Scandinavian Association of Pollination Ecology

SCAPE 2011

25th annual meeting

held at Vingstedcentret, Denmark

27 – 30 October 2011

Organizers: Jens M. Olesen, Yoko L. Dupont, Melanie Hagen, Bodil K. Ehlers, Claus Rasmussen

Programme Scape 2011

Thursday, 27th October

Dinner: **18:00**

Poster presentations: **19:30 –**

Friday, 28th October

Breakfast: **7:30 – 9:00 am**

Session 1: **9:00-10:30** **Chairperson: Jane Stout**

Anna Sofie Persson - Effects of landscape context on populations of bumblebees.

Yoko L. Dupont, Christian Damgaard, Vibeke Simonsen, Dennis Boll and Marianne Bruus Pedersen - Quantitative historical decline of bumblebees

Dara A. Stanley & Jane C. Stout - Bees and Biofuels: The effects of replacing conventional agriculture with bioenergy crops on pollinators at the field scale.

Beate Strandberg – Ecoserve: organic hay fields as resources for pollinators.

coffee break: **10:30 – 11:00**

Session2: **11:00 – 12:00** **Chairperson: Stein Joar Hegland**

Toke Thomas Høye - Shorter flowering season in a warmer Arctic

Claus Rasmussen - Climate change and pollination networks in Greenland

Nadine Prill, James Bullock & Roosa Leimu - How can fragmented plan t populations cope with climate change?

Lunch: **12:00-13:00**

Session3: 13:00 – 14:20 Chairperson: Bodil Ehlers

Marianne Bruus Pedersen – The toxicity of pesticides on different pollinators

Sarah Papiorek, Klaus Lunau - The sensory exclusion of non-pollinating bees in ornithophilous plant species and their ecological implications.

Amparo Lázaro, Rebekka Lundgren & Ørjan Totland (presenting author) - Experimental reduction of pollinator visitation modifies the interactions between plant species for pollination

Kristin Marie Lassen - Separation of pollinators in time using bags of cheesecloth (muslin) on *Parkia biglobosa* in Burkina Faso 2011 and 2012.

Short break: 14:20 - 14:40

Session 4: 14:40 – 15:40 Chairperson: Roosa Leimu

Méndez, M., García-Camacho, R., Giménez-Benavides, L., Milla, R., Santamaría, S. & Torices, R. - Contrasting pollination patterns in two high mountains of the Iberian Peninsula (S Europe).

Anna Jakobsson & Jon Ågren - Does pollination in road-verges decrease with distance to semi-natural grassland?

Sven Hanoteaux, Eva-Maria Hoch, Katja Tielbörger & Merav Seifan - Density and spatial distribution of an attractive species: effects on plant-pollinator interaction structure in grasslands.

Coffee break – 15:40 – 16:20

Session5: 16:20 – 17:20 Chairperson: Jens Mogens Olesen

Francisco G. Gonzálvez & Miguel A. Rodríguez-Gironés - Flower inspection and predation risk assessment during the foraging activity of solitary bees.

Navarro-Cano JA, Posledovich D, Toftegard T, Gotthard K, Wiklund C & Ehrlén J - Host plant selection traits and environment-mediated shifts in an olygophagic butterfly.

Eva Grøndahl & Bodil K. Ehlers - Three way interactions between *Thymus, Medicago* and *Sinorhizobium* - local adaptation to thyme oil

Dinner: 18:00

Open poster session: 19:30 – open end

Saturday, 29th October

Breakfast: 7:30 – 9:00 am

Session 6: 9:00-10:30 Chairperson: Martina Stang

Sam Tarrant & Jeff Ollerton (presenting author) - Stability and resilience of plant-pollinator networks tested using experimental removal of core floral resources.

Melanie Hagen – The spatio-temporal behavior of networks crossing habitat borders

Bo Dalsgaard, Else Magård, Jon Fjeldså, Ana M. Martín González, Carsten Rahbek, Jens M. Olesen, Jeff Ollerton, Ruben Alarcón, Andrea Cardoso Araujo, Peter A. Cotton, Carlos Lara, Caio Graco Machado, Ivan Sazima, Marlies Sazima, Allan Timmermann, Stella Watts, Brody Sandel, William J. Sutherland, & Jens-Christian Svenning - Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity.

Kristian Trøjelsgaard Nielsen – Macroecology of pollination networks

coffee break: 10:30 – 11:00

Session 7: **11:00 – 12:00** **Chairperson: Anders Nielsen**

Alfredo Valido, María C. Rodríguez-Rodríguez & Pedro Jordano - Impact of introduced honeybees on mutualistic networks in Teide National Park (Tenerife, Canary Islands).

Lea Gallop – Ecological supernetworks crossing borders

Peter Borgen - How to find governing questions for pollinations research based on management needs.

Lunch: **12:00-13:00**

Session 8: **13:00 – 14:30** **Chairperson: Renate Wesselingh**

Klaus Lunau - Ways out of the pollen dilemma.

Åsa Lankinen - Benefits of delayed stigma receptivity in *Collinsia heterophylla*, a mixed-mating species

Somme Laurent, Van Rossum Fabienne, Mayer Carolin, Leprince Nathalie, Jacquemart Anne-Laure - Pollen dispersal pattern assessment in four insect-pollinated bog species

Rocío Pérez-Barrales and Juan Arroyo - Flower phenotypic integration in *Narcissus* under contrasting pollinator arrays across the Mediterranean.

Coffee break: **14:30 – 15:00**

Field walk: **15:00 – 18:00**

25th Anniversary Dinner: **18:00**

!!!!!!!CHANGE TO WINTERTIME – ONE MORE HOUR TO SLEEP (OR PARTY)!!!!!!

Sunday, 30th October

Breakfast: 7:30 – 9:00 am

Session 9: 9:00 – 10:30 Chairperson: Jon Ågren

Nina Sletvold, Judith Trunschke, Carolina Wimmergren, Jon Ågren - Pollinator-mediated selection in *Gymnadenia conopsea*: separating the effects of diurnal and nocturnal pollinators

Karin Gross, Mimi Sun & Florian P. Schiestl - Pollinator-mediated selection on floral scent and morphology at different altitudes in the rewarding orchid *Gymnadenia odoratissima*

Amy L. Parachnowitsch, Robert A. Raguso & André Kessler - Floral attraction in *Penstemon digitalis*: display, scents, and colour.

Annette Kolb, Anna-Karin Borg-Karlson & Johan Ehrlén - Selection on plant visual traits and floral scent: effects via seed development and antagonistic pathways.

coffee break: 10:30 – 11:00

Session 10: 11:00 – 12:00 Chairperson: Johan Ehrlen

Richard Waterman - The effects of pollination on evolutionary and contemporary patterns of orchid diversity

Alexandra Ley & D.J. Harris - Flower morphological diversity in *Aframomum* – potential for adaptations to different pollinators as driving speciation agents.

Madjidian J.A, Smith H.G., Andersson S. and Lankinen Å. - Indirect and direct selection on mate choice.

Lunch: 12:00-13:00

Abstracts: Poster Session(alphabetical order)

Farming practices and pollination success
Georg Andersson, Henrik Smith, Maj Rundlöf

During the last century there has been a major intensification in agricultural landscapes and large declines in semi-natural habitats. This has a potential to affect not only biodiversity but also the ecosystem functions performed by species, such as pollination.
Studies of landscape effects on biodiversity most often focus on the spatial distribution and quality of habitats, but the time-scale is not equally well studied. How historical processes affects the configuration of biodiversity and ecosystem functions is of great importance to more efficiently set up management to prevent further losses. In Europe organic farming is one of the environmental schemes argued to benefit biodiversity (Bengtsson *et al.,* 2005), but effects have been shown to depend on landscape context (Rundloef *et al.,* 2007).
How ecosystem functions are affected by landscape context and management is not equally well studied. In this research project I study how organic farming, and the time since transition from conventional farming, affect the pollination function.
We used organic farms, situated in landscape with similar structure but with different time since transition from conventional to organic. A set of conventional farms were used as control. To examine the effects on pollination we set up experiments on strawberries in pots situated along the transects of the field borders.
The study showed significant effect on pollination quality of farming practice where strawberries on organic farms produced more full pollinated fruit. However the effect appeared to take place rapidly since there was no effect of time since transition.

Flower colours do not structure plant communities in temperate grasslands
Julia Binkenstein & H. Martin Schaefer

Flowers pollinated by insects and other animals depend on attractants like colours and scent to draw pollinators. Considering the colour diversity of a rich flowering grassland it seems obvious to hypothesise that floral colour divergence is non-random and of adaptive significance. Selective pressures may have favoured divergence of flower colours to promote flower constancy of pollinators. However, especially rare plants may profit from convergence on the flower colours of common species to avoid receiving only exploratory visits from pollinators. To assess whether the assemblage of flowering plants is based on patterns of divergence or convergence in flower colours of rare and common plants, we collected data on blossom cover and flower reflectance spectra of flowering herbs in three different sites in Germany. We analysed reflectance data of colours as they are perceived by bees and studied the floral colour composition of 54 plant communities based upon flower colour loci of each plant species in bee colour space. First results revealed that the occurrence of rare plant species is not determined by divergence or convergence on sympatric and simultaneously flowering common species. Thus, in contrast to previous studies our results suggest that plant communities of temperate grasslands are not structured by a strong selective pressure on the flower colour of rare plants to secure pollination in the presence of common plants.

Mitigating decline in wild plant pollination in agricultural landscapes
Lina Herbertsson

is the title of my PhD project, that is just in the starting up phase. The focus will be on the importance of pollinators for wild plant pollination in farmed landscapes and how to mitigate the declines of pollinators and wild plant pollination. The project will determine if there is parallel variation in pollinator communities and pollination success of focal plant species, and which influence mass-occurring species, e.g. honey bees and oilseed rape, have on pollination networks and on reproductive success in insect pollinated wild plants.

Herbivore-induced changes in floral traits: Ecological costs or benefits?
Mathias Hoffmeister & Robert R. Junker

Herbivore-induced defense reactions in vegetative plant parts have been intensively studied, but whether herbivory similarly affects reproductive parts has rarely been considered. Systemic wound responses are mediated via signaling molecules like jasmonates which also play important roles in flower development. Potential changes in floral traits in response to elevated levels of endogenous jasmonates, may alter pollinator behaviour with consequences for plants' reproductive success. We tested whether herbivory by *Aphis fabae* on *Vicia faba* induces changes in floral scent and how this affects the behaviour of *Bombus terrestris.* Headspace bouquets of pairs of infested and uninfested plants were directed into a Y-shaped arena of an olfactometer and bumblebees' decisions towards these olfactory stimuli were recorded. Afterwards sampled volatiles were analyzed by GC/MS. Scent bouquets of infested and uninfested plants pairs differed strongly, and bumblebees showed a significant preference for uninfested plants. We further tracked changes in the size of the melanin spot in the otherwise white petal after jasmonic acid (JA) treatment of leaves. Spot sizes were evaluated prior to and after the treatments from subsequently emerged flowers of the same plants. In JA-treated plants spot sizes were stronger increased than in control plants. Our findings suggest that herbivore-induced changes in floral traits may lead to reduced pollinator-visits with potential negative effects on the reproductive success of the plants. The benefits of induced defenses against herbivores may thus also impose ecological costs via an altered appearance of the flowers.

Parallel ecotype differentiation in the hemi-parasitic plant *Rhinanthus serotinus*?
Anneli Jonstrup, Stefan Andersson and Mikael Hedrén

Ecotypic variation has been described for hundreds of species, but yet little is known about the selective mechanisms underlying the variation. For instance, it’s thought that morphologically similar ecotypes can arise repeatedly if populations are subjected to similar selective regimes. Nevertheless, only a few studies have addressed the question and most of them have targeted animals. The focus of this project is to test the hypothesis using the plant *Rhinanthus serotinus* as study organism.

Rhinanthus serotinus is an annual hemi-parasitic plant, that shows a high level of ecotypic variation. To start with, I focus on two specialized forms that occur in Sweden: 1) an early-flowering unbranched form that probably reflects adaptation to mowing, and 2) an unbranched late-flowering form that could reflect adaptation to an environment influenced by cold upwelling water in calcareous fens. I use a combination of molecular markers and extensive common garden experiments to evaluate whether each of these ecotypes has evolved from the ancestral highly-branched form on recurrent occasions. The overall aim of the study is to increase the understanding of a significant portion of the evolutionary diversity, i.e. the occurrence of specialized, and in many cases unique, ecotypes within widespread species.

Coevolution and conservation: local adaptation and inbreeding in a plant-herbivore-parasitoid interaction

Aino Kalske, Pia Mutikainen, Anne Muola, Liisa Laukkanen, Roosa Leimu

Habitat fragmentation is one of the major factors responsible for the current extinction crises. Fragmentation reduces population sizes and increases their distances. As a consequence, genetic variation decreases within populations and genetic differentiation increases among populations. Reduced genetic variation together with increased inbreeding often lead to reduced fitness in small populations. It is not well known how these fragmentation effects influence species interactions, such as those between plants and herbivores. The geographic mosaic theory of co-evolution provides an ideal framework to examine species interactions in fragmented landscapes. This theory postulates that co-evolution (reciprocal evolution between interacting species) is the major force in the organization of biological communities and of biodiversity. Therefore, if we want to understand the effects of fragmentation on biodiversity, examining fragmentation effects on the evolution of interacting species is of fundamental importance. We investigate how the effects of inbreeding, levels and distribution of genetic variation, and third trophic-level interactions influence plant-herbivore co-evolution. We focus on local adaptation in these antagonistic trophic interactions, because ongoing local adaptations can be considered an essential starting point for co-evolutionary dynamics. Our study system consists of the long-lived perennial herb *Vincetoxicum hirundinaria* (Asclepiadaceae) and its specialist herbivore, the folivorous moth *Abrostola asclepiadis* (Lepidoptera) and its parasitoids. We address several specific questions related to the impact of inbreeding on species interactions and their evolution. Our approach combines conservation genetics and co-evolutionary theory and provides a novel platform on which to investigate the effects of fragmentation on biodiversity.

Nectar robbery influences pollinator behaviour and pollen transport – experimental study on *Aconitum napellus* spp. *lusitanicum*

Carolin Mayer, Charles Dehon, Olivier Naveau, Anne-Laure Jacquemart

It has been thought that nectar robbery is detrimental for a flower and its reproductive success. However, evidence is rising that even floral parasites sometimes contribute to pollination or change the behaviour of actual pollinators which increases the chance of cross pollination (Maloof & Inouye 2000). A species that could profit from higher amounts of outcross pollen is *Aconitum napellus* spp. *lusitanicum* (Ranunculaceae), a species suffering from inbreeding depression which has been reported to be pollinated but also robbed mainly by bumble bees (Le Cadre et al. 2008).

We tested whether simulated nectar robbery would influence flower visitor behaviour and the distance and amount of possible pollen transport. We set up experimental patches of five plants each where about 50% of the flowers were: 1) artificially robbed 2) protected against robbery 3) left untreated. Preliminary results show that bumble bees (*Bombus pascuorum*) spent less time on artificially robbed flowers.

In a second experiment, we marked anthers of flowers that had been artificially robbed or left untreated (control) with fluorescent dye and collected the stigmas of flowers along a transect the day after. The proportion of stigmas with dye as well as the abundance of dye declined much quicker with distance for the robbed transect (less than 70% at 10 m compared to still 100 % at 35 m and high dye abundance with > 100 particles only up to 5 m compared to 13 m) indicating that flower visitors indeed left the unrewarding patch quicker and flew farther.

Le Cadre S, Tully T, Mazer SJ, Ferdy J-B, Moret J, Machon N (2008) Allee effects within small populations of *Aconitum napellus* ssp. *lusitanicum*, a protected subspecies in northern France. The New Phytologist 179:1171-1182.
Maloof JE, Inouye DW (2000) Are nectar robbers cheaters or mutualists? Ecology 81:2651-2661.

Diversity relationships for plant & pollinator mutualists in grasslands: an empirical approach.

Sarah E. Mullen and Jane C. Stout

Documented global declines in pollinators have led to concerns about the provision of pollination services to both crops and wild plant species. Recent demonstrations of parallel declines in plants and their pollinator communities, using historical data, have highlighted the mutual dependence of both groups and suggest a causal link in plant and pollinator decline. Demonstrating causality has been difficult given the considerable impracticalities involved. Testing for relationships between plant and pollinator diversity, however, can shed light on the degree of dependence of both guilds on species diversity in the other and can help predict the potential responses of either guild to such losses. We tested for relationships between plant and flower diversity and pollinator diversity in 20 semi-natural grasslands in the Irish midlands. Preliminary results suggest that a relationship exists between flowering plant species richness

and flowering plant abundance and a) pollinator taxonomic group richness and b) pollinator species richness at a site. This suggests some degree of interdependence between pollinator and flowering plant diversity. The findings highlight the potential importance of flowering plant diversity for maintaining functionally diverse pollinator communities. Conservation efforts could benefit from focusing on the conservation of functional groups in order to maintain complementarity and promote diversity in other groups.

Latitudinal variation in thermal reaction norms of eclosion time in Swedish populations of the Orange-tip butterfly *Anthocharis cardamines*

Posledovich D, Toftegaard T, Navarro-Cano JA, Ehrlén J, Wiklund C, Gotthard K

Climate change can influence the strength of species interactions by altering the phenology of interacting species, and thus leading to phenological asynchrony between herbivores and their host plants. Temperature is one of the main climatic factors that determines the rate of developmet and growth as well as survivorship of both herbivorous insects and their host plants. The aim of our study was to investigate latitudinal variation in thermal reaction norms of post-diapause development rates in the Orange-tip butterfly (*Anthocharis cardamines*) along a ~ 1000 km south-north latitudinal gradient in Sweden. These results will later on be compared to thermal reaction norms of plant development of several host plant species from the same locations along the gradient. We recorded the timing of the butterflies' eclosion in four different temperature treatments. We found that the difference in development rate between the populations was greatest in the warmest treatment and smallest in the coldest one. In addition, we found that the population from the south developed faster than the central population, which in turn developed faster the northern population. This shows that there is a co-gradient pattern in thermal norms of reaction in the Orange-tip butterfly in Scandinavia. To investigate the effects of temperature on the phenological matching between this butterfly and its host-plants these results will be supplemented with the results from the host plant phenological state experiment.

Plant-pollinator interactions in an alpine community of Picos de Europa (in Spain)

Silvia Santamaría, Marcos Méndez, Raúl García-Camacho, Luis Giménez-Benavides, Rubén Milla & Rubén Torices

We described the structure of an alpine plant-pollinator network located at El Jou de Los Cabrones (2050 m; Picos de Europa National Park, N Spain).
We found a high proportion of high mountain plant and insect specialists and 8,75% endemic plant species. Small flies were the dominant pollinators. Nevertheless, a Correspondence Analysis revealed four sets of plant species visited by *Macroglossum stellatarum*, *Apis mellifera* and *Bombus* spp., big flies and wasps, or ants and beetles, respectively. This network showed a high number of plant species (77) and relatively high connectance (9.98 %) and connectivity (4). The network was significantly nested and was organized into five modules. Added to this, three

network roles were identified: peripheral nodes (65.63% of species), connector nodes (28.75%) and network hub nodes (5.63%). We did not identify any module hub node.

Floral display increases indirect costs in two pairs of sympatric large-flowered Mediterranean *Cistus* species: a petal removal experiment

Alberto L. Teixido, Marcos Méndez

Larger floral displays receive more pollinator visits, but investment in attraction may also involve indirect costs in terms of fruit and seed production, especially in hot and dry ecosystems. In this context, smaller displays could play an important role to buffering such costs. We conducted an experimental approach in two pairs of sympatric *Cistus* species, a large-flowered Mediterranean genera, and each pair differing in floral display. On every individual we conducted two treatments, flowers with removed petals (R flowers) and control non-manipulated flowers (C flowers), and next we hand-pollinated. We also recorded individual mean flower size and number of flowers. Then we compared fruit and seed production between treatments, individual within-populations and coupled-species. For all species, fruit set significantly decreased in R flowers and was significantly negatively correlated with flower size. In addition, both larger-flowered and with higher number of open flowers species tended to lose more fruits and to have a higher correlation between relative loss and floral display. For seed number, differences did not show such evidence. Overall, however, correlation between relative loss and floral display followed the same trend that fruit set did. Our results support the notion that investment in attraction implies indirect costs and go further, reporting higher costs both in larger-flowered individuals and species and/or with higher number of open flowers. Mediterranean stressful conditions may limit flower size and exert relevant selective pressures towards smaller corollas, maintaining intraspecific variation. Likewise, for sympatric sister species differing in floral display, higher attraction involves higher costs.

Consequences of invasion by a mass flowering plant on native plant-pollinator networks: a quantitative approach

Erin Jo Tiedeken, Jane C. Stout

Alien invasive species tend to occur at high abundances in exotic habitats, thus flowering invasive plant species that are visited by native pollinators can facilitate or disrupt native flower visitation and fertilization. These species have been shown to integrate into native plant-pollinator networks and significantly affect network structure. The copious rewards offered specifically by a mass-flowering invasive species could cause it to have different and potentially severe impacts on native plant pollinator community structure; network structure may change significantly over the flowering season when the rewards offered by a mass flowering invasive are no longer available. We used two sets of highly resolved plant-pollinator networks from woodland communities in southeast Ireland invaded by *Rhododendron ponticum* (Ericaceae) to investigate the impacts of a mass flowering alien invasive plant on network structure.

Quantitative connectance significantly increased at our sites after conclusion of *R. ponticum* flowering. There were no significant differences in interaction evenness, interaction strength asymmetry, or generality when *Rhododendron ponticum* was flowering vs. when it finished and was no longer a member of the community. We found evidence that at high levels of invasion a mass flowering species appears to decrease connectance and possibly robustness of plant pollinator communities but that communities can become more generalized after *R. ponticum* flowering concludes. Communities appear to be tolerant to the temporal variation in floral abundance over the flowering season and well able to adjust to changes in levels of floral resources.

Do herbivore-induced changes in floral volatiles impact on pollinator behaviour?
Judith Trunschke and Florian Schiestl

Plants live in association with diverse mutualistic (pollinators) and antagonistic (herbivores) partners, and volatile organic compounds provide an important basis for plant-insect communication. For example, floral scent plays a key role for pollinator attraction, whereas herbivory often provokes the production of repellent compounds. This systemic response might also be reflected in floral scents, putting plants into a so-called signalling dilemma between defence and attraction. Despite their apparent interrelation only little is known about the effects of herbivory on pollinators mediated by floral scent. Within this project we will investigate herbivore-induced changes in floral volatiles (HICFV) and consequences for plant-pollinator interactions in the specialized *Silene latifolia – Hadena bicruris* and the generalized *Brassica rapa – Apis mellifera* systems. Specifically we ask the following questions: 1) How do floral volatiles change after herbivore attack? 2) How do HICVF affect pollinator attractiveness and behaviour? 3) Do invasive herbivores differentially impact pollinator selection on HICFV? To address these questions we will induce a standardized damage by native and invasive root and shoot feeding larvae. Consecutively emitted floral volatiles will be analysed using gas chromatography – mass spectrometry (GC-MS), and alterations in pollinator preferences will be assessed in behavioural assays. We expect an increase of defence volatile compounds and subsequent discrimination by pollinators against damaged plants, whereby local pollinators should be less affected by HICFV evoked by native herbivores compared to invasive herbivores. This study will provide novel insights into the evolution of floral scent under the perspective of its functional trade-off between defence and attraction.

The bigger the better? Pollinators' efficiency in a red-listed Fritillary (*Fritillaria meleagris* L., Liliaceae)

Marcin ZYCH, Małgorzata STPICZYŃSKA, Katarzyna ROGUZ, Krystyna JĘDRZEJEWSKA-SZMEK & Jan GOLDSTEIN

Fritillary (*Fritillaria meleagris* L., Liliaceae) is a critically endangered plant in the Polish flora, red-listed in most of the European countries of its range. In spite of the literature data where it is usually described as protogynous and out-crossed species pollinated by *Bombus terrestris* L. and (perhaps) other bees, long-term field studies reveal it can produce self-seeds and there is no evidence of floral dichogamy. Although in the natural population the largest *Fritillaria* pollen loads are carried by solitary bees, based on pollen loads, visitation frequency and seasonal abundance it is estimated that the key pollinators are queen bumblebees. As visitation frequency in natural population is low, there is, however, no direct evidence of their importance, especially regarding pollen pick-up and deposition. Our *ex-situ* experiment conducted in an artificial population established in the botanic garden showed that although there are no significant differences in pollen loads deposited on virgin stigmas between key flower visitor groups (solitary bees vs. bumblebees) during a single visit, the latter export very little quantity of pollen (no significant differences when compared to unvisited flowers), whereas after a visit by solitary bees approx. 40% of all available pollen is removed from anthers. We conclude that although both visitor groups can effectively pollinate the flowers, the costs of pollination service of solitary bees are much higher for the plant.

Abstracts: Talks

Friday, 28th October

Session 1: Friday 9:00-10:30 Chairperson: Jane Stout

Session 1: Friday 9:00-10:30
Effects of Landscape context on populations of bumblebees
Anna Sofie Persson

To investigate recent declines in bumblebee populations, I carried out landscape analyses, made field studies of bumblebees (*Bombus spp.*), flowering plants and pollination in an agricultural region in southernmost Sweden. Studies were carried out in landscapes of contrasting agricultural intensity and land-cover configuration; "simple" landscapes highly dominated by large crop fields, and "complex" with mixed farming, grasslands and smaller fields.

Factor Analysis of land-cover and measures of agricultural practice showed that intensity is not to be equated with landscape complexity. A relatively complex landscape could thus provide high yields from farming, while retaining small non-crop elements. This is promising for persistence of farmland biodiversity.

Total number of bumblebees was ca. 30 times lower in simple compared to complex landscapes in July. However, numbers did not differ significantly in June, despite ca. 30 times more of flowering plants in complex landscapes. This may be explained by the larger area of oilseed rape grown in simple landscapes, which may aid early colony growth. Effects of landscape context on bumblebees was modified by colony-based, ecological and life-history traits. Species with early emerging queens, large colonies, under-ground nests or short colony reproductive cycle, produced equal numbers of male offspring in both simple and complex landscapes. However, all species produced smaller workers in simple landscapes. This may be caused by a shortage of food, which hampers larval growth and adult size. It may also be an adaptive strategy to produce more but smaller workers under food stress. Individual-based traits of workers: thorax width and proboscis length modified foraging habitat preferences. Likely because composition of flowers differed among habitats and therefore also differed in value depending on bumblebee species.

Higher abundance and richness of wild bees were found near domestic gardens in simple landscapes, compared to 140m further away. Also, seed set of *Campanula persicifolia* was higher nearer a garden. Gardens may thus act as refuges for wild bees, constitute sources of pollinators to surrounding habitats and benefit pollination in these landscapes. However, pollination of wild plants may already be hampered in simple landscapes, since seed set of *C. persicifolia* was lower already at 140m from a garden.

Measures to enhance bumblebee populations and pollination in farmland regions should focus on increasing landscape complexity by restoring and recreating flower-rich non-crop habitats. Importantly, this must be implemented over whole regions and match the spatial scales

and phenology at which declining species operate and flowering plants must also meet the preferences of these species.

Session 1: Friday 9:00-10:30

Quantitative historical decline of bumblebees

Yoko L. Dupont, Christian Damgaard, Vibeke Simonsen, Dennis Boll and Marianne Bruus

Pollinator decline due to environmental changes is a major concern for maintenance of crop production in addition to communities of wild flowers. However, despite widespread perceptions among both scientists and the public regarding recent pollinator decline, few studies have documented historical changes in pollinator assemblages. To date, most evidence is "qualitative", i.e. based on red list assessments and museum collections documenting change in species composition, but not abundance. In the current study, we take advantage of a detailed historical study of bumblebees from the 1930's (Skovgaard 1936 *Det Kongelige Danske Videnskabernes Selskabs Skrifter*), which is a remarkably detailed account of bumblebees in red clover fields in Denmark. We repeated the same sampling protocol at nearly the same localities at present, hence setting up a "historical experiment". We clearly document declines of long-tongued bumblebees in both abundance (bees/m^2) and species richness, while populations of short-tongued bumblebees were little affected. Why some species of bumblebees, but not others, has declined historically has been discussed among bumblebee ecologists. Our own (preliminary) lines of investigation highlight the differential use of habitat (land use) types by different bumblebee species, in addition to the influence of pesticides.

Session 1: Friday 9:00-10:30

Bees and Biofuels: The effects of replacing conventional agriculture with bioenergy crops on pollinators at the field scale

Dara A. Stanley & Jane C. Stout

Pollinators and the services they provide are increasingly threatened by many human activities including land use change and agricultural intensification. A major shift in agricultural land use is beginning with the widespread promotion and cultivation of bioenergy crops as an alternative fuel source to combat climate change, with potentially major implications for biodiversity. This study focuses on the impact of two bioenergy crops – the annual, high-input, mass-flowering winter oilseed rape (*Brassica napus*) and perennial, low-input, non-flowering *Miscanthus giganteus*, on pollinators and pollination. We use diversity and abundance measures and pollinator community analyses to examine the impacts of these contrasting energy crops, compared to the crops they replaced, at the community level in Ireland. Pan traps, transect walks and trap nests were all used to adequately sample the pollinator communities in all sites during summer 2009. Observations of nest searching bumblebees were also carried out in spring 2010. While different pollinator groups respond differently, differences were found between energy crops and the crops they replace in a heterogeneous agricultural landscape at both the species and community level. The findings are discussed in the context of ongoing agricultural impacts on

pollination systems, with implications for farmland management to combat pollinator decline. This project is part of the SIMBIOSYS project which is focusing on key human enterprises in Ireland, and their affects on associated ecosystem services (www.simbiosys.ie).

Session 1: Friday 9:00-10:30
EcoServe – organic hay fields as resources for pollinators
Beate Strandberg

Organic hay fields potentially sustain a diverse pollinator fauna. In the recently started three-year project EcoServe (Ecosystem Functions and Services of Biodiversity in Grasslands) we investigate the potential improvements for wild pollinators by establishment of organic hay fields with a large proportion of selected herbs beneficial for pollinators. We test the importance of the floristic composition and diversity and the influence of cutting regime (number and timing of hay cuttings) for pollinator diversity.

Session 2: Friday 11:00 – 12:00 Chairperson: Stein Joar Hegland

Session2: Friday 11:00 – 12:00
Shorter flowering season in a warmer Arctic
Toke Thomas Høye

Earlier flowering has recently been reported across biomes, and such shifts under climate change may potentially uncouple the phenology of plants and pollinators. Arctic phenological responses have been shown to outpace responses from lower latitudes, and this could render plant-pollinator interactions particularly vulnerable to phenological uncoupling here. Also, flowering phenology is mostly studied at the local scale although pollinators typically operate at the landscape scale. Here, we investigate variation in the duration of flowering at local and landscape scale in six common plant species during 1996–2009 at Zackenberg in high-arctic Greenland. Duration of flowering was related negatively to temperature during flowering at both spatial scales in individual species and across all species. At the landscape scale, duration of flowering was also related positively to timing of snowmelt in five of six species as well as across species. In three species there was an interaction between temperature and snowmelt. Community-wide duration of flowering declined significantly during the study period while mean summer temperatures increased significantly and timing of snowmelt advanced. We conclude that recent warming has resulted in shorter flowering seasons at Zackenberg which could increase the risk of flowering not occurring when pollinators have their peak resource demand.

Session2: Friday 11:00 – 12:00

Climate change and pollination networks in Greenland

Claus Rasmussen

Climate change does not only affect single species in isolation but entire ecological networks, most often consisting of hundreds of species and their interactions. Since climate changes are strongest in the Arctic we expect to see the most severe natural disturbances here. Fourteen years ago (1996-1997), a 2-year study of an entire network of 31 plant species interacting with 76 pollinating animal species at Zackenberg, NE Greenland was conducted. Since then climate change has caused strong responses from both plants and animals. The previous study gives us an un-foreseen but unique opportunity to analyze climatically induced changes at network level by repeating (2010-2011) the previous study and to perform a comparative analysis of these network data, spanning a 14-year period in which the arctic environment has experienced strong climatic changes. The insight gained may tell us how highly complex natural systems react to climate change globally now and in the future. Field work is now completed and most identifications done for comparing data. Actual comparative analyses is at its initial stage.
Nadine Prill, James Bullock & Roosa Leimu - How can fragmented plan t populations cope with climate change?

Session2: Friday 11:00 – 12:00

How can fragmented plant populations cope with climate change?

Nadine Prill, James Bullock & Roosa Leimu

Human activities impose substantial impacts on the environment. There is increasing evidence that global change drivers, such as climate change and habitat fragmentation, cause major threats to biodiversity and ecosystem functioning. Habitat fragmentation reduces population size, which can lead to the loss of genetic diversity and increasing levels of inbreeding. The isolation of fragmented populations reduces gene flow amongst them, leading to increasing genetic differentiation of isolated populations over time. The genetic consequences of habitat fragmentation are, therefore, likely to compromise the ability of plants to respond to environmental changes, such as those exerted by climate change. However, the combined effects of habitat fragmentation and climate change on plants and their interactions with other organisms have remained unclear. In a common garden experiment with 96 inbred and outbred families from six populations of *Brassica nigra*, we studied the interactive effects of drought, herbivory and experimental inbreeding as well as within- and between-population outbreeding. Key functional plant traits were measured, including height, leaf mass per unit area, biomass, fitness parameters and herbivore damage. In addition, we investigated the impacts of inbreeding and outbreeding on phenotypic plasticity, one of the ways in which plants can cope with changing environments. Finally, we studied whether inbreeding and outbreeding can constrain the evolution of defence against multiple herbivores. In this talk, I will present the first findings of this experiment.

Session3: Friday 13:00 – 14:20 Chairperson: Bodil Ehlers

Session3: Friday 13:00 – 14:20
Testing pesticide effects on pollinators
Marianne Bruus Pedersen

Pesticide regulations take into account possible effects on honeybees, but not necessarily other pollinators. Since other pollinators may be active at other times than honeybees and some species spend their larval stages in agricultural crops, pesticide exposure may differ from that of honeybees. Furthermore, physiological differences may result in different sensitivity to pesticides. In two projects we investigate the toxicity of selected pesticides to mason bees (*Osmia rufa*), syrphids (*Episyrphus balteatus*) and butterflies (*Pieris brassicae* and *Pieris napi*). This involves establishment of synchronized cultures of the insects and supply of their food sources, adaptation of application techniques and development of testing systems.

Session3: Friday 13:00 – 14:20
The sensory exclusion of non-pollinating bees in ornithophilous plant species and their ecological implications.
Sarah Papiorek, Klaus Lunau

Hummingbird-pollinated plants suffer from nectar robbing or nectar thieving by non-pollinating agents, especially large bees. To prevent negative effects resulting in reduced reproductive success, flowers pollinated by hummingbirds exhibit distinct characteristics not only adapted to their pollen vector, but also to exclude bees as visitors of these flowers.
Sensory exclusion of flowers pollinated by birds is conceivable, since trichromatic bees and tetrachromatic birds exhibit not only disparate photoreceptor sensitivity functions but also disparate preferences for color features, i. e. hue, saturation and brightness. We show that both red and white hummingbird-pollinated flowers differ from bee-pollinated flowers in their reflection properties. In addition we substantiate with preference tests involving hummingbirds and neotropical orchid bees foraging at artificial red and white flowers with deviant reflection properties in the UV waveband the sensory exclusion of bees through hummingbird-pollinated flowers by color. The underlying color preference in bees might provide hummingbirds with an ecological private niche consisting of flower colors that are non-attractive for bees.
Furthermore, we studied mechanical exclusion of bees through hummingbird-pollinated flowers. Due to preliminary results, conical cell structures of the epidermal surface of flower petals, which are common in the majority of angiosperms, are absent in hummingbird-pollinated flowers. The impact of conical epidermal cell structure on color and grip for bees are discussed.

Session3: Friday 13:00 – 14:20

Experimental reduction of pollinator visitation modifies the interactions between plant species for pollination

Amparo Lázaro, Rebekka Lundgren and Ørjan Totland (presenting author)

1. The interactions between plant species for pollination depend on the relative abundance of both pollinators and plants in the community. Therefore, a reduction in pollinators, as expected under the current pollinator loss scenario, may affect the way the plant species interact for pollination, influencing their relative attractiveness and modifying the associations and densities at which individual fitness is maximized.
2. We experimentally reduced pollinator visitation in two communities of southern Norway to test whether the strength and direction of the intra- and inter-specific relationships for pollination were modified by the experimental change in pollinator abundance. We measured visitation and fertilization rates for three plant species both inside 30 dome-shaped cages partially covered with fishnet (Experimental plots) and in 30 Control plots in each community. These variables were later related to the local conspecific density, the density of the three most abundant neighbours, and plant diversity.
3. Our experiment influenced both the intra and inter-specific interactions for pollination in all the study species. The relationships were often non-linear, showing either saturating or bell-shaped curves. A slight tendency towards increased competitive interactions inside the Experimental plots was detected for fertilization rate in one community, but the main difference between Control and Experimental plots was the intensity of the interactions. Relationships were always stronger inside the experimental plots for fertilization rate, suggesting that the neighbours have a stronger role on the fitness of individual plants when pollinators are scarce. However, the relationships were not always stronger inside the Experimental plots when the visitation rates were analyzed, which we attribute to differences among species in natural visitation frequency.
4. The reduction in the availability of pollinators modifies the interactions between plants for pollination in a complex way. The combined effect of plant and pollinator abundances on the interactions for pollination deserves future exploration, because it could be the key to understand the structure of the interactions at the community level, its spatio-temporal variation, and its potential modifications under a pollinator loss scenario.

Session3: Friday 13:00 – 14:20

Separation of pollinators in time using bags of cheesecloth (muslin) on *Parkia biglobosa* in Burkina Faso 2011 and 2012.

Kristin Marie Lassen

An experiment based on the separation of pollinators in time using bags on *P. biglobosa* in 2011 revealed some difficulties. The talk will explain the employed setup and the experienced difficulties in details. I will also mention the results from an experiment in The Gambia in 2003, which was based on separation of pollinators due to size and not time. I hope that the discussions at SCAPE will help me in adjusting the setup of experiments for 2012.

The greatest difficulty was that the bats, which are the main pollinators during the night, left the trees at the same time as the honey bees arrived in the early morning. Hence it was

difficult in a short time to protect flowers pollinated by bats from the bees, and at the same time unbag flowers protected from the bats giving access to the bees. Another problem was to find the capitula which had been open during night and later during early morning should be enclosed by a bag. The honey bees arrive between 05:30 and 06:00 when it is still dark and difficult to see the labels attached to the peduncles of the flowers. Since some of the trees have flowers fertile for more than one night the ones pollinated early in the morning should be enclosed by the same bags about one hour later. The design of the bags is important in order to avoid the material to touch the flowers. However, the present design is both laborious and inflexible.

Session 4: Friday 14:40 – 15:40 Chairperson: Roosa Leimu

Session 4: Friday 14:40 – 15:40

Contrasting pollination patterns in two high mountains of the Iberian Peninsula (S Europe)

Méndez, M.; García-Camacho, R.; Giménez-Benavides, L.; Milla, R.; Santamaría, S.; Torices, R.

Pollination patterns at a community scale have been explored for a limited set of high mountain systems. Flies are considered to be the most frequent pollinators in these systems. However, data on Mediterranean mountains is mostly lacking. We conducted pollination interaction observations in two contrasting mountain systems in the Iberian Peninsula: at 2050 m a.s.l. in Picos de Europa, a mountain of Atlantic climate influence in N Spain, and at 2850 m a.s.l. in Sierra Nevada, a mountain of Mediterranean climate influence in S Spain. Flies were predominant visitors (ca. 70% of visits) in Picos de Europa. By contrast, in Sierra Nevada, flies were common visitors but a high percentage of floral visits was carried out by two ant species and one species of bumblebee. Compared to Picos de Europa, Sierra Nevada was also characterized by a much lower relative importance of syrphid flies (lower amount of species and visits). It is striking that the diversity of bumblebees was much higher in Picos de Europa (12 spp.) than in Sierra Nevada (4 spp.), while their importance as pollinators was lower.

Session 4: Friday 14:40 – 15:40

Does pollination in road-verges decrease with distance to semi-natural grassland?

Anna Jakobsson and Jon Ågren

Road-verges harbour many grassland plant species and could be an important alternative habitat to traditionally managed semi-natural grasslands. But do herbs in road verges receive effective pollination services? Small fragments of grasslands may not provide enough nectar or pollen to support large pollinator populations, and may rely on dispersal of pollinators from larger grassland areas. If so, pollinator visits and seed production in road-verges would decline with distance to semi-natural grasslands. However, such a relationship could depend on qualities of the surrounding landscape. In 2010 the effects of distance to semi-natural grasslands on seed production and pollinator visits were investigated for three self-incompatible species; *Armeria maritima*, *Lotus corniculatus* and *Lychnis viscaria*. In order to reduce genetic and nutrient effects on seed production, plants were raised from a common seed source in pots with standardized

soil. Stations with potted plants were placed in road-verges at five different distances, 0, 100, 200, 400 and 800 m from a semi-natural grassland. Three such transects were made in each of two landscape types, one with high intensive farming and few natural habitats and one with low intensive farming. All species showed decreased seed production with increased distance to grasslands and for two species there were a stronger negative effect of distance in the intensively farmed landscape. The observation data was not that straightforward, but supports the seed production data to some degree.

Session 4: Friday 14:40 – 15:40

Density and spatial distribution of an attractive species: effects on plant-pollinator interaction structure in grasslands.

Sven Hanoteaux, Eva-Maria Hoch, Katja Tielbörger & Merav Seifan

A majority of plant species in grasslands are dependent on insects for their pollination. The major pollinator functional groups are known to be polylectic. As such, the reproductive success of grasslands species might be affected, not only by the plant species' own traits but also by the presence and identity of its neighbors. Driven by the pollinator's abundance and preferences, the pollination success of grassland species is likely to be affected by the abundance and spatial distribution of attractive plant species. In order to test for these potential effects, we constructed a field experiment in which *Centaurea cyanus* was introduced in grasslands at two density levels and using two different spatial distributions, aiming at investigating its effects on the plant pollinator interaction structure in two grasslands of the Swabian Alb (Germany). By comparing different network metrics (at the network and species level) among treatments, we discuss the potential implications of the introduction of attractive species in European grasslands such as shifts in competition and changes in recorded specialization indices.

Session5: Friday 16:20 – 17:20 Chairperson: Jens Mogens Olesen

Session5: Friday 16:20 – 17:20

Flower inspection and predation risk assessment during the foraging activity of solitary bees

Francisco G. Gonzálvez & Miguel A. Rodríguez-Gironés

Foraging animals face a trade-off between increasing intake rate and decreasing predation risk. Animals can reduce mortality assessing predation risk at foraging patches before exploiting them. In order to detect predators ambushing at flowers, pollinators must be able to detect visual and/or chemical cues correlated with the presence of predators. Flower inspection, however, takes time and therefore introduces a missed-opportunity cost. In this work we will focus on the use of flower inspection as a strategy to detect and avoid ambush predators by solitary bees. By constructing a model we first developed a theoretical frame of flower inspection in response to certain cues associated with the presence of predators. We then conducted an experimental study on the flower inspection behaviour of the solitary bee, *Nomia strigata*, when visiting flowers

with and without visual and chemical cues from the aggressive, *Oecophylla smaragdina* and non-aggressive ant, *Polyrhachis dives*. The experimental results confirmed the predictions of our model; while bees exhibited strong inspection behaviour in response to cues from the more aggressive ant species they did not alter their behaviour when facing cues uncorrelated with the presence of predators.

Session5: Friday 16:20 – 17:20

Host plant selection traits and environment-mediated shifts in an olygophagic butterfly

Navarro-Cano JA, Posledovich D, Toftegard T, Gotthard K[2], Wiklund C, Ehrlén J

Climate change imposes a selection pressure on traits important for the temporal matching between different trophic levels. For plant-insect interactions, phenology-related traits such as the strength of flowering timing and hatching usually determine the degree of synchronization. Selection on synchrony is likely to vary with the degree of specialization and the local context. We studied oviposition rate as an index of host preference in a system consisting of the orange tip butterfly *Anthocharis cardamines* and its host crucifers. We combined field data from orange tip-host interacting populations along a 900 km S-N climatic gradient with information from a cage experiment examining host plant preference in butterfly females under controlled conditions. We aimed i) to assess whether the host selection is consistent under different environmental conditions along the climatic gradient; ii) to determine which traits govern butterfly host plant selection among and within species; iii) to determine whether the importance of these traits remains constant across the different studied regions.
The data analysis indicated significant shifts in the ranking of host preference throughout the studied gradient. The traits controlling host selection had a similar among-location effect but the magnitude and direction of the effect differed within species. The cage experiment revealed the host rank hierarchy of the butterfly, which has been proposed to be evolutionarily conserved.

Session5: Friday 16:20 – 17:20

Three way interactions between *Thymus, Medicago* and *Sinorhizobium* - local adaptation to thyme oil

Eva Grøndahl and Bodil K. Ehlers

I will present preliminary results from a study on the interaction between the aromatic *Thymus vulgaris*, an annual medic (*Medicago truncatula*) and its root symbiont *Sinorhizobium*. *Thymus vulgaris* is a dominating component of the Mediterranean garrigue vegetation. It produces aromatic oil, containing monoterpenes, which affects the performance (growth, survival) of other plants, and microorganisms.

Annual plant species of the genus *Medicago* are commonly found in Mediterranean thyme communities, in fact they often grow very close to thyme plants (within 1 square meter). *Medicago* has a symbiosis with the nitrogen fixing bacteria *Sinorhizobium meliloti* – which is essential for nitrogen uptake in the nutrient poor garrigue. In this study we wanted to examine if *Medicago* shows patterns of adaptation to its thyme neighbor, and if any adaptive response was

dependent on the rhizobium, and whether the rhizobium was either "experienced" or "naive" with respect to thyme monoterpenes.

Using a G*G*E design, we tested the fitness of 13 genotypes of *Medicago truncatula*, 7 of which are ”experienced”, and 6 which are ”naive” to thyme. All genotypes were grown on soil either amended with thyme monoterpene or not. In addition, each plant received a rhizobium treatments which was either: no rhizobium, a mix of thyme experienced *Sinorhizobium* genotypes, or a mix of thyme naive *Sinorhizobium*. The experiment was carried out as a fully factorial design. We found a large effect of *Medicago* genotype on plant fitness. Thyme naive rhizobium overall had a more positive effect on plant fitness than thyme experienced ones, irrespective of whether the soil was amended with thyme oil or not. We found a small, but significant difference in *Medicago* fitness between naive and experienced plant genotypes on soil amended with thyme oil. Thyme experienced *Medicago* genotypes perform better on thyme soil than thyme naive ones. I will present more results on this experiment at the meeting.

Saturday, 29th October

Session 6: Saturday 9:00-10:30 Chairperson: Martina Stang

Session 6: Saturday 9:00-10:30

Stability and resilience of plant-pollinator networks tested using experimental removal of core floral resources

Tarrant, S. and Ollerton, J. (presenting author)

Resilience and stability of ecological complexes are key concepts within biodiversity and are considered to be important to the continued functioning of natural communities. Networks of plants and their pollinator are frequently nested in structure and are highly variable in both space and time. Both of these features (plasticity and nestedness) have been suggested to promote stability and resilience, making them relatively robust to natural or anthropogenic disturbance. Simulation studies of the removal of pollinators and consequential loss of plants have been undertaken, but empirical field studies that manipulate plant-pollinator communities are only just being attempted. In this study we examine the effect of the sudden removal of the floral resources provided by a core generalist plant species from a plant-pollinator assemblage. The was to determine how the plant-pollinator community would respond to the loss of the most abundant floral resources. Our experimental design involved surveying a grassland plant-pollinator network before (pre-removal), during (post-removal) and after (re-growth) extirpation of the floral resources provided by the most generalist plant Field Scabious *Knautia arvensis* (Dipsacaceae). Our findings were that: (i) there was no significant difference in mean pollinator richness during the three phases of the experiment; (ii) there was a significant difference in mean pollinator abundance between the re-growth phase and the earlier two phases, but not between the pre-removal and post-removal phase; (iii) the interaction network was significantly nested in structure in the pre-removal and re-growth phases, but not in the post-

removal phase; (iv) experimental removal of *Knautia arvensis* inflorescence caused an increase in the number of individual insects visiting flowers of the previously second most generalist plant species, *Centaurea nigra* (Asteraceae) though this effect did not cascade down to the remaining plant species. Our study has demonstrated that plant-pollinator interaction networks are relatively robust to short timescale, local disturbances. This may be evidence that the long term persistence and stability of this vital class of ecological interaction is due to the plasticity of interactions and their nested structure.

Session 6: Saturday 9:00-10:30
The spatio-temporal behavior of networks crossing habitat borders
Melanie Hagen & Jens M. Olesen

Habitat borders are a main feature of landscapes and separate habitats from each other. While some borders might be easy to cross for some species, they might be insuperable for others. Habitat borders may not only be species specific, but dynamic on a temporal scale. While the border might be rather impenetrable in a certain season, it might be blurred during another season. In the case of flower visiting bees, these patterns might be due to seasonal changes or differences in the availability of foraging and nesting sites in neighboring habitats. In a tropical rainforest in Western Kenya we found obvious community differences between the forest and the surrounding farmland in terms of flowering plants and their pollinating bees. While large numbers of flowering plants and bee species were found in the farmland throughout the year, the pattern was highly dynamic within the forest, with very small numbers of flowering plants and bees in the rainy season, and larger numbers of both in the dry season.

Here we want to demonstrate the dynamics of plant-pollinator interactions between neighboring habitats using a network approach and investigate the seasonal variation in network composition, especially modularity across habitats. We will focus on the seasonal dynamics in the topological role of species within and among modules (hubs, connectors and peripherals).

Session 6: Saturday 9:00-10:30
Specialization in Plant-hummingbird Networks is Associated with Species Richness, Contemporary Precipitation and Quaternary Climate-change Velocity
Bo Dalsgaard, Else Magård, Jon Fjeldså, Ana M. Martín González, Carsten Rahbek, Jens M. Olesen, Jeff Ollerton, Ruben Alarcón, Andrea Cardoso Araujo, Peter A. Cotton, Carlos Lara, Caio Graco Machado, Ivan Sazima, Marlies Sazima, Allan Timmermann, Stella Watts, Brody Sandel, William J. Sutherland, & Jens-Christian Svenning

Large-scale geographical patterns of biotic specialization and the underlying drivers are poorly understood, but it is widely believed that climate plays an important role in determining specialization. As climate-driven range dynamics should diminish local adaptations and favor generalization, one hypothesis is that contemporary biotic specialization is determined by the degree of past climatic instability, primarily Quaternary climate-change velocity. Other prominent hypotheses predict that either contemporary climate or species richness affect biotic

specialization. To gain insight into geographical patterns of contemporary biotic specialization and its drivers, we use network analysis to determine the degree of specialization in plant-hummingbird mutualistic networks sampled at 31 localities, spanning a wide range of climate regimes across the Americas. We found greater biotic specialization at lower latitudes, with latitude explaining 20-22% of the spatial variation in plant-hummingbird specialization. Potential drivers of specialization - contemporary climate, Quaternary climate-change velocity, and species richness - had superior explanatory power, together explaining 53-64% of the variation in specialization. Notably, our data provides empirical evidence for the hypothesized roles of species richness, contemporary precipitation and Quaternary climate-change velocity as key predictors of biotic specialization, whereas contemporary temperature and seasonality seems unimportant in determining specialization. These results suggest that both ecological and evolutionary processes at Quaternary time scales can be important in driving large-scale geographical patterns of contemporary biotic specialization, at least for co-evolved systems such as plant-hummingbird networks.

Session 6: Saturday 9:00-10:30

Macroecology of pollination networks
Kristian Trøjelsgaard Nielsen & Jens Mogens Olesen

Many species assemblies show strong macroecological patterns, e.g. increasing species richness with decreasing latitude, but whether this latitudinal diversity gradient scales up to entities as complex as networks is little explored. We investigated this using a dataset of fifty-three networks of interacting plants and pollinators. Each network was organized as a presence/absence matrix, consisting of *P* plant species, *A* pollinator species and their links. From these matrices, various network parameters were estimated. Additionally, data about geography (latitude, longitude, altitude), climate at network site (temperature, precipitation) and methodology (number of observation days, study-plot size) were gathered. Analyses were done using simultaneous autoregressive modelling (SAR).

No strong latitudinal gradients were observed for any network descriptor except modularity, which decreased with latitude. Mean no. links per plant species $<L_p>$, *A* and *A*:*P*-ratio peaked at mid-latitude. Above 500 m a.s.l., *A*, *A*:*P*-ratio, and mean no. links per pollinator species $<L_a>$ decreased with altitude, whereas L_p increased. Some parameters displayed mid-ambient peaks like $<L_p>$ with temperature, and *A*:*P*-ratio and nestedness with precipitation.

Pollination networks showed macroecological patterns, but their overall complexity did not increase towards the tropics. Instead their complexity peaked at mid-latitude, at mid-level temperature and precipitation and at an altitude of 500 m.

Session 7: Saturday 11:00 – 12:00 Chairperson: Anders Nielsen

Session 7: Saturday 11:00 – 12:00

Impact of introduced honeybees on mutualistic networks in Teide National Park (Tenerife, Canary Islands)

Alfredo Valido, María C. Rodríguez-Rodríguez & Pedro Jordano

The mutualistic interactions between flowering plants (17 species) and their floral visitors were intensively recorded during the spring in the sub alpine scrubland of the Teide National Park (Tenerife, Canary Islands). The central aim of this study was to determine the structural and functional impacts of the introduced honeybees on the mutualistic native pollination network of this protected area. The main results indicate that both the structural and functional pollination network parameters were markedly different under the massive presence of the introduced *Apis mellifera* (Apidae), related to significantly reduced diversity of native flower visitors. Thus, the relatively higher abundance and the dominant behaviour of *A. mellifera* might negatively affect this insular native mutualistic system. Our results also suggest that these structural consequences were translated into functional changes in plant reproductive success. Thus, those plants of *Spartocytisus supranubius* (Fabaceae) being highly visited by *A. mellifera* were characterized by a significantly lower seed-set than those flowers (within the same individual plant) exposed to only native floral visitors. The same negative effect was also found along a decreasing-distance gradient respect to beehives, since the nearest plants of *S. supranubius* to beehives (< 500 m) were characterized by a significantly reduced seed-set than those with a lower (or null) floral visitation by *A. mellifera* (> 1 km).

Session 7: Saturday 11:00 – 12:00

Ecological SUPER-networks – *crossing borders*

Lea Gallop, Yoko L. Dupont, Melanie Hagen & Jens M. Olesen

In most ecological network studies there is a focus on just one interaction type within one kind of habitat when studying the stability, robustness, build up and break down of a system in nature. Studying one interaction networks dose not give a thorough understanding of how real systems in nature are constructed. To come closer to a more comprehensive understanding of a real world system the network study in this talk is scaled up to a super network including three bipartite networks (plant-pollinator, plant-herbivore and plant-pathogen networks). Furthermore, the network is crossing a habitat border to illustrate that networks span different habitats. The study was done in Moesgaard Have in Denmark with a total of 697 interactions between plants and their interaction partners. The super network was analysed for a list of network parameters including nestedness and degree distribution. It was analysed for modularity and the turnover rates of species and their links between plots were calculated. The results show that a super network has some of the same characteristics as a classic bipartite pollination network. The super network is significantly modular and nested and the degree distribution follows a power law or a truncated power law depending of trophic level. The super network spans the habitat border, with some modules restricted to a specific habitat type and others occurring on both sides of the

border. There is a high turnover rate at the habitat border indicating that many species go extinct and colonize the network when crossing the habitat border.

Session 7: Saturday 11:00 – 12:00

How to find governing questions for pollination research, based on management needs

Peter Borgen Sørensen

There are many evidences for claiming that pollination is important for society to provide a supporting function to several ecosystem services. However, there is a missing link between the research activity to understand pollination and the need of knowledge to support ecosystem services. This presentation will show a method that can solve this missing link, illustrated based on the survey of Mayer, et al, 2011 and discussed by Biesmeijer et al, 2011. Ranking of the questions done based of aggregation level is done in the following way. An aggregated question could be "How important are wild pollinators for crop yield?" while a more specific question could be "How important is Bombus Terrestris for oils seed rape production?". It is clear that the first question is addressing a larger area of knowledge by including all wild pollinators and all crop types, while the second question is only addressing one species of pollinator and one crop type. However, the first question is containing the second question in such a way that the second question needs to be answered as a subsequent step together with other questions to make the answer of the first question. If the listing of questions is incomplete it introduces uncertainty due to unrecognized ignorance as described by Walker et al., 2003, because the missing question will cause damage on the subsequently analysis to find answers by not taking into account the "missing" question. Thus, if the listing of questions is incomplete it opens up for highly critical and hidden uncertainty and the work done by Mayer et al., 2011 is forming an excellent raw material but the outcome should be closely analyzed to discover incompleteness in the listing of questions and the ranking method is highly useful for this purpose. In the hieratical system of questions, the top ranked more general questions has to be "important" for the society and thus the cascade of lower ranked lesser general questions are the research questions needed to answer the questions raised as important by the society. So, the top layer is related to "relevance" for society and the bottom layers are related to activities that are needed to satisfy the relevance. The ranking of questions can in this way form a method for integrating different types/sources of questions to display relationships, synergy and relevance.

Acknowledgment

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Session 8: Saturday 13:00 – 14:30 Chairperson: Renate Wesselingh

Session 8: Saturday 13:00 – 14:30
Ways out of the pollen dilemma
Klaus Lunau

The pollen dilemma of bee- and hoverfly-pollinated plants arises, because bee-pollinated flowers expend pollen for sexual reproduction as well as for the attraction and reward of pollinators and because pollen emptied flower are no longer attractive for pollen-eating or pollen-collecting flower-visitors as potential import carriers of pollen. Pollen that is eaten by hoverflies or collected by bee is no longer available for pollination. There are various solutions to the pollen dilemma: 1. The change-the-pollinator way out implies discouraging bees and hoverflies and attracting pollinators that do neither eat nor collect pollen. 2. The pollen-mimicry way out comprises the separation between attraction and rewarding with pollen signals. Flowers use pollen mimicry to attract pollinators and concurrently display cryptically coloured real pollen and anthers. The flowers then reward attracted flower-visitors with nectar. Alternatively flowers develop heteranthy with feeding anthers and pollination anthers. 3. The malvaceous way out of the pollen dilemma includes the production of pollen grains that bees do not collect. Flowers of some species of the Malvaceae family offer large, echinaceous pollen grains. These pollen grains adhere very well to the bristles of a bee`s body, but they are not collected by bees. We tested two hypotheses about the bees´ refusing of collecting malvaceous pollen: The toxic-pollen hypothesis assumes that malvaceous pollen is bitter-tasting or toxic and bees refuse to collect this pollen as a provision of brood cells; the non-collectable pollen hypothesis assumes that the pollen grains are not collected, because the pollen grains cannot be packed into the corbiculae. We found that bees readily collect malvaceus pollen following two treatments which were the bending of the spines and the removal of the pollenkitt. Tests with pollen surrogates show, that bees do not constantly use chemical stimuli for the detection of pollen and readily collect inert substances like glass powder. Malvaceous pollen thus represents a rare example of mechanical defense of pollen against pollen collection by corbiculate bees.

Session 8: Saturday 13:00 – 14:30
Benefits of delayed stigma receptivity in *Collinsia heterophylla*, a mixed-mating species
Åsa Lankinen, Josefin A. Madjidian and W. Scott Armbruster

Delaying stigma receptivity could be beneficial because it leads to protandry, thereby increasing outcrossing rates or reducing interference between the sexual functions. Another advantage of this pistil trait is that it may enhance pollen competition either between donors or between self pollen. Competition between self pollen may be of particular importance in species with mixed mating system because it can lead to reduced inbreeding depression, potentially contributing to

persistence of a mixed-mating system. Species of *Collinsia* (Plantaginaceae) show extensive variation in mating system; this variation is associated with variation in floral morphology and development, and with timing of self-pollination. Large-flowered, more out-crossing species also tend to delay stigma receptivity, but benefits of this trait are not fully understood. In the large-flowered species, *Collinsia heterophylla*, a crossing experiment suggested that delayed stigma receptivity did not prevent geitonogamous selfing because early-arriving pollen survived on the stigma until receptivity. However, results of other crosses suggested that intense pollen competition between self pollen can reduce inbreeding depression. This potential benefit of enhancing pollen competition may contribute to maintenance of the mixed-mating system in this species and should select for traits that intensify pollen competition. Another set of crosses showed that delaying stigma receptivity resulted in higher paternal diversity within a seed capsule, which was associated with increased seed set. Our results indicate several advantages of delayed stigma receptivity connected to the ability to enhance pollen competition between both self and outcross pollen in *C. heterophylla*.

Session 8: Saturday 13:00 – 14:30

Pollen dispersal pattern assessment in four insect-pollinated bog species

Somme Laurent, Van Rossum Fabienne, Mayer Carolin, Leprince Nathalie, Jacquemart Anne-Laure

Over the last centuries, habitat fragmentation through human activities, resulting in small and isolated plant populations, are major threats to plant-pollinator networks. The degree of response to habitat fragmentation, depending from one species to another, is related to specific life traits like reproductive system, adaptability or pollination mode. Plants can propagate through vegetative multiplication, sexual reproduction or both. Vegetative multiplication leads to clonal patches within population enhancing the risk of self-pollination through geitonogamy between inflorescences of the same genet, depending on pollinator behaviour. Pollen dispersal is often the major contributing factor to gene flow. Measuring pollen dispersal within populations is essential to assess gene flow and maintenance of genetic diversity.

We assessed pollen flow through fluorescent dye as pollen analogues in four model plants growing in highly fragmented bogs in High Belgium and differing in compatibility system and pollinator guild: *Comarum palustre*, a self-compatible, insect-pollinated and generalist species; *Menyanthes trifoliata*, an insect-pollinated and generalist species, showing floral dimorphism unabling self-pollination and self-compatibility; *Vaccinium uliginosum*, self-compatible, pollinated by specialist insects (e.g. *Bombus* species); and *Vaccinium oxycoccos*, also self-compatible but barely visited by specialist insects. Pollen transfer limitations were also assessed in each population of the four species.

No species did suffer from pollen limitation. Furthermore, fluorescent pollen analogues were dispersed over the whole populations in almost all investigated study sites for the four species. This suggests at least that a sufficient pollen transfer still remains.

Session 8: Saturday 13:00 – 14:30

Flower phenotypic integration in *Narcissus* under contrasting pollinator arrays across the Mediterranean

Rocío Pérez-Barrales and Juan Arroyo

The "Correlation Pleiades" hypothesis proposed by R. L. Berg (1960) states that pollinators with close fit with their flowers might exert higher selective pressures than those with a loose fit. These different selective pressures may be reflected on the structure of correlation among different traits, that is, different degrees of phenotypic integration. *Narcissus* shows a great diversity of pollinators, what makes it a very suitable group of plants to test this hypothesis on phenotypic integration. Also, this diversity of pollinators seems to be related to the expression of style polymorphism in *Narcissus*. We test the phenotypic integration hypothesis at population level in two species of *Narcissus: N. payraceus* from the western and *N. tazetta* from the eastern Mediterranean range. We predict that populations where long-tongued pollinators are more active will present a higher integration values that those with medium and short-tongued pollinators. We discuss the results with respect the ecological and evolutionary significance of the "Correlation Pleiades hypothesis" and the importance of different pollinators on moulding sexual polymorphism and flower shape.

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Sunday, 30th October

Session 9: Sunday 9:00 – 10:30 Chairperson: Jon Ågren

Session 9: Sunday 9:00 – 10:30

Pollinator-mediated selection in *Gymnadenia conopsea*: separating the effects of diurnal and nocturnal pollinators

Nina Sletvold, Judith Trunschke, Carolina Wimmergren, Jon Ågren

Floral evolution should reflect interactions with the most important pollinators, but few have quantified the contribution of specific pollinators to current selection on floral traits. To compare selection mediated by diurnal and nocturnal pollinators on floral traits in the rewarding orchid *Gymnadenia conopsea*, we manipulated the environment by conducting supplemental hand-pollinations and selective pollinator exclusions in two populations in central Norway. In both populations, plants exposed to diurnal pollinators produced more seeds than plants exposed to nocturnal pollinators. Both diurnal and nocturnal flower visitors mediated selection on traits expected to influence attraction and pollination efficiency. The relative strength of selection exerted by diurnal and nocturnal visitors varied among traits and populations, but the direction of selection was consistent. The results suggest that both pollinator groups drive floral evolution in the studied populations, and illustrate how experimental manipulations can promote a quantitative understanding of the contribution of different pollinators to selection on floral traits.

Session 9: Sunday 9:00 – 10:30

Pollinator-mediated selection on floral scent and morphology at different altitudes in the rewarding orchid Gymnadenia odoratissima

Karin Gross, Mimi Sun & Florian P. Schiestl

In animal pollinated plants, pollinators represent one of the main driving forces in flower evolution. Pollinator guilds may differ regionally and thus may lead to the evolution of differences in floral traits among populations. To quantify phenotypic selection on floral traits, we collected floral scent and measured plant, inflorescence, and flower size in Swiss lowland and mountain populations of the rewarding orchid Gymnadenia odoratissima. Fruit set was counted as an estimate of fitness. In general, lowland plants were larger and emitted higher amounts of scent than mountain plants. We found positive directional selection on physiologically active scent compounds as well as on plant and inflorescence size in lowland and mountain populations. However, we also showed opposing directions of selection gradients between lowland and mountain populations on flower size (lowland: positive, mountain: negative) as well as on some "non-active" and one "active" scent compound, and on labellum lobe length (lowland: negative, mountain: positive). Moreover, selection gradients on "active" scent compounds differed among mountain populations (positive in two and negative in one - population). This study is one of the first showing that pollinators select for floral scent but differently depending on the type of compounds. Our results also suggest that pollinators select for different floral traits at different altitudes. However, differences in floral traits between lowland and mountain population not always comply with the direction of selection imposed by the respective pollinators.

Session 9: Sunday 9:00 – 10:30

Floral attraction in *Penstemon digitalis*: display, scents, and colour

Amy L. Parachnowitsch, Robert A. Raguso and André Kessler

Flowers are complex signals however much of our knowledge of the evolutionary ecology of these signals has been limited in two ways. First, pollinators have generally been credited as the main agents driving the wide diversity of flowers. Second, studies generally have focused on single aspects of the floral phenotype such as visual cues. Using *Penstemon digitalis* as a study system, we are exploring the role of floral morphology, scent and colour in attracting both pollinators and antagonists. Moreover, we examine how these plant-insect interactions may lead to evolution of floral characters through natural selection. *Penstemon digitalis* is a bumblebee-pollinated wild flower found in eastern North American and is attacked by a pre-dispersal seed herbivore that consumes developing seeds. We have found within and among population variation in each measured component of the floral phenotype. Pollinators-mediated selection on display leading to higher fitness in plants with larger and more flowers. Conversely, we have found no evidence for herbivore-mediated selection suggesting that for *P. digitalis*, herbivores will not constrain pollinator-mediated selection on display size. Plants with more flowers also generally produce a stronger scent. We have found selection to increase scent independent of correlations with display, suggesting that these two components could be separate targets of

selection. However we did not directly measure the agents of selection on scents so do not know if pollinators also prefer stronger scented flowers. Conversely, despite strong variation in colour, there was no selection suggesting that it is neutral with regards to fitness.

Session 9: Sunday 9:00 – 10:30
Selection on plant visual traits and floral scent: effects via seed development and antagonistic pathways
Annette Kolb, Anna-Karin Borg-Karlson & Johan Ehrlén

Evolutionary explanations of plant reproductive traits have usually emphasized visual characteristics of plants and selection by insect pollinators. In recent years, studies have been broadened by incorporating also interactions with antagonists and by studying plant olfactory cues. Here, we examined if visual and olfactory traits of the perennial herb *Primula veris* correlated with reproductive success, in terms of fruit and seed set, and predator avoidance. Both visual and olfactory traits were correlated with plant reproductive success. Moreover, visual and olfactory traits influenced total seed production both via fruit and seed set and via predator avoidance, and in one case the same trait influenced total seed production both positively and negatively through effects on different components of fitness. Our results suggest that selection on plant reproductive traits by both mutualists and antagonists simultaneously act on visual and olfactory traits.

Session 10: Sunday 11:00 – 12:00 Chairperson: Johan Ehrlen

Session 10: Sunday 11:00 – 12:00
The effects of pollination on evolutionary and contemporary patterns of orchid diversity
Richard Waterman

I present results from a recent study of South African orchids demonstrating the key role that pollinators play in both plant speciation, and community assembly. Phylogenetic analyses show that recently diverged orchid species tend either to use different pollinator species or to place pollen on different body parts of the same species, consistent with a role of pollination-mode shifts in driving orchid speciation. Field experiments provide support for the hypothesis that colonization of new geographical areas requires adaptation to new pollinator species, whereas co-occurring orchid species share pollinator species by placing pollen on different body parts. Given this essential role in maintaining orchid diversity, it is essential to understand how pollinator interactions may be influenced by climate change. I present preliminary results from a study of British orchids , investigating links between flowering phenology, pollinator adundance and orchid reproductive success.

Session 10: Sunday 11:00 – 12:00

Flower morphological diversity in Aframomum – potential for adaptations to different pollinators as driving speciation agents?

A.C. Ley and D.J. Harris

Aframomum (~70 spp., Zingiberaceae: ~53 genera) is a genus of perennial rhizomatous herbs from the understorey and edges of tropical African rainforests. The family is well known for a high diversity in floral morphology and pollination systems in Asia, however, less is known in Africa. Phylogenetic studies suggest a recent diversification in the genus possibly corresponding with climate change during the period from the late Oligocene to the Miocene. In this project we want to explore the potential of pollinator mediated diversification versus climate change as driving force for speciation using flower morphological, ecological and population genetic data. As a first step we submitted 13 taxa to a detailed morphological survey on traits relevant for pollination. A PCA suggested five floral types based solely on slight changes in the relative length of dorsal petal and labellum. A further 59 species were subsequently each attributed to one of these five types based on digital photos (24 species) and monographic descriptions (35 species). Mapping floral types onto the phylogeny demonstrated repeated parallel developments of types. Nevertheless, regarding the number of species in *Aframomum* switches between floral types potentially indicating speciation via differential pollinator adaptations were rare due to the preponderate presence of one single floral type (~90% of taxa: purple tube type). Thus additional speciation hypotheses such as allopatric speciation during ice ages have to be tested via phylogeographic approaches.

Session 10: Sunday 11:00 – 12:00

Indirect and direct selection on mate choice

Madjidian J.A, Smith H.G., Andersson S. and Lankinen Å.

Indirect partner choice and sexual antagonism may act simultaneously, but few empirical studies have investigated how these two selective forces interact. Furthermore, empirical evidence of sexual antagonism is scare in plants. The hermaphroditic *Collinsia heterophylla* shows delayed stigma receptivity, a female choice character that intensifies pollen competition. We have previously demonstrated a potential sexual conflict over timing of stigma receptivity, as pollen from certain pollen donors can grow in the pistil at early floral development, at a maternal cost of lowered seed set. Here, we will present a study assessing the co-occurrence of indirect mate choice and sexual antagonism during pollen competition. In a greenhouse experiment we performed controlled two-donor crosses at several stages of floral development in order to investigate siring success across varying degrees of stigma receptivity. We further compared siring success to the sexually antagonistic traits of the two sexual functions, namely, the ability of pollen to germinate early, and the ability of pistil to delay stigma receptivity in presence of pollen (evaluated in a separate crossing experiment). In order to explore benefits of delaying stigma receptivity (female choice character) we measured fitness of the resulting offspring. The results suggest that both mate choice and sexual antagonism occur during pollen competition in *C. heterophylla*, indicating that sexual conflicts may have important evolutionary consequences also in plants.

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