Pijl, L. 1979. The principles of pollination ecology. Pergamon Press, London.
Gallai, N., Salles, J.-M., Settele, J., Vaissiêre, B. E. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics, 68: 810-821.
Garcia-Camacho, R., Totland, Ø. 2009. Pollen limitation in the alpine: a meta-analysis. Arctic, Antarctic, and Alpine Research. 41: 103-111.
Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S. K., Kennedy, C. M., Krewenka, K. M., Krishnan, S., Mandelik, Y., Mayfield, M. M., Motzke, I.,

Munyuli, T., Nault, B. A., Otieno, M., Petersen, J., Pisanty, G., Potts, S. G., Rader, R., Ricketts, T. H., Rundlöf, M., Seymour, C. L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C. H., Viana, B. F., Wanger, T. C., Westphal, C., Williams, N., Klein, A. M. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science, 339: 1608-1611.

Gederaas, L., Moen, T. L., Skjelseth, S., Larsen, L.-K. (eds.) 2013. Alien species in Norway – with the Norwegian Black List 2012. Norwegian Biodiversity Information Centre, Norway.

Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis. Trends in Ecology and Evolution, 20: 367-373.

Gjershaug, J. O., Ødegaard, F. 2012. Vurdering av risiko for biologisk mangfold ved innførsel av mørk jordhumle *Bombus terrestris* til Norge. NINA Report, 895: 42 pp.

Hegland, S. J., Totland, Ø. 2007. Pollen limitation affects progeny vigour and subsequent recruitment in the insect-pollinated herb *Ranunculus acris*. Oikos, 116: 1204-1210.

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L., Totland, Ø. 2009. How does climate warming affect plant-pollinator interactions? Ecology Letters, 12: 184-195.

Hegland, S. J., Totland, Ø. 2012. Interactions for pollinator visitation and their consequences for reproduction in a plant community. Acta Oecologica, 43: 95-103.

Henry, M., Beguin, M., Requier, F., Rollin, O., Odoux, J-. F., Aupine, l. P., Aptel, J., Tchamitchian, S., Decourtye, A. 2012. A common pesticide decreases foraging success and survival in honey bees. Science, 336: 348-350.

Holzschuh, A., Dormann, C. F., Tscharntke, T., Steffan-Dewenter, I. 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. Proceedings of the Royal Society B, Biological Sciences, 278: 3444-51.

Hovd, H. 2006. Field margins in central Norway – creation, management and flora. PhD thesis, Norwegian University of Life Sciences, Ås.

Jauker, F., Bondarenko, B., Becker, H. C., Steffan-Dewenter, I. 2012. Pollination efficiency of wild bees and hoverflies provided to oilseed rape. Agricultural and Forest Entomology, 14: 81-87.

Kells, A. R., Holland, J. M., Goulson, D. 2001. The value of uncropped field margins for foraging bumblebees. Journal of Insect Conservation, 5: 283-291.

Klein, A. -M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B, Biological Sciences, 274: 303-313.

Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Dudash, M. R., Johnston, M. O., Mitchell, R. J., Ashman, T. L. 2005. Pollen limitation of plant reproduction: pattern and process. Annual Review of Ecology, Evolution and Systematics, 36: 467-497.

Kohler, F., Verhulst, J., Van Klink, R., Kleijn, D. 2007. At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? Journal of Applied Ecology, 45: 753-762.

Kuussaari, M., Heliölä, J., Luoto, M., Pöyry, J. 2007. Determinants of local species rich-

ness of diurnal Lepidoptera in boreal agricultural landscapes. Agriculture, Ecosystems & Environment, 122: 366-376.
Körner, K. 2003. Alpine plant life: functional plant ecology of high mountain ecosystems (2nd ed.). Springer, Berlin, Germany.
Kålås, J. A., Viken, Å., Henriksen, S., Skjelseth, S. (eds.) 2010. The 2010 Norwegian Red List for Species. Norwegian Biodiversity Information Centre, Trondheim, Norway.
Lázaro, A., Nielsen, A., Totland, Ø. 2010. Factors related to the inter-annual variation in plants' pollination generalization levels within a community. Oikos, 119: 825-834.
Lundemo, S., Totland, Ø. 2007. Within-population spatial variation in pollinator visitation rates, pollen limitation on seed set, and flower longevity in an alpine species. Acta Oecologia, 32: 262-268.
Løken, A. 1949. Bumble bees in relation to *Aconitum septentrionale* in Central Norway (*Øyer*). Nytt Magasin for Naturvidenskapene, 87: 1-60.
Løken, A. 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). Norwegian Journal of Entomology, 20: 1-218.
Marshall, E. J., Moonen, A. 2002. Field margins in northern Europe: their functions and interactions with agriculture. Agriculture, Ecosystems & Environment, 89: 5-21.
Meekers, T., Hutchings, M. J., Honnay, O., Jacquemyn, H. 2012. Biological flora of the British Isles: *Gymnadenia conopsea* s. l ., 162: 1269-1288.
Millennium Ecosystem Assessment 2005 Ecosystems and Human Well-being: Synthesis, World Resources Institute. http://www.millenniumassessment.org/documents/document.356.aspx.pdf
Nielsen, A. 2007. The spatio-temporal variation of the plant-pollinator system of a boreal forest landscape. Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås.
Nilsson, L. A. 1983. Mimesis of bellflower (*Campanula*) by the red helleborine orchid *Cephalanthera rubra*. Nature, 305, 799-800.
Norderhaug, A., Johansen, L. 2011. Semi-natural sites and boreal heaths. In: Lindgaard, A., Henriksen, S. (eds.) The 2011 Red List for Ecosystems and Habitat Types. Norwegian Biodiversity Information Centre, Trondheim, Norway.
Petanidou, T., Godfree, R. C., Song, D. S., Kantsa, A., Dupont, Y. L., Waser, N. M. 2012. Self-compatibility and plant invasiveness: Comparing species in native and invasive ranges. Perspectives in Plant Ecology, Evolution and Systematics, 14: 3-12.
Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W. E. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution, 25: 345-353.
Persson, A., Smith, H. 2013. Seasonal persistence of bumblebee populations is affected by landscape context. Agriculture, Ecosystems & Environment, 165: 201-209.
Pettersson, M. W., Cederberg, B., Nilsson, L. A. 2004. Grödor och vildbin i Sverige. Svenska Vildbiprojektet vid Artdatabanken, SLU & Avdelningen för Växtekologi, Uppsala Universitet.
Richards, A. J. 1997. Plant breeding systems (2nd ed.). Chapman and Hall. London.

UK.
Rundlöf, M., Nilsson, H., Smith, H. G., 2008. Interacting effects of farming practice and landscape context on bumblebees. Biological Conservation, 141: 417-426.
Saville, N. M., Dramstad, W. E., Fry, G. L. A., Corbet, S. A. 1997. Bumblebee movement in a fragmented agricultural landscape. Agriculture, Ecosystems & Environment, 61: 145-154.
Sletvold, N., Ågren, J. 2010. Pollinator-mediated selection on floral display and spur length in the orchid *Gymnadenia conopsea*. International Journal of Plant Sciences, 171: 999-1009.
Sletvold, N., Trunschke, J., Wimmergren, C., Ågren, J. 2012a. Separating selection by diurnal and nocturnal pollinators on floral display and spur length in *Gymnadenia conopsea*. Ecology, 93: 1880-1891.
Sletvold, N., Grindeland, J. M., Zu, P., Ågren, J. 2012b. Strong inbreeding depression and local outbreeding depression in the rewarding orchid *Gymnadenia conopsea*. Conservation Genetics, 13: 1305-1315.
Steffan-Dewenter, I., Tscharntke, T. 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia, 122: 288-296.
Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., Tscharntke, T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology, 83: 1421-1432.
Steffan-Dewenter, I., Westphal, C. 2008. The interplay of pollinator diversity, pollination services and landscape change. Journal of Applied Ecology, 45: 737-741.
Svensson, B., Lagerlöf, J., Svensson, B. G. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agriculture, Ecosystems & Environment, 77: 247-255.
Sydenham, M. A. K. 2012. Living on the edge – the value of field edges as resource patches for solitary bees (Hymenoptera: Apiformes). Master thesis, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås.
TEEB. 2010. The Economics of Ecosystems and Biodiversity: Mainstreaming the Economics of Nature: A synthesis of the approach, conclusions and recommendations of TEEB, UNEP. http://bit.ly/TEEB_synthesis
Thijs, K. W., Brys, R., Verboven, H. A. F., Hermy, M. 2011. The influence of an invasive plant species on the pollination success and reproductive output of three riparian plant species. Biological Invasions, 14: 355-365.
Totland, Ø. 1993. Pollination in alpine Norway: flowering phenology, insect visitors, and visitation rates in two plant communities. Canadian Journal of Botany, 71: 1072-1079.
Totland, Ø. 2001. Environment-dependent pollen limitation and selection on floral traits in an alpine species. Ecology, 82: 2233-2244.
Van Swaay, C. A. M., Van Strien, A. J., Harpke, A., Fontaine, B., Stefanescu, C., Roy, D., Maes, D., Kühn, E., Õunap, E., Regan, E., Švitra, G., Heliölä, J., Settele, J., Pettersson, L.B., Botham, M., Musche, M., Titeux, N., Cornish, N., Leopold, P., Julliard, R., Verovnik, R., Öberg, S., Popov, S., Collins, S., Goloshchapova, S., Roth, T.,

Brereton, T., Warren, M. S. 2012. The European butterfly indicator for grassland species 1990-2011. Report VS2012.019, De Vlinderstichting, Wageningen.

Vandepitte, K., Roldán-Ruiz, I., Jacquemyn, H., Honnay, O. 2010. Extremely low genotypic diversity and sexual reproduction in isolated populations of the self-incompatible lily-of-the-valley (*Convallaria majalis*) and the role of the local forest environment. Annals of Botany, 105: 769-76.

Vilà, M., Bartomeus, I., Dietzsch, A. C., Petanidou, T., Steffan-Dewenter, I., Stout, J. C., Tscheulin, T. 2009. Invasive plant integration into native plant-pollinator networks across Europe. Proceedings of the Royal Society B, Biological Sciences, 276: 3887-3893.

Vos, J. M., Keller, B., Isham, S. T., Kelso, S., Conti, E. 2012. Reproductive implications of herkogamy in homostylous primroses: variation during anthesis and reproductive assurance in alpine environments. Functional Ecology, 26: 854-865.

Waser, N. M., Ollerton, J. (eds.) 2006. Plant-pollinator interactions: from specialization to generalization. University of Chicago Press, Chicago, USA.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. Journal of Applied Ecology, 46: 187-193.

Whitehorn, P. R., O'Connor, S., Wackers, F. L., Goulson, D. 2012. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. Science 336: 351-352.

Willmer, P. 2011. Pollination and floral ecology. Princeton University Press. Princeton. USA.

Öckinger, E., Smith, H. G. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology, 44: 50-59.

Ødegaard, F. 2012. Faglig grunnlag for handlingsplan for rødknappsandbie *Andrena hattorfiana* og ildsandbie *Andrena marginata*. NINA Report, 759, 59 pp.

Ødegaard, F., Sverdrup-Thygeson, A., Hansen, L. O., Hanssen, O., Öberg, S. 2009. Kartlegging av invertebrater i fem hotspot-habitattyper. Nye norske arter og rødlistearter 2004-2008. NINA Report, 500, 102 pp.

Aarstad, P. A., Bjørlo, B. 2012. Bruk av plantevernmidler i jordbruket i 2011. Norway Statistics.

Appendices

Appendix 1 Scientific names and common names of plant species in figure 1.
Appendix 2 Pollinator species observed on flowering plant species sorted by order. Numbers refers to figure 1.

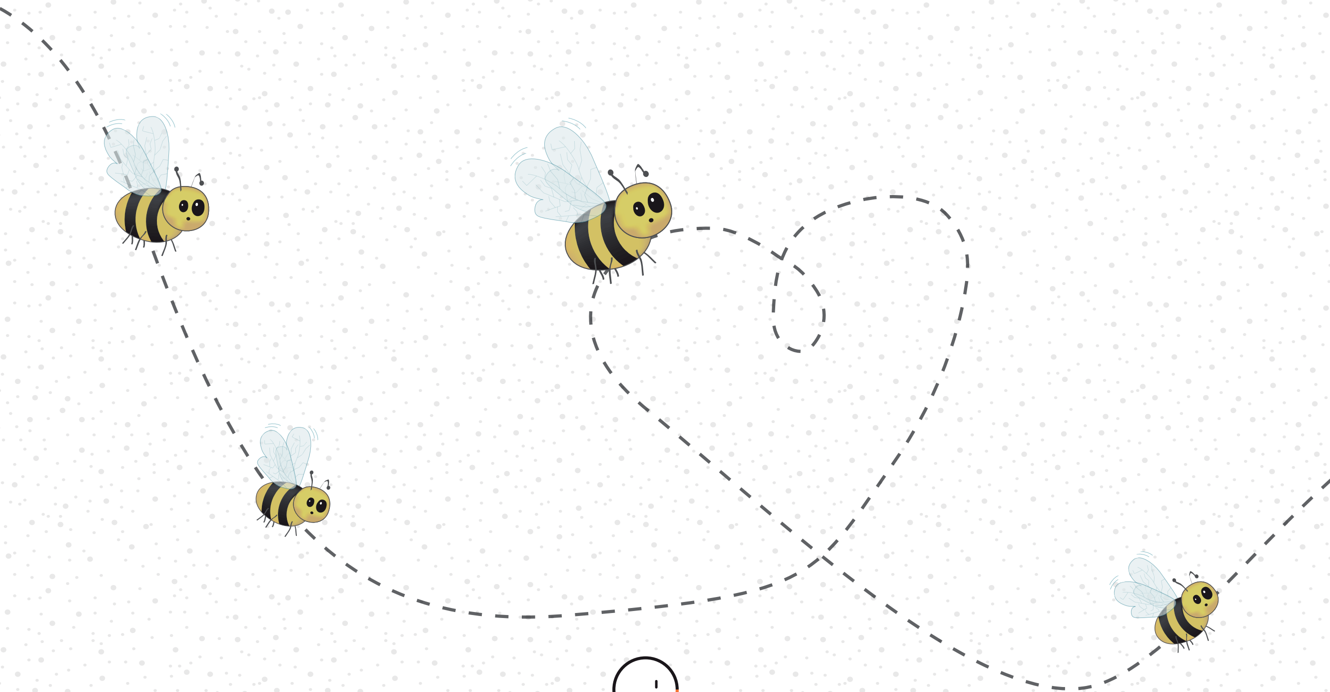
Appendix 1 Scientific names and common names of plant species in figure 1.

Scientific names	**Common names**
Melampyrum	Cow-wheat
Calluna vulgaris	Heather
Potentilla erecta	Tormentil
Chamaepericlymenum suecicum	Dwarf cornel
Rubus idaeus	Raspberry
Rubus chamaemorus	Cloudberry
Vaccinium vitis-idaea	Cowberry
Trientalis europaea	Chickweed-wintergreen
Solidago virgaurea	Goldenrod
Maianthemum bifolium	May lily
Vaccinium myrtillus	Bilberry
Orthilia secunda	Serrated wintergreen
Chamerion angustifolium	Rosebay willowherb
Vaccinium uliginosum	Bog bilberry
Linnaea borealis	Twinflower
Galeopsis tetrahit	Common hemp-nettle

Appendix 2 Pollinator species observed on flowering plant species sorted by order. Numbers refers to figure 1.

Nr	Order and species
	Coleoptera - beetles
1	*Chrysanthia viridissima*
2	*Epuraea aestiva*
3	*Byturus tomentosus*
4	*Dasytes niger*
5	*Anoplodera sanguinolenta*
7	*Chrysanthia geniculata*
8	*Malthodes fuscus*
9	*Meligethes denticulatus*
10	*Anaspis rufilabris*
11	*Anoplodera maculicornis*
12	*Anthaxia quadripunctata*
13	*Anthonomus rubi*
14	*Ligyrocoris silvestris*
15	*Lythraria salicariae*
16	*Meligethes aeneus*
17	*Rhagonycha atra*
18	*Trichius fasciatus*
	Diptera - true flies
19	*Thricops cunctans*
20	*Episyrphus balteatus*
21	*Rhamphomyia umbripennis*
22	*Thricops innocuus*
23	*Thricops semicinereus*
24	Tachinidae
25	Cecidomyiidae
26	*Parasyrphus lineolus*
27	*Melanostoma scalare*
28	*Phaonia angelicae*
29	*Phaonia consobrina*
30	Drosophilidae
31	*Syrphus ribesii*
32	Ceratopogonidae
33	*Rhamphomyia hybotina*
34	Empididae
35	*Syrphus torvus*
36	*Eupeodes corollae*
37	*Melanostoma* sp.
38	*Coenosia means*
39	*Phaonia meigeni*
40	*Sphaerophoria* sp.
41	*Chrysotoxum bicinctum*
42	*Platycheirus albimanus*
43	*Sericomyia silentis*
44	Simuliidae
45	Chironomidae
46	*Dasysyrphus pinastri*
47	Dolichopodidae
48	*Fannia rondanii*
49	Lauxaniidae
50	*Melanostoma mellinum*
51	*Thricops* sp.
52	*Hydrotaea militaris*
53	*Nematocera*
54	*Phaonia hybrida*
55	Phoridae
56	*Sepsis orthocnemis*
57	*Sphaerophoria taeniata*
58	*Volucella bombylans*
59	Chamaemyiidae
60	*Cheilosia longula*
61	Chloropidae
62	*Chrysotoxum fasciolatum*
63	*Fannia parva*
64	*Fannia postica*
65	*Haematobosca stimulans*
66	*Parasyrphus macularis*
67	*Parasyrphus vittiger*
68	*Pipiza quadrimaculata*
69	*Pipiza* sp.
70	*Platycheirus* sp.
71	*Sericomyia lappona*
72	*Sphegina clunipes*
73	*Volucella pellucens*
74	*Acalyptrate*
75	*Alliopsis billbergi*
76	*Alliopsis silvestris*
78	Anthomyiidae
79	Bibionidae
80	*Bicellaria* sp.
81	*Coenosia pulicaria*
82	*Dasysyrphus tricinctus*
83	*Didea alneti*
84	*Eristalis rupium*
85	*Eupeodes nielseni*
86	*Fannia umbrosa*
87	Heleomyzidae
88	*Helina ciliatocosta*
89	*Heterostylodes pratensis*
90	*Hilara interstincta*
91	*Hydrophoria lancifer*
92	*Hylemya nigrimana*
93	*Hylemya vagans*
94	*Lasiomma atricaudum*
95	Muscidae
96	*Paragus haemorrhous*
97	*Parasyrphus* sp.
98	*Phaonia alpicola*
99	Piophilidae
100	*Platycheirus holarcticus*
101	*Rhingia campestris*
102	*Sepsis punctum*
103	*Sphaerophoria batava*
104	*Sphaerophoria philantha*
105	*Sphaerophoria virgata*
106	*Syrphus vitripennis*
	Hemiptera - hemiptera
6	*Auchenorrhyncha*
107	Cicadidae
108	*Lygus punctatus*
109	Miridae
	Hymenoptera - ”wasps”
110	*Bombus pratorum*
111	*Bombus lucorum*
112	*Bombus pascuorum*
113	*Formica lemani*
114	*Bombus hypnorum*
115	*Apis mellifera*
116	*Psithyrus norvegicus*
117	*Myrmica ruginodis*
118	*Andrena*
119	*Bombus hortorum*
120	*Bombus lapidarius*
121	Chalcidoidea
122	*Formica* cf. *polyctena*
123	Braconidae
124	*Leptothorax acervorum*
125	Vespidae
126	*Bombus jonellus*
127	*Halictus*
128	*Formica* cf. *aquilonia*
129	*Formica* sp.
130	Ichneumonidae
131	*Psithyrus bohemicus*
	Lepidoptera - butterflies and moths
132	Micropterigidae
133	*Dyscia fagaria*
134	*Erebia ligea*
135	Geometridae
136	Lychenidae
137	Pyralidae

This report summarizes the state of knowledge in Norway concerning insect pollination. It explains what pollination is and the significance it has for plants and insects. It goes on to examine pollination as an ecosystem service and the consequences human pressures have on this complex interaction. The report identifies gaps in our knowledge about insect pollination in Norway and proposes measures to remedy them.



NORWEGIAN BIODIVERSITY
INFORMATION CENTRE

Published by:
Norwegian Biodiversity Information Centre
Phone: +47 73 59 21 45
E-mail: Postmottak@artsdatabanken.no
Web: www.biodiversity.no

ISBN 978-82-92838-36-5
9 788292 838365 >