PROGRAMME

THURSDAY, 23.10.2014

15:00-18:00 Arrival and registration

18:00-19:30 Dinner

19:30-20:30 SESSION 1 Chair:

19:30 **Anne Muola:** No spatial variation in outcrossing rate in the mixed-mating perennial *Vincetoxicum hirundinaria*.

19:50 **Judith Trunschke:** Deceptive orchids experience stronger pollinator-mediated selection than rewarding species do.

20:10 **Marion Chartier:** The floral morphospaces – a modern comparative approach to study angiosperm evolution.

21:00- Get-together

FRIDAY, 24.10.2014

07:30-08:45 Breakfast

09:00-10:30 SESSION 2 Chair:

09:00 **Diane Campbell:** Natural selection of floral trait associations shaped by interactions with multiple species.

10:00-10:30 Coffee break

10:30-11:50 SESSION 3 Chair:

10:30 **Marcin Zych:** Cryptic floral adaptations may explain geographic variation in pollinator guild of a generalist umbellifer.

10:50 **Marcos Mendez:** The dark side of pollination networks: adding nocturnal pollinators.

11:10 **Sarah Papiorek:** The impact of floral colouration on network structures on a Caribbean Island.

11:30 **Jens Mogens Olesen:** Double mutualists.

12:00-13:30 Lunch

13:30-14:30 SESSION 4 Chair:

13:30 **Saskia Klumpers:** Flower morphology, floral nectar and pollinator behavior: an optimal foraging approach to pollination networks.

13:50 **Lisa Evans:** Variation in learning performance and its effect on foraging behaviour in the bumble bee *Bombus terrestris*.

14:10 **Klaus Lunau:** Why it is important to distinguish innate, spontaneous and learnt preferences of flower visitors.

14:30-15:00 Coffee break

15:00-11:50 SESSION 5 Chair:

15:00 **Anna Jakobsson:** Do landscape composition and abundance of *Salix caprea* affect pollination of natives in marginal habitats?

15:20 **Laura Moquet:** Importance of floral resources for the maintenance of plant-pollinator interactions in heathland.

15:40 **Pierre Ouvrard:** Effects of a Belgian AES (flowered margins) on pollinator populations and *Brassica napus* yields; preliminary results.

16:10- POSTER SESSION

18:00-19:30 Dinner

19:30- Pub

SATURDAY, 25.10.2014

07:30-08:45 Breakfast

09:00-10:30 SESSION 6 Chair:

09:00 **Mario Velljo-Marin:** Buzz-pollination and the evolution of flower form in *Solanum*.

10:00-10:30 Coffee break

10:30-11:50 SESSION 7 Chair:

10:30 **Florian Etl:** Pollination biology and fruit dispersal of *Alocasia sarawakensis* (Araceae), in a lowland rainforest on Borneo.

10:50 **Magne Friberg:** Floral scent in a geographic mosaic of coevolution.

11:10 **Amy Parachnowitsch:** Dissecting floral scent: how connected are olfactory and visual signals?

11:30 **Peter Hambäck:** Plant-insect interactions in spatially heterogeneous environments: the role of search cues.

12:00-13:30 Lunch

13:30-15:00 Field trip in the close surroundings

15:00-16:00 SESSION 8 Chair:

15:00 **Anders Nielson:** Pollination; an ecosystem service affected by climate change.

15:20 **Julie Sørlie Paus-Knudsen/Helge Lone:** Effects of pesticides on domesticated and wild pollinators/Valuation of ecosystem services: The effect of pollination in Norwegian agriculture.

15:40 **Dara Stanley:** Investigating sublethal pesticide effects on bumblebee foraging and pollination service.

16:00-16:30 Coffee break

16:30-17:10 SESSION 9 Chair:

16:30 **Jeff Ollerton:** Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes.

16:50 **Alfredo Gozales:** Woodland as providers of ecosystem services.

17:10 **Jonas Kuppler:** Infiltrated by invaders: a trait-based community approach for understanding niche competition of flower visitors in the Hawaii Volcanoes National Park.

17:30-17:40 Leg stretcher

17:40-18:40 SESSION 10 Chair:

17:40 **Gita Benadi:** When can pollination niches facilitate plant coexistence?

18:00 **Agnes Dellinger:** Move out without a pollinator: effects of reproductive systems on ecological niche use in invasive species.

18:20 **Robert Junker:** The functional diversity of floral and vegetative traits along an altitudinal gradient suggests that habitat filtering and competition avoidance additively act on plant community assembly.

19:00- SCAPE banquet

SUNDAY, 26.10.2014

07:30-08:45 Breakfast

09:00-10:00 Concluding discussion

10:00-10:30 Coffee

10:30 Departure

NO SPATIAL VARIATION IN OUTCROSSING RATE IN THE MIXED-MATING PERENNIAL *VINCETOXICUM HIRUNDINARIA*

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A mixed-mating system is relatively common among plants. Being able to self and outcross simultaneously has its advantages under different environmental conditions. Still, factors contributing to the maintenance of stable mixed-mating system are not well understood. Our earlier pollination experiments and allozyme studies indicate that in the SW archipelago of Finland, the perennial herb *Vincetoxicum hirundinaria* has a mixed-mating system with varying levels of self-fertilization within and among populations. In this area, population size, age and isolation vary and there is also extensive spatio-temporal variation in herbivore pressure. Moreover, artificially selfed offspring suffer from inbreeding depression, especially under herbivory. In order to understand whether opposing selection pressures caused by herbivory and survival in highly fragmented environment maintain a mixed-mating system in *V. hirundinaria* we investigated variation in outcrossing rate with microsatellite analysis of 153 progeny arrays from 13 populations in the SW archipelago of Finland. We hypothesised that outcrossing rate is negatively related to population size, age and isolation, and positively related to levels of herbivory. Surprisingly, there was no spatial variation in outcrossing rates. In fact, we found only two plants in two populations that produced offspring via selfing. However, especially in small populations the amount of fertile individuals with high proportion of homozygous loci was relatively large indicating either mating among relatives or selfing in past. Our results thus indicate that although outcrossing rather than selfing might be rule for *V. hirundinaria*, small populations might still be prone to decreased heterozygosity that may eventually affect their capability to adapt to different biotic or abiotic conditions.

DECEPTIVE ORCHIDS EXPERIENCE STRONGER POLLINATOR-MEDIATED SELECTION THAN REWARDING ORCHIDS DO

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In animal-pollinated plants, the strength of pollinator-mediated selection is expected to increase with the degree of pollen limitation. To test the hypotheses that (1) female fitness of deceptive species is more strongly pollen limited and more variable compared to that of rewarding species, and (2) this is associated with stronger net and pollinator-mediated selection, we experimentally quantified pollinator-mediated selection on five traits important for pollinator attraction and pollination efficiency (flowering start, plant height, flower number, flower size and spur length) in natural populations of six deceptive and six rewarding orchid species in SE Sweden. Mean pollen limitation was more than seven times higher and the variance in relative female fitness was more than twice as high in the deceptive species compared to the rewarding species. As predicted, both net and pollinator-mediated selection on floral traits were stronger in the deceptive species. Within reward category there was little variation in pollen limitation, and only a weak correlation between pollen limitation and strength of selection. The results suggest that the degree of pollen limitation influences the strength of selection imposed by pollinators, and more generally that the intensity of biotic interactions is an important determinant of the selection regime in plant populations.

THE FLORAL MORPHOSPACE - A MODERN COMPARATIVE APPROACH TO STUDY ANGIOSPERM EVOLUTION

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Morphospaces are mathematical tools allowing for the study of morphological diversity and for the evaluation of evolved shapes among theoretically possible ones. Although widely used in zoology, morphospaces are relatively rarely applied in plant science. An exception is the use of morphospaces for the study of floral traits selection by pollinators. However, almost nothing has been attempted at the level of broad-scale patterns of floral structure and evolution. We review earlier morphospace applications in plant science and highlight two very different, practical examples: (i) A broad-scale investigation of morphological diversity across the angiosperms. Here, we use modern statistical tools applied to the first and only angiosperm-wide floral morphospace published by Stebbins in 1951 (Evolution 5: 299-324). Despite the incompleteness of Stebbins' dataset, our analyses highlight major, angiosperm-wide trends in the diversity of floral morphology. (ii) A study on pollinator driven selection in the flowers of two *Arum* species and their hybrids. Here, we construct and analyze floral structure, scent, and pollinator spaces with the aim to understand the way these traits are inherited by the hybrids and how they are related to their pollination ecology.

NATURAL SELECTION OF FLORAL TRAIT ASSOCIATIONS SHAPED BY INTERACTIONS WITH MULTIPLE SPECIES

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Flowers differ in a multitude of traits, including shape, color, rewards, and scent. Specific trait combinations can be subject to correlational selection in which the effect of one trait on fitness depends on another trait. I consider first whether pollinator visitation patterns produce such correlational selection, and second whether the presence of additional interacting species makes it more likely that correlational selection occurs. Increasing the indole scent produced by *Ipomopsis tenuituba*, but not *Ipomopsis aggregata*, attracts hawkmoth pollinators to flowers, and white color increases hawkmoth feeding at dusk. The effects of scent and color on visit rate are, however, additive, so these traits do not experience correlational selection based on hawkmoth visitation. Correlational selection of flower tube shape and color based on bee and fly visitation to *Polemonium foliosissimum* was also weak. The general paucity of demonstrations of correlational selection could reflect failure to consider selective agents across the lifecycle. In theory, directional selection acting in sequence, such as selection by pollinators and then by seed predators, can generate stabilizing and correlational selection. In *Ipomopsis*, flower traits, including shape and the scent compound of alpha-pinene are also under selection by a fly that is a seed predator. Field tests of whether hummingbirds, hawkmoths, and fly seed predators together generate correlational selection are in progress. Whereas pollinators and herbivores can both select on the same floral trait, it will be particularly important to incorporate both kinds of interactions when studying the evolution of associations between multiple traits.

CRYPTIC FLORAL ADAPTATIONS MAY EXPLAIN GEOGRAPHIC VARIATION IN POLLINATOR GUILD OF A GENERALIST UMBELLIFER

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In terms of the pollination system umbellifers (plants of the Carrot family, Apiaceae) are regarded generalists, since their (usually dichogamous) flowers are visited by a wide range of insects representing several taxonomic orders. However, recent analyses of insect effectiveness revealed that the plants may be effectively pollinated by a narrow assemblage of flower visitors. In our study we focused on *Angelica sylvestris* L., a common European species, putatively an example of "adaptive generalization" (*sensu* Gómez & Zamora 2006). In three populations of the species, located along approx. 500 km long transect, over three years we analysed floral visitor assemblages, assessed insect effectiveness, and studied nectar and scent composition. We showed that despite similar taxonomic composition of insect visitor assemblages, our study populations are pollinated by different pollinator guilds. This indicates that despite apparent generalization on the species level, our study populations may be locally adapted to the most effective pollinators, which is likely to be caused by differences in nectar and scent profiles.

THE DARK SIDE OF POLLINATION NETWORKS: ADDING NOCTURNAL POLLINATORS

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The ongoing interest in community approaches to plant-pollinator interactions has yielded a burst of studies on plant-pollinator networks. However, most of this work has focused on diurnal pollinators whereas the potentially important role of nocturnal pollinators has been neglected. We are interested in quantifying the changes in network structure produced by the addition of data on nocturnal pollinators to three diurnal plant-pollinator networks in Spanish high mountains. We documented the diurnal interactions between plants and pollinators in three high mountain communities and simultaneously collected moths using light traps for pollen extraction. Nocturnal pollination was present in the three communities, involving both plant species with or without nocturnal pollination syndromes. Addition of the nocturnal pollination interactions to the diurnal networks moderately modified almost all their descriptive properties. Nocturnal pollinators did not preferentially attach to the most (diurnally) connected plant species but to plants covering the whole spectrum of degree in the networks. In the two modular networks, addition of nocturnal pollinators caused a decrease in the number of modules and changes in the role of ca. 20% of the species, including the loss of module hub roles of some plant and pollinator species. These results indicate that our perception of network structure, including modularity and robustness to species extinction, is highly biased and that nocturnal pollinators should be regularly added to plant-pollinator studies to get a more balanced view of this important ecological interaction.

THE IMPACT OF FLORAL COLOURATION ON NETWORK STRUCTURES ON A CARIBBEAN ISLAND

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Colour is one of the most obvious advertisements of flowers and responsible for the attraction of flower visitors. As physiological colour-vision systems as well as neuronal processing differ among flower visitors, floral colouration selectively attracts specific visitors. Flower-visiting birds have a tetrachromatic colour vision system, whereas bees exhibit a trichromatic colour-vision system without a photoreceptor-type sensitive in the red wavelength range. In addition bees exhibit preferences for distinct colour parameters, whereas the foraging behaviour of birds relies more on experience, including the association of floral colour with expected rewards. Consequently, the colouration of bird-pollinated flowers may not only be adapted to potential pollinators, but may also filter non-pollinating bees from effective foraging at these flowers, ultimately giving an advantage for the pollinating birds by offering large amounts of floral rewards which cannot be exploited by bees. In this study, we measured the spectral reflectance of flowers in two distinct habitats (one lowland and one highland) site on Dominica, Caribbean Islands. The sites differ markedly in climatic conditions and habitat structure, resulting in distinct relative composition of the pollinator fauna: whereas bees are frequent visitors in the lowland site, bees are not present in the highland site. In contrast, hummingbirds are common flower-visitors in both sites, but differ in their morphological properties and concomitant in their energy-demand between the two sites. It has previously been shown that abiotic factors, i.e. temperature and rainfall, may account for the divergence of flower-visitors in the two sites. Here, we test whether floral colouration also differs between the two sites and how floral colouration may impact network structure in addition to morphological and environmental factors. Preliminarily analysed results suggest that highland bird-pollinated flowers display colours which are less attractive for bees, although competition by bees is non-existent. Moreover, the colour of lowland and highland bird-pollinated flowers does not differ significantly. These results are discussed with respect to evolutionary constraints of bird-pollinated flowers and to other flower visitors in the highland.

DOUBLE MUTUALISTS

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Islands have a lower species density than adjacent mainland. Thus species experience interaction release, i.e. many species are more generalised and perform more ecological functions than related mainland species. I will give some examples from Galapagos and New Zealand and discuss the consequences of this to the stability of island ecosystems.

FLOWER MORPHOLOGY, FLORAL NECTAR AND POLLINATOR BEHAVIOR: AN OPTIMAL FORAGING APPROACH TO POLLINATION NETWORKS

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Most pollinators are known to forage non-randomly among flowering plants in a community, visiting only a subset of the species. The range of plant species that pollinators can visit is strongly influenced by morphological constraints. Floral nectar may also influence pollinator choice behavior, as it is - for the majority of pollinators - the most important energy source. Optimal foraging theory states that pollinators should forage, among the plants they can visit, in such a way as to maximize their energy gain per unit time. Therefore, nectar-feeding pollinators should prefer plant species that yield the highest net energy (or sugar) gain. Energy gain depends on flower handling time and travel time as well as on nectar obtained per flower. This study was designed to get more insight into the energy gain of pollinators when foraging on different plant species and how this determines pollinators' flower choice. In this study we focused on a natural community of a group of generalized plant species, the Asteraceae. We investigated the relationship between flower morphology, nectar production and size-matching between pollinators and plants. We also investigated how these traits affect flower handling time. We show that nectar production increases allometrically with nectar tube depth and width. In addition, deeper flowers are visited by larger pollinators. We argue that, for the Asteraceae, it is important to have a good understanding of the functional flower morphology. Also, we show that different insect groups differ in their flower handling time. Our results indicate that, even in the generalized Asteraceae, flower handling time increases with increasing flower depth, size-matching and nectar production. However deeper flowers are energetically more profitable. We discuss the implications of our results for the structure of pollination networks.

VARIATION IN LEARNING PERFORMANCE AND ITS EFFECT ON FORAGING BEHAVIOUR IN THE BUMBLE BEE *BOMBUS TERRESTRIS*

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Foraging is a complex task all animals undertake, requiring them to make comparative judgments about the abundance and/or quality of resources in changeable conditions. We might therefore expect individuals or groups with higher cognitive capabilities to be better able to deal with such complex foraging decisions. However, in many social insect groups we see appreciable variation in learning ability among closely related individuals (e.g. foraging workers within a bumble bee colony). Using bumble bees we investigated how this variation in cognitive performance among foraging individuals could have adaptive value for the colony. Are those individuals that perform best in associative learning tasks responsible for collecting most of the food for the colony? Having assessed individual learning performance in the lab we monitored the foraging behaviour of the same individuals in the field using radio frequency identification (RFID) tagging technology. We hypothesized that fast learning individuals would perform better in the field, seeing as foragers must learn which flowers provide rewards, where to find them, and how to extract nectar and/or pollen. Our results indicate that individual learning performance does predict foraging behaviour, but perhaps not in the way we expected.

WHY IT IS IMPORTANT TO DISTINGUISH INNATE, SPONTANEOUS AND LEARNT COLOUR PREFERENCES OF FLOWER VISITORS

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Flower colour is probably the most important signal for flower visitors to locate flowers. Many flower visiting insects are prepared to find flowers for the first time and possess innate colour preferences. Being rewarded at flowers generates a learnt colour preference, whereby the number of learning trials, absolute versus differential conditioning, amount of reward and other factors may influence the strength of learnt colour preferences. My talk is focused on spontaneous colour preferences which are shown by experienced flower visitors and may deviate from innate as well as from learnt colour preferences. Behavioural colour preference tests show that pre-trained bumblebees (*Bombus terrestris*) and honeybees (*Apis mellifera*) exhibit spontaneous colour preferences for more spectrally pure colours, but not for colours of a deviant (shorter or longer) dominant wavelength, e.g. a more bluish test colour as compared to the training colour. The spontaneous colour preferences are altered by the quality of reward. In dual choice test it was demonstrated that the bumblebees' spontaneous preference shifted to less spectrally pure colour if these colours are rewarded with higher concentrated sugarwater than the initially preferred spectrally pure colours. Compared to honeybees and bumblebees, which are highly flexible in the modulation of their colour preference, the hoverfly *Eristalis tenax* shows an innate proboscis reflex towards UV-absorbing yellow colours, which cannot be conditioned towards other colours despite intense training and differential conditioning. It is discussed how plants can exploit these spontaneous colour preferences for discouraging, attracting and guiding flower visitors.

DO LANDSCAPE COMPOSITION AND ABUNDANCE OF *SALIX CAPREA* AFFECT POLLINATION OF NATIVES IN MARGINAL HABITATS?

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Pollinator assemblages in agricultural landscapes benefit from proximity to and increasing proportions of natural and semi-natural habitats, and corresponding patterns for yield in insect-pollinated crops has been frequently demonstrated. Less studies has been devoted to effects on pollination services to native plants in marginal habitats, although such habitats, like road-verges and field boundaries, are common in agricultural landscapes and can harbour a substantial part of the plant species pool. We investigated the effect of landscape composition and the suggested pollinator key flower resource *Salix caprea* on pollination in the native plants *Armeria maritima* spp *maritima* and *Lotus corniculatus*. Using hand pollination and potted plants we estimated pollen limitation in arrays of the study species placed in road-verges in twenty and twenty-four independent landscapes in two counties. We found no effects of landscape composition or abundance of *Salix* on pollen limitation in *Armeria*, and in *Lotus* the only relationship found was that of increasing pollen limitation with increasing forest cover. This could be due to flowering *Vaccinium* species in the forest competing with *Lotus* for bumblebees during the experimental period. Effects of pollen limitation on seed production was generally low in both study species and since number of pollen donors, resources and genetic differences was controlled for we conclude that levels of pollinator visitation in the studied landscapes, some of which are among the most intensively farmed areas in Sweden, are sufficient. Whether *Salix caprea* generates higher growth rate of pollinator populations and increased pollination of plants needs to be further studied.

IMPORTANCE OF FLORAL RESOURCES FOR THE MAINTENANCE OF PLANT-POLLINATOR INTERACTIONS IN HEATHLANDS

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Pollinators play fundamental ecosystem services as they contribute to the reproduction of 78% of Angiosperms in temperate area. Nevertheless, evidence about their decline has accumulated worldwide during the past three decades. The fragmentation and destruction of biotopes are factors that explain this decline. In this context, the aim of my study is to analyse the influence of landscape and population structure on plant-pollinator interactions in semi-natural habitats that decreases across Europe: heathlands. Social insect visitors like bumblebees exclusively forage on floral resources and depend on both quality and quantity of pollen and nectar for colony development and population survival. To investigate if heathland surface and landscape mosaic may affect the bumblebee diet, we study the proportion of the different plant species in their diet as well as the nutritive qualities of these resources. My first results showed that plant species greatly differed in their resource qualities. For example, pollen from Ericaceae species (*Calluna vulgaris, Vaccinium myrtillus*) was of poor quality with low polypeptide content. On the contrary, *Narthecium ossifragum,* presented high quality pollen with high essential amino acid and polypeptide content. It seems that co-flowering plant species at both local and landscape levels are of crucial importance for pollinator survival. Future management plans for heathland restoration need to consider the maintenance of floral diversity but also a landscape mosaic offering resources of different quality.

EFFECTS OF A BELGIAN AES (FLOWERED MARGINS) ON POLLINATOR POPULATIONS AND *BRASSICA NAPUS* YIELDS; PRELIMINARY RESULTS

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The situation of pollinator insects worldwide is currently very worrying for both, wildlife and agriculture. The decline of pollinator populations will be quickly very damageable for fruits and seeds production of about 85% of crops plants in temperate zones. We already have a pollination deficit in several farming areas. In the same time entomophilous crops, and so the need of insect pollinators increase faster than the global food demand. Oilseed rape (*Brassica napus* L.) is one of these crops that know an amazing expansion, mainly due to its use as energy crop. Supporting these insect populations is so very important and a common consciousness of this problem seems to appear. That starts to be conceptually included in the Agricultural Common Policy (ACP) schemes. Can we really support these populations without a full revision of our current agriculture practices? Are the present actions useful to support insect biodiversity and to improve crops pollination? The lake of data about these practices is considerable. I will investigate these questions through the evaluation of a Belgian agro-environmental measure (according to ACP): the flowered managed margins for pollinators (AES 9 c) and a target crops: oilseed rape. The observations of my first year are a bite concerning:

- the effective attractiveness of *Brassica napus* for pollinators is questioned
- the real importance of pollinators on a usually recognize as highly attractive crop appear not so strong
- and so the pollination deficit that is evaluated as increasing in several recent papers could be less evident.

BUZZ-POLLINATION AND THE EVOLUTION OF FLOWER FORM IN *SOLANUM*

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More than 20,000 species of plants possess flowers that release pollen only through small openings (pores or slits) in the anther's tips. Bees visiting these species use high-frequency vibrations or "buzzes" to extract pollen from anthers. Buzz-pollinated flowers have evolved independently many times and include agricultural crops such as tomatoes and potatoes. Despite its widespread taxonomic distribution in plants and importance to natural and agricultural systems, the ecology and evolution of buzz-pollination has received limited attention. Here I will present an overview of buzz-pollination from both plant and animal perspectives, and illustrate how selection through buzz-pollinators has caused some striking example of convergent evolution across angiosperms. I will then use species in the genus *Solanum* (Solanaceae) to illustrate how selective pressures imposed by buzz-pollinators have also triggered the specialisation of floral organs and the division of labour within flowers.

POLLINATION BIOLOGY AND FRUIT DISPERSAL OF *ALOCASIA SARAWAKENSIS* (ARACEAE), IN A LOWLAND RAINFOREST ON BORNEO

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We have investigated the reproductive ecology of *Alocasia sarawakensis* (Araceae), a perennial, terrestrial herb endemic to the lowland rainforests of Borneo. We conducted our investigation in the Danum Valley Field Centre, Sabah, Malaysia and report for the first time the thermogenetic pattern of the inflorescences of *A. sarawakensis* during anthesis and also characterize the main pollinators: flies of a yet undescribed species of the genus *Colocasiomyia* (Diptera, Drosophilidae). The inflorescences attract numerous individuals of these flies during early morning hours. Attraction of the flies is accomplished by a strong scent emission that follows an increase in temperature of the appendix up to 44°C. In addition, we recorded unique spathe movements, which most likely act as a pollinator management device and as an exclusion mechanism for other floral visitors. Pollinator exclusion experiments resulted in zero fruit set and therefore indicate a strong mutualistic plant-pollinator relationship. As *Colocasiomyia* flies also use the inflorescence as rendezvous and breeding site, we interpret the pollination system as a case of nursery mutualism. Our field observations further indicate that seeds of this species are exclusively dispersed by birds. A total of nine bird species were observed removing fruits, indicating that *A. sarawakensis* is an important food resource for the local lowland rainforest avifauna. Spiderhunters (Nectarinidae, *Arachnothera*) dominated in visitation rates and total seed removal. This may be due to the characteristic beak morphology found in this genus, which allows easy removal of the often relatively inaccessible fruits.

FLORAL SCENT IN A GEOGRAPHIC MOSAIC OF COEVOLUTION

M. Friberg

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Scent is a major component of the floral phenotype, and many floral volatiles function as pollinator attractants on both specialized and generalized pollination systems. Other volatiles could act as repellents against herbivores and seed predators, and the field of chemical ecology has made great headway by focusing on linking the chemical characteristics of certain flowers to the physiology and behavior of their pollinators and seed predators. At the same time, fewer studies have investigated the evolution of floral scent from an ecological and life-history perspective. For example, little is known still about how, whether and why the scent signal varies among populations, and to what extent this variation can be attributed to variation in the local community of mutualist and antagonist insects that are interacting with the focal plant species. Such local variation in plant-insect communication could have profound effects on diversification of traits and species on both sides of the plant-insect interaction. Here, I will present several datasets focused on describing and understanding the geographic variability of floral scent. Examples come from plant species involved in specialized coevolutionary interactions as well as from species involved in more generalized mating systems and species evolving towards increased selfing.

DISSECTING FLORAL SCENT: HOW CONNECTED ARE OLFACTORY AND VISUAL SIGNALS?

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A flower's visual and scent signals may be linked; for example via shared pathways for pigments and scents, however the evidence is mixed for this hypothesis. Another way visual and scent signals maybe linked arises from where within a flower floral scent is emitted. For example, petal size could affect both visual and olfactory signals for those scents emitted from petals because larger petals also provide more surface area for scent release. The available evidence is scarce but indicate the presence of a spatial variation in floral scent production among floral tissues. Thus, floral scent can be both emitted from or completely lacking from each component part of the visual display, and it is unclear how frequently visual and olfactory signals are linked in general. Here we survey the tissue-specific floral scent production by dissecting flowers of several more or less distantly related species into the visual display and non-visual parts to ask whether floral scents vary between these classes. Preliminary results suggest that variation in floral scent emissions from visual and non-visual parts is common. Additionally, visual and scent signals are likely not highly correlated traits in most systems, suggesting that both need to be measured for full characterisation of floral phenotypes.

PLANT-INSECT INTERACTIONS IN SPATIALLY HETEROGENEOUS ENVIRONMENTS: THE ROLE OF SEARCH CUES

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The strength of species interactions varies with aspect of spatially heterogeneity, such as patch size and habitat complexity, and with species traits. The responses depends both on active decisions made by the forager and on the mode of search. For instance, insects using mainly visual cues for locating resource may respond differently to the same spatial heterogeneity than insects using mainly olfactory cues. We have developed a theory for explaining variation in insect responses to patch size, resource density and within-patch complexity. This theory is derived from basic information properties of different types of cues, and predicts different responses by different groups of insect herbivores. For instance, we have predicted different responses by aphids, butterflies and nocturnal moths, and have used own and other data to test predictions. In general, visually searching insects such as many butterflies have a stronger response to patch size than olfactory searching insects such as many moth species. Out analyses also suggest that difference in the responses caused by search depend on other traits such as mobility. I will in this talk outline the basic ideas behind the model and reason how various species traits may be connected to spatial patterns in insect density and therefore in strength of plant-insect interactions. The main focus of the model development has been on insect herbivores but aspects may be extended to plant-pollinator interactions.

POLLINATION; AN ECOSYSTEM SERVICE AFFECTED BY CLIMATE CHANGE

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Plants and their pollinators and indeed the subtle ways in which they interact can be affected by climate change. Such changes may have consequences for wild plant communities, insect populations as well as for food production. Both flowering phenology and insect population development and behavior may change in response to altered temperature and precipitation regimes. In two recent reviews we have discuss the potential for climate induced spatial and temporal mismatches between plants and their pollinators and highlighted the paucity of empirical studies looking into this issue. The PolliClim project aims at studying several aspects of climate induced changes in plant pollinator interactions encompassing entomophilous crops, wild plans, honeybees and wild pollinators. Here I will present the general framework of the project, some of the challenges we have met and the potential I still see for the remaining 2.5 years of the project period. It might even be time for a presentation of some preliminary results. I will also introduce two master students just enrolled on the project that will present the idea of their projects in separate talks.

VALUATION OF ECOSYSTEM SERVICES: THE EFFECT OF POLLINATION IN NORWEGIAN AGRICULTURE

Helge Lone[a]

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I wish to explore the effect of pollination services in Norwegian agriculture. The questions I want to address are; What is the effect of pollination in Norwegian agriculture? How are pollination services affected by changes in climate, and what possible consequences will this have for future output in the agricultural sector? What is the marginal utility of pollination in agricultural production? The valuation of ecosystem services is a fairly recent topic. Past efforts have often emphasized the necessity of ecosystem services without attempting to evaluate them. Given the complexity of natural ecosystems, attempts to do so will often be prone to error and oversimplification. However, recent efforts have attempted to do so none the less in order to provide a credible framework for decision makers and policy. The knowledge of pollinations effect in agricultural production is limited. It is understood as a necessary component, but has rarely been valued in the same way as other factors of production. The majority of Norwegian agricultural production is pollinated by wind rather than insects. The reason for this is that Norwegian agriculture consists primarily of grain production, rather than fruit and berry crops. Even so insect pollination plays an important role in our ecosystem. And it is vital to the limited production of fruits and berries that we do have.

EFFECTS OF PESTICIDES ON DOMESTICATED AND WILD POLLINATORS

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35% of global production comes from crops that depend on pollinators. Agricultural productivity is under threat due to a decline in pollinator population. Understanding the causes of decline is important, nevertheless our current understanding of the reason is poor across the globe. There is a growing understanding that chemicals toxic for pollinators are present in nectar and pollen. In this research we will look at the behavior effects or the accumulation of toxic chemicals in both domestic and wild pollinators, depending on the toxins used in agricultural management in Norway. The project is still a work in progress, and whether we will look at behavior effects or accumulation is still open. We will sample plant-pollinators interactions in the area around Oslo and/or the west coast of Norway. The entomophilous crop species being used is raspberry, an increasingly important fruit in Norwegian agriculture. In this work we wish to get more information on the effects chemicals used in agricultural management have on biodiversity and ecosystems services.

VALUATION OF ECOSYSTEM SERVICES: THE EFFECT OF POLLINATION IN NORWEGIAN AGRICULTURE

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INVESTIGATING SUBLETHAL PESTICIDE EFFECTS ON BUMBLEBEE FORAGING AND POLLINATION SERVICES

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Bumblebees are essential pollinators of many important agricultural crops and wild plants. While foraging in agricultural farmland bees are likely to be exposed to pesticides applied for crop protection. The systemic nature of neonicotinoid pesticides means they can be found in the nectar and pollen of mass flowering crops where bees and other pollinators become orally exposed while foraging. Although bees typically encounter these pesticides at sublethal levels, exposure may still have impacts on important behaviours such as foraging, which in turn could have consequences for the delivery of pollination services to other plants visited by exposed individuals. We examined the impact of two field realistic doses of a neonicotinoid pesticide, thiamethoxam, on bumblebee foraging behaviour and the pollination services they delivered to apple trees in a caged experiment. Bumblebee colonies were either exposed to a pesticide (two levels of exposure, n=8 colonies/ level) or kept untreated (n=8 control colonies) in the lab for 13 days before they were moved to the field for behavioural observations. Apple seed set and quality measurements of tested trees were also measured at the end of the growing season. Our results indicate varying effects of pesticide exposure on both bumblebee foraging behaviour and the pollination services they provide. This has implications for both pesticide usage policy, and the management of pollination services to both crops and wild plants.

EXTINCTIONS OF ACULEATE POLLINATORS IN BRITAIN AND THE ROLE OF LARGE-SCALE AGRICULTURAL CHANGES.

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Pollinators are fundamental to maintaining both biodiversity and agricultural productivity, but habitat destruction, loss of flower resources, and increased use of pesticides are causing declines in their abundance and diversity. Previous research has focussed on changes in pollinator assemblages over relatively modest time scales and geographical ranges, whilst analyses of regions are rare and our understanding of the effects of human-mediated actions over longer periods is limited. We determined the rate of extinction of bee and flower-visiting wasp species in Britain using the approximately c. 500,000 records held by the Bees, Wasps and Ants Recording Society (BWARS), probably the most detailed available for a single country. Twenty-three bee and flower-visiting wasp species are extinct in Britain, including formally widespread species. Since the mid 19th century the pattern of extinctions has been characterised by intervals of relative stability, in which few species were lost, interspersed with times when over three species per decade went extinct. A novel breakpoint analysis was used, in which a piecewise linear model is fitted to data to reveal periods of approximately constant extinction rate, separated by breakpoints where the rate changes. The most rapid phase of extinction correlates with changes in agricultural policy and practice beginning in the 1920s. This comes before the agricultural intensification prompted by the Second World War, often cited as the most important driver of biodiversity loss in Britain. The recent slowing of the rate of extinction may be due to prior loss of the most sensitive species and/or effective conservation programmes.

WOODLAND AS PROVIDERS OF ECOSYSTEM SERVICES

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The main objective of my research is to understand the ecosystem services provided by woodlands in England, particularly the provision of pollination and pest control in apple orchards. My first year's field work has focused on sampling one organic orchard and one adjacent woodland, both located in the South West UK. Next year I will work on replicate orchards: 10 orchards with adjacent woodlands and 10 orchards without woodlands as controls. The methodology during my first year included the establishment of random transects of 50 meters long, along which quadrats were used every 10m to estimate vegetation abundance and to collect leaf miners, aphids and caterpillars; pollinators were caught by random walks through transects and birds and bark dwelling insects were also sampled. The food web approach I intend to use will show the extent to which both the pollinators and parasitoids are linked to plants other than apple and the data will provide an audit not only of the species present in an orchard, but how they interact with each other. Pollinators and parasitoids were at lower abundance in the adjacent woodland in comparison to the orchard. That said, several pollinator nests were observed in the woodlands, especially in spring and late summer, which could mean that the woodlands provide a shelter for those species overwinter and a source of pollinators for orchards and other ecosystems during summer.

INFILTRATED BY INVADERS: A TRAIT-BASED COMMUNITY APPROACH FOR UNDERSTANDING NICHE COMPETITION OF FLOWER-VISITORS IN THE HAWAII VOLCANOES NATIONAL PARK

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Biological invasions are a major threat of natural ecosystems. Native Hawaiian communities are characterized by high endemism and relatively poor species richness, and are particularly susceptible to introduced species that fill vacant niches or displace native organisms. Naturalized alien flower-visiting species often severely interfere with native co-evolved interactions due to competition for resources. In order to reveal the competition potential of native and invasive flower-visitors, we first analyzed the niches of species based on functional plants traits (flower morphology, resources, scent, colour) and environmental parameters (weather, habitat); and second, we quantified the degree of niche overlap of native and introduced species. Thus, by using a novel non-parametric statistical approach, we aimed to understand the mechanisms underlying niche displacements and invasions. Our preliminary results show that invasive species (i.e. honeybees, carpenter bees, syrphids) tend to visit more plant species (native and invasive) and that their activity periods were less constraint by weather conditions compared to native bees (genus *Hylaeus*). This indicates that invasive flower-visitors occupy larger niches than native ones and therefore may have a higher competition potential. This could lead to the displacement of native flower-visiting species and the disruption of important co-evolved interactions.

WHEN CAN POLLINATION NICHES FACILITATE PLANT COEXISTENCE?

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Plant-pollinator interactions are often thought to have been a decisive factor in the diversification of flowering plants, but to be of little or no importance for the maintenance of existing plant diversity. In a recent opinion paper, Pauw (2013) challenged this view by proposing a mechanism of diversity maintenance based on pollination niche partitioning. Here, we investigate under which conditions the mechanism suggested by Pauw can promote plant coexistence using a mathematical model of plant and pollinator population dynamics. Our numerical simulations show that this mechanism is most effective when the costs of searching for flowers are low, pollinator populations are strongly limited by resources other than pollen and nectar, and plant-pollinator interactions are sufficiently specialized. We review the empirical literature on these three requirements, discuss additional factors that may be important for diversity maintenance through pollination niche partitioning, and provide recommendations on how to detect this coexistence mechanism in natural plant communities.

MOVE OUT WITHOUT A POLLINATOR: EFFECTS OF REPRODUCTIVE SYSTEMS ON ECOLOGICAL NICHE USE IN INVASIVE SPECIES

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Baker's law postulates a colonization advantage of self-compatible over self-incompatible species as the former may establish in the absence of conspecifics and pollinators. Species reproducing asexually by seed (apomicts) do also benefit from these advantages. In addition, apomicts do not suffer from inbreeding depression and, due to the lack of gene flow, may maintain a stable (frozen) array of different genetic lineages adapted to slightly different niche optima (Frozen Niche Variation Model). This disposition may enable apomicts to rapidly colonize new habitats and expand their niches as their gene-pools will not be swamped by possibly less well adapted genotypes. We have compiled worldwide occurrence datasets of 14 congeneric invasive species pairs consisting of one sexual and one apomictic species and sharing a similar native range. Climatic niches of each species are characterized by using PCA-based-methods on environmental variables and niche metrics are calculated by applying kernel smoothers. These measures will be used to analyse patterns of niche occupancy and niche breadth between sexual and apomictic species pairs. Based on Baker's law and the Frozen Niche Variation Model, we hypothesize that apomicts should show more pronounced niche shifts and in particular a tendency to broaden their realized niches in the invaded ranges.

THE FUNCTIONAL DIVERSITY OF FLORAL AND VEGETATIVE TRAITS ALONG AN ALTITUDINAL GRADIENT SUGGESTS THAT HABITAT FILTERING AND COMPETITION AVOIDANCE ADDITIVELY ACT ON PLANT COMMUNITY ASSEMBLY

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Communities are composed of species that are able to survive and reproduce under the local conditions. The establishment of species is either controlled by the environment (habitat filtering – narrow range of functional traits across species) or by interspecific competition for resources or mutualistic partners such as pollinators leading to a limited similarity of functional traits. Therefore, the functional diversity of vegetative and floral traits in plant communities may respond to different selection regimes enabling plants to cope with abiotic factors, e.g. smaller leaves in areas with higher mean annual temperatures (low functional diversity), or to attract pollinators by displaying floral signals such as colour and scent (high functional diversity). Within that framework, we quantitatively measured several floral and vegetative traits of plant species in eight communities along an elevational gradient in the Austrian Alps. The main findings were 1) that the functional diversity of floral traits exceeds that of vegetative traits supporting the notion that vegetative traits are more filtered by the habitat than floral traits. 2) The importance of habitat filtering increases with increasing altitude suggesting that the environmental conditions in higher altitudes exert stronger selection on traits. 3) The functional diversity of floral scent emission and pigmentation within communities was dependent on the flower visitors' equipment with olfactory and visual receptors because these contribute to a species-specific perception of scents and colours. Thus, the evaluation of species-specific perception on flower signals may help to understand evolutionary and ecological processes in community assembly. The study suggests that vegetative traits are rather controlled by the habitat, whereas the diversity of floral traits within a community reflects the need of plant species to compete for pollinators by displaying unique and salient floral signals. Our results thus provide insights into assembly processes of plant communities and are suited to pinpoint functional traits that help the plant to establish and sexually reproduce under given conditions.

PIGMENT CONCENTRATION IN PETALS – IMPACT ON FLORAL SIGNALLING

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The colour of flowers is one of the most important enticements to attract potential pollinators. Floral colours are caused by pigments in organelles of the petals and occur in various colour shades dependent of pigment composition and pigment concentration. In this study we considered the influence of variable pigment concentrations on the manifestation of floral colour considering three common colour attributes, namely the peak wavelength (respective to subjective colour impression 'hue'), colour purity (respective to 'saturation') and colour intensity (respective to 'brightness'). We tested the spontaneous response to variable pigment concentrations of inked papers in honeybees and bumblebees. The worker bees showed preferences for colours displaying a middle concentration of pigments. We discuss these results with respect to the parameters determining colour preferences in bees and with respect to the ecological function of floral pigment concentration within the scope of honest flower signals.

I CALL CHEAT: IS *PENSTEMON DIGITALIS* USING SCENT TO BE DISHONEST?

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The function for nectar volatile organic compounds (VOC's) has been hypothesised as either an attractant or deterrent of nectar-feeding animals. Nectar with a unique odour distinct from the rest of the floral blend could function as an honest cue of resource availability. However what if nectar scent is not correlated with resource quality or quantity? Using the protandrous North American species *Penstemon digitalis,* I suggest floral scents could aid in cheating pollinating insects. Previous work has shown selection pressure to increase emissions of the nectar scent compound S-(+)-linalool in *P. digitalis*. Flowers produce more nectar in the female-phase yet emit no significant difference in scent between the two sexual phases. In addition, nectar removal has no impact in the strength of odour emission from the flower. Therefore these findings suggest that pollinators cannot discriminate between nectar-rich and nectar-poor flowers through the emitted scent. I hypothesise that *P. digitalis* could be transiently using linalool to cheat, that is pollination may not always be rewarded.

AMONG-POPULATION VARIATION IN DIURNAL AND NOCTURNAL FLORAL SCENT IN THE FRAGRANT ORCHID *GYMNADENIA CONOPSEA*

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Gymnadenia conopsea is a nectar-rewarding and fragrant orchid, highly variable in terms of morphology and phenology. The contribution from diurnal and nocturnal pollinators to seed production and selection on floral traits varies among populations, and *G. conopsea* thus constitutes an attractive system for exploring the relative role of diurnal and nocturnal pollinators in driving floral differentiation. In particular, floral scent is thought to evolve in response to pollinator-mediated selection. As a first step toward understanding evolution of floral scent in *G. conopsea*, we investigated whether (1) floral scent varies qualitatively and quantitatively within and among populations, and (2) the cycle of scent emission differs among populations located at different latitudes. We expected that in southern locations the peak of scent emission should be during night to attract nocturnal pollinators, while in northern populations the peak should be reduced and/or shifted toward an earlier period of the day, as the nocturnal pollinators are less abundant and contribute less to reproductive success at this latitude. Using dynamic headspace sampling, we collected scent samples at day and night for ca 20 individuals in each of six populations at different latitudes, four in southern Sweden and two in mid-Norway. Preliminary data indicate qualitative and quantitative differences in floral scent between day and night, and that this daily variation is consistent among populations, independently of latitude. Scent profiles were similar to previously reported analyses from populations in central Europe. This suggests conservatism of floral scent throughout the distributional range, despite mosaic variation in the composition of pollinator communities encountered by this semi-generalist orchid species.

EFFECTS OF PHENOLOGICAL MATCHING ON TRAIT SELECTION IN A PLANT-HERBIVORE SYSTEM

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During the summer of 2014, we conducted experiments in order to record how herbivore mediated genotypic and phenotypic selection on plant flowering traits depend on the degree of phenological matching between plants and herbivores. As study system, we used *Cardamine pratensis*, a perennial grassland herb, and the butterfly herbivore *Anthocaris cardamines,* who is sensitive to the phenological stage of the plant. The butterfly oviposits upon flower buds, and the butterfly larvae consume most of the developing reproductive tissues, leading to negative effects on several components of fitness. In the experiments, we introduced female *A. cardamines* to *Cardamine* populations in different phenological stages. Each experiment was conducted with a different mean phenology of the plant population, while the butterfly phenology was manipulated and held constant. We hope that the analyses of the data will provide insights to the effects of synchrony on butterfly preference and how this might affect herbivore-mediated selection on flowering time, by experimentally linking synchrony directly to trait selection.

POLLINATOR DECEPTION INCREASES OUTCROSSING – AN EXPERIMENT USING ROBOTIC FLOWERS

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Effect of spatial structure of plant populations (homogenous/patchy) and rewarding of pollinators (reward/no reward) on the degree of cross-pollination was tested in this factorial experiment. The study was carried out in laboratory conditions with bumblebees (*Bombus terrestris*) and with a new type of artificial flowers. The system we developed is automatized and mechanistically reliable with controllable filling rates and infra-red sensors as motion detectors. In non-rewarding treatments pollinators moved longer distances between visitations than in rewarding treatments, indicating higher outcrossing. In patchy-rewarding treatment most movements between flowers happened inside a patch. With no reward, a higher proportion of movements happened between patches and with much greater variance. In both spatial structures rewarding of pollinators induced short flight distances with small variance between individual bumblebees. In non-rewarding treatments it was not only the average flight distances that were higher, but also the variance between individual bumblebees was much greater. This suggests higher likelihood for long flight distances and in plant´s point of view, possibly a higher quality of pollen. Our results indicate considerable variability in the learning abilities of naive bumblebees.

THE COST OF VEGETATIVE PROPAGATION IN CONDITIONS WHERE THE OFFSPRING BRING NO PROFIT FOR THE PARENTAL PLANT

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Clonal growth is advantageous where horizontal spread is favoured over vertical growth and in stressful environments. How quickly plants spread depends on species and on plant size so must the price of vegetative propagation also depend on species. There is no studies, where the cost of vegetative propagation is shown when parent plant can´t use assimilates from siblings. The aim of our study was to find out - how costly is it for clonal plants to produce off-springs if they bring no profit for parental plant. We conducted an experiment where the half of plants of *Elymus repens* (guerrilla plant) and *Alopecurus pratensis* (phalanx plant) were planted through the cover laid on the soil (fertile and unfertile soil) and half of plants directly to the soil. Different growth forms reacted differently. *Alopecurus pratensis* as a plant with tussocky growth form choose possibility to escape from stressful environment with help of seeds. Covered plants flowered and produced more seeds in fertile and in unfertile soils, but there was no difference between covered and uncovered treatment on total plant biomass. *Elymus repens* as a plant with long rhizomes reacted differently and the soil fertility played bigger part in it. In fertile soils plant total biomass was lower in covered treatment and in unfertile soils the total length of rhizomes was longer and also those plants had more seeds. We conclude that it is costly for plants to produce siblings without of their help, but it depends on soil fertility and plant form.

ANDROMONOECY BEYOND SOLANUM: A TENTATIVE REVIEW

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Andromonoecy is a sexual system in which individual plants bear both hermaphroditic (h) and male (m) flowers. The main (non exclusive) hypotheses for the evolution of andromonoecy are: (1) sexual allocation related to reallocation of resources away from flowers with low potential female success to increase their potential male succes, (2) increase of male success (pollen export), (3) increase of pollinator attraction, (4) minimization of herbivory on female flowers. Although these hypotheses were put forward about 30 years ago, the extent to which they have been tested is variable and, in general, low. *Solanum* has been considered as a model genus for studying andromonoecy but we lack a more general view of this sexual system. A tentative review of andromonoecy in 48 species from 15 families indicated that m flowers were, in general, smaller (including androecium) than h flowers. In general, m flowers had less, not more, pollen than h flowers and its size, viability or germination were not consistently higher than the one of h flowers. Data on the relative performance and siring ability of m vs. h flowers pollen are almost lacking. Studies addressing the role of m flowers as pollinator attractors are equally scarce and yield mixed results. Overall, production of m flowers seems to be related to sequential adjustment of resources but the extent to which this leads to an increase of male reproductive success is still uncertain due to the scarcity of empirical evidence.

COMPARATIVE DEMOGRAPHY AND ENVIRONMENTAL PRESSURES IN SEVERAL SPECIES OF SCANDINAVIAN ORCHIDS

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Environmental pressures such as climate or anthropogenic disturbance have the potential to greatly alter demographic structure. However, populations of different species are likely to respond differently to these pressures due to variation in life history strategies. These differences may be present even when species are closely related. Variation may also occur between populations of the same species at different locations. We used a matrix modeling approach parameterized by generalized linear mixed models (GLMM) to examine the effects of climate and mowing on five closely related species of orchids at two sites in Norway. The two sites consisted of a lower altitude costal site and a higher altitude interior site. Preliminary results show differences both in the direction and magnitude of environmental effects on the population growth rates of each species. Precipitation in particular shows strong effects in species thought to exhibit a strong preference for either high or low water levels. Differences within species at different sites were also notable. These results underscore the need to understand local effects as well as species-level dynamics to accurately assess effect of changes in larger scale factors such as climate on demography.

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