



SCAPE 2007

Århus, Denmark

Organizers: **Jens M. Olesen**
Yoko L. Dupont
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Bodil K. Ehlers

Program for the "SCAPE meeting 2007" at Fuglsøcentret, Aarhus. Denmark

Friday 16. November

16:00 Arrival and registration.

18:00 Dinner.

20:00-21:30 Poster session. Chairperson: Virginia González-Álvaro.

- ◆ *Pollen amino acids, plant taxonomy and specialisation in solitary bees.* Christiane Weiner, M. Werner, A. Hilpert, K.E. Linsenmair, and N. Blüthgen.
- ◆ *Seasonal variation in neighborhood size of Common Ash (Fraxinus excelsior).* Grazyna Bochenek.
- ◆ *Scent and Sensibility: The effects of Thymes aromatic oils on associated plants.* Catrine Groenberg Jensen and Bodil Ehlers.
- ◆ *Two Caribbean plant-pollinator networks.* Tanja Ingversen.
- ◆ *Effects of land use on pollination networks and individual specialization of flower visitors.* Michael Werner, C. Weiner, K.E. Linsenmair, and N. Blüthgen.
- ◆ *Displacement of a native by an alien bumblebee: lower pollination efficiency overcome by higher visitation frequency.* Josefin Madjidian, Carolina Morales, Henrik Smith.
- ◆ *A possible breakdown of heterostyly in Waltheria ovata at the Galápagos Islands?* Christina Bramow, Signe Brandt Larsen and Marianne Philipp.
- ◆ *Comparision of the visitors of Heracleum mantegazzianum and H. sphondylium.* Uli Zumkier.
- ◆ *The fig wasp community of Ficus thonningii: Between-habitat diversity and its impact on the fig/fig wasps mutualism in Kakamega forest, Western Kenya.* Yvonne Hiller and Manfred Kraemer.
- ◆ *The effects of different densities of invasive plant on native plant pollination.* Dara Stanley.

Saturday 17. November

8:00-8:40 Breakfast

8:40-10:00 4 talks: General pollination. Chairperson: Yoko L. Dupont.

- *The ecology of "special" rewards in the tropics: plant-pollinator co-specialisation and web symmetry.* W. Scott Armbruster.
- *Stamen mimicry and pollen eating insects.* Klaus Lunau.
- *Specialized pollination of orchids by euglossine bees in Mexico.* Charlotte Skov.
- ➤ *The parallel evolution of plant-pollinator interactions in African Marantaceae.* Alexandra Ley and Regine Claßen-Bockhoff.

10:00-10:20 Coffee break

10:20-11:20 3 talks: Breeding systems. Chairperson: Roosa Leimu.

- *Andromonoecy and architectural effects in the wild olive.* Carlos Granado-Yela, Balaguer, L., García-Verdugo, C., Vargas, P., Pérez Corona, M.E., Manrique-Reol, E. and Méndez, M.
- *Effects of population size and co-flowering species on reproductive success in a common and an endangered orchid (*Spiranthes spiralis* and *S. romanzoffiana*).* Karl Duffy.
- *Positional effects on fruit mass of *Tragopogon porrifolius* L.* Rubén Torices and Marcos Méndez.

11:20-11:30 short break

11:30-12:10 2 talks: Pollen dispersal/limitation. Chairperson: Roosa Leimu.

- *Pollen limitation within a plant community.* Stein J. Hegland and Ørjan Totland.
- *Pollen donor efficiency in *Silene acaulis*.* Marianne Philipp.

12:15-14:45 lunch and afternoon break

14:45-15:50 3 talks: Networks. Chairperson: Martina Stang.

- ➤ *Spatio-temporal variations in plant-pollinator systems.* Anders Nielsen.
- ➤ *Plant-pollinator networks: adding the pollinator's perspective.* Ana M. Martín González.
- *Regional spatial-scale patterns in bee species composition in Kakamega Forest area, Kenya.* Melanie Hagen and Manfred Kraemer.

15:50-16:10 coffee break

16:10-17:10 3 talks: Networks. Chairperson: Alfredo Valido.

- *Modules in pollination networks.* Jens M. Olesen.
- ➤ *Modularity of pollination networks: Do modules reflect "syndromes"?* Yoko L. Dupont and Jens M. Olesen.
- *Are modules explained by floral properties?* Virginia González-Álvaro and Jens M. Olesen.

17:10-17:30 short break

17:30-18:10 2 talks: Bird pollination. Chairperson: Alfredo Valido.

- ➤ *The structure of nectar bird communities in Wallacea.* Daniel W. Carstensen.
- ➤ *Bird-flower interactions in the Canary Islands.* M^a Candelaria Rodríguez and Alfredo Valido.

18:30 dinner and party

Sunday 18 November

8:00-9:00 h Breakfast

9:00-10:00 3 talks: Invaders. Chairperson: Jane C. Stout.

- ➤ *Bumblebee foraging behaviour on alien *Impatiens glandulifera*: implications for native plant pollination.* Caroline N. Nienhuis and Stout, J.C.
 - *Comparison of floral visitors between the invasive *Senecio inaequidens* and the native *S. jacobaea*.* Valérie Vanparys and Jacquemart A.-L.
- ➤ *Effects of alien invasive *Rhododendron ponticum* on survival and resource sharing in Irish bumble bees.* Anke C. Dietzsch and Jane C. Stout.

10:00-10:30 Coffee break

10:30-11:10 2 talks: Habitat fragmentation/spatial variation. Chairperson: Manja Kwak.

- *Pollination and herbivory in fragmented populations of a perennial forest herb: Balancing effects on plant reproductive success?* Annette Kolb.
- ➤ *Spatial variation in the interaction between *Vincetoxicum hirundinaria* and its specialist herbivores: leaf chemistry, plant fitness and herbivore damage.* Anne Muola, Laukkanen, L., Riipi, M., Mutikainen P. and Leimu, R.

11:10-11:30 Concluding remarks and planning of the next SCAPE meeting.

11:45 Lunch and departure.

ABSTRACTS - Poster session

Pollen amino acids, plant taxonomy and specialisation in solitary bees

C. Weiner, M. Werner, A. Hilpert, K.E. Linsenmair, N. Blüthgen

Lehrstuhl für Tierökologie und Tropenbiologie, Biozentrum, Universität Würzburg, 97074 Würzburg, Germany.

Knowledge about taxonomic and ecological trends in pollen composition could be important for understanding host plant selection of oligolectic bees. In this study, pollen samples from 73 species were analysed for free and protein-bound amino acids. The composition of amino acids varied significantly between plant species, but taxonomically related species had a similar composition. However, pollen sources of oligolectic bees, on average, did neither show a more balanced or significantly different amino acid composition nor higher total concentration of amino acids compared to pollen sources solely used by polylectic bees.

Seasonal variation in neighborhood size of Common Ash (*Fraxinus excelsior*)

Grazyna Bochenek.

University of Göteborg, Sweden.

In any given population of *Fraxinus excelsior* individual trees will flower at different times. It depends on various microclimatic and genetic factors that are difficult to partition. However, it is usually characteristic to some individuals to be "early" or "late". This phenological variability may imply that certain mother trees generate a larger share of the total genetic variation in a population than others. Theoretically, individuals flowering in the local peak season will produce seeds through inbreeding or biparental inbreeding and therefore contribute less to genetic variation of the population. On the other hand, trees that flower in the beginning or at the end of the flowering season may receive pollen, though very little, from distant populations.

To study seasonal difference in neighborhood area we chose two previously mapped and genotyped *Fraxinus excelsior* populations: "Delsjön" and "Eklanda" stands located in the outskirts of Göteborg (Sweden): During three successive flowering periods, the populations have been visited, and the date when each studied tree opened its buds was recorded. In this way, trees flowering outside the local pollen peak were identified. Three trees from each group: "early" or "late" were marked, and their fruits were collected in the autumn. Embryos from 20 seeds from each tree were genotyped using five highly polymorphic microsatellite loci. By comparing the obtained data with the list of genotypes of all male trees in the populations, the potential fathers were identified. In the poster we are presenting the estimated influence of flowering phenology on the distance between mating trees and possible input from foreign populations.

Scent and Sensibility. The effects of Thyme oil on associated plants

Catrine Groenberg Jensen and Bodil Ehlers

Department of Ecology and Genetics. University of Aarhus, Denmark.

Plants of the genus *Thymus* produce aromatic oil containing terpenes. Terpenes can have allopathic effects on its biotic environment, including the associated plants in its close vicinity. Associated plants of Thyme have recently been shown to exhibit local adaptation to the presence of specific thyme terpenes. However little is known regarding levels of genetic variation for local adaptations to these aromatic oils. The monoterpene carvacrol is the main constituent of the aromatic oil in Danish *Thymus pulegoides* populations. In our study we examined the effects of carvacrol on the performance of *Agrostis capillaris* originating from populations where *T. pulegoides* is either

present (“experienced” *Agrostis*) or absent (“naïve” *Agrostis*). We found that carvacrol treatment significantly reduced above ground biomass compared to control treatment in 3 populations. Moreover we found a significant effect of family (half-sibs) in all populations, but only in one population were the interaction between treatment and family significant. Our preliminary results show that carvacrol significantly affect the performance of *Agrostis*, and that there is genetic variation present for the response to growing with carvacrol. On the variable measured (above ground biomass) we find no evidence for a difference between the two “experienced” and the one “naïve” population, and hence no indication of local adaptation to carvacrol. These results are the first results of an ongoing study including three associated species from several different populations.

Two Caribbean plant-pollinator networks.

Tanja Ingversen, Dept. Ecology and Genetics, University of Aarhus, Denmark.

A Jamaican plant-pollinator network (45 pollinator, A , and 29 plant species, P ,) and a Dominican ($A = 44$, $P = 31$) network were both analyzed for a set of parameters. Plants were found to be more generalized than pollinators, and most specialists interacted with generalist species of the other assemblage which made the network asymmetrical. A successive removal of species according to decreasing degree and betweenness showed that *connector* species (*i.e.*, those with high betweenness) were most important to network stability. Significant modularity was only observed in the Jamaican network and did not influence its stability with respect to simulated species extinction.

Effects of land use on pollination networks and individual specialization of flower visitors

M. Werner, C. Weiner, K.E. Linsenmair, N. Blüthgen

Lehrstuhl für Tierökologie und Tropenbiologie, Biozentrum, Universität Würzburg, 97074 Würzburg, Germany.

In a recently initiated project, specialization of flower visitors will be compared across grasslands and forests along a gradient of land use intensity. We will focus on resource-based mechanisms that may determine pollinator communities including all flower visiting insects in different habitats.

The project is part of the ‘Biodiversity Exploratories’ funded by the German Research Council, addressing the relationship between land use, biodiversity change, and ecosystem functioning for selected taxa and guilds across three large-scale and long-term research sites. The sites are distributed from southwest to northeast Germany, comprising the biosphere reserves Schorfheide/Chorin, Swabian Mountains and the Hainich-Dün region.

The specialization of flower visitors will be investigated on species, population and individual level and related to land use type and landscape context. We will analyze the surrounding environment of each site for important structures that influence the distribution of flower visitors, e.g. mass flowering crops such as oil seed rape and potential larval habitats. For analysis of specialization and flower constancy, we will use direct observation methods and identification of pollen that had been collected by pollinators (e.g. by investigating feces of hoverflies).

In a pilot study from May to August 2007, 20 extensively and 20 intensively used meadows were compared. The abundance of important pollinator taxa (hoverflies, honeybees, bumblebees and solitary bees) was highly variable in space and time, but their average abundance did not differ significantly between both habitat types.

Displacement of a native by an alien bumblebee: lower pollination efficiency overcome by higher visitation frequency

Josefin Madjidian, Carolina Morales, and Henrik Smith

Dept. of Plant Ecology and Systematics, University of Lund. Lund, Sweden.

The displacement of a native by an alien pollinator might affect the pollination of plants, if native and alien visitors differ in pollination effectiveness. Since its invasion in 1994 into South-West Argentina, the introduced European bumblebee *Bombus ruderatus* has continuously increased in abundance, along with a parallel decrease in the abundance of the native *Bombus dahlbomii*. In order to evaluate the impact of the ongoing displacement of the native by the alien bumblebee, we compared the pollinator effectiveness (i.e. the combination of pollinator efficiency per visit and visitation frequency) of both bumblebee species, as well as related pollinator traits that might account for potential differences in pollinator efficiency. Native *B. dahlbomii*, which has a larger body and spent more time per flower, was the more efficient pollinator compared to the alien *B. ruderatus*, both in terms of quantity and quality of pollen deposited per visit. On the other hand, *B. ruderatus* was a much more frequent flower visitor than *B. dahlbomii*, which has resulted in that *B. ruderatus* nowadays is a more effective pollinator of *A. aurea* than its native congener. Nevertheless, comparisons with historical records of *B. dahlbomii* abundances prior to *B. ruderatus* invasion suggest that the overall pollination intensity of *A. aurea* might have declined as a consequence of the displacement of its main pollinator by the introduced congener.

A possible breakdown of heterostyly in *Waltheria ovata* at the Galápagos Islands?

Christina Bramow, Signe Brandt Larsen and Marianne Philipp

Department of Biology. University of Copenhagen. Denmark.

According to Baker's rule (Baker 1955), self-compatibility should be necessary for long-dispersing species, as it provides reproductive assurance when the density of mates is low. It is therefore surprising that *Waltheria ovata*, with its highly specialised breeding system, has successfully colonized all of the Galápagos Islands, situated more than a thousand kilometres off the shore of Ecuador. *Waltheria ovata* is in possession of a heterostylous breeding system that assures outcrossing by the two morphs that differ reciprocally in heights of stigma and anthers, referred to as pin and thrum. The system is accompanied by an incompatibility system preventing intramorph fertilizations. In pollination experiments we examined the ability of seed set following passive and active self-pollination. We also examined the seed set following intra- and intermorph pollinations. We found that *Waltheria ovata* is able to set seed after intramorph pollination. This suggests that the heterostylous breeding system has changed in response to the difficulties in the establishment of *Waltheria ovata* at the isolated Galápagos Islands. There might be an evolutionary potential for development of monomorphic populations of *W. ovata*.

Comparison of the visitors of *Heracleum mantegazzianum* and *H. sphondylium*

Uli Zumkier

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Invasive to many countries, the Giant Hogweed (*Heracleum mantegazzianum*) is known for its threat for human health and biodiversity. While these aspects are well explored little is yet known on the pollinators of the invader. Also unknown is the impact of the invader on co-occurring native plants with a similar flowering-phenology and -time, in this case *Heracleum sphondylium*. The experiments in this study are made in order to analyze the relationship of the two plants based on

the following hypotheses: 1. *H. mantegazzianum* and *H. sphondylium* have a common range of visitors and share their pollinators. 2. The invasive plant is more attractive to pollinators leading to negative competition effects for the native plant. Data of the first year of the field study conducted to validate the first hypothesis will be presented.

The range of pollinators for the two plants is similar, ten morphospecies, that visited these plants regularly, could be distinguished. During an observation period of 10 min. there was an average of about 9 visits on *H. sphondylium* while about 16 visits on *H. mantegazzianum* were recorded. The higher number of visitors for *H. mantegazzianum* is not surprising, as umbels of the invader compared to the native plant are much larger. Flies (especially *Lucilia* sp.) and hoverflies (*Eristalis* sp.) were the most frequent visitors on both plants. Diversity (expressed as Renyi-index) of the visiting insect species does not differ. However, there are significant differences in the abundance of certain species. Especially honeybees (*A. mellifera*) seem to prefer *H. mantegazzianum* to *H. sphondylium*. In a given time visits of honeybees occur on *H. mantegazzianum* ten times more often than on *H. sphondylium*. In conclusion the spectrum of visitors seems to be the same, but each species may have a preference for a certain plant. If these interactions have an effect on the pollination of the two plant species has yet to be revealed.

The fig wasp community of *Ficus thonningii*: Between-habitat diversity and its impact on the fig/ fig wasps mutualism in Kakamega forest, Western Kenya

Yvonne Hille and Manfred Kraemer

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Fragmentation in rain forests usually results in differences and losses of plant and animal species richness. Especially species-specific interactions may be affected by fragmentation and deserve extraordinary attention and applied conservation efforts. Whether effects of habitat fragmentation exist in the fig/ fig wasps mutualism, the influence of different stages of fragmentation were investigated on *Ficus thonningii* and its fig wasp community.

My studies reveal that fig wasp diversity differs along forest distance gradients. The proportion of the pollinator wasps is the lowest in the primary forest (Kakamega forest), where the smallest figs are most abundant. This is due to high pollinator parasitism rates recorded in small figs and consequently in the primary forest. Bigger figs exclude parasitoids, depending on the length of their ovipositor. This is attributed to enlarges in fig walls of fruits. The lowest proportion of pollinator parasitism rates and high proportion of pollinator wasps are found in the highly fragmented habitat (Farmland), due to the occurrence of big sized figs. Finally, seed set of *F. thonningii* is randomly distributed in different fig diameters. However, the best ratio of seeds and seed parasitism rates to attain the best benefit for its reproduction is achieved in intermediate and big figs. Consequently the highest seed sets were found in the fragmented habitat type with forest character (Kisere) and in the highly fragmented habitat.

Decrease in fig diameters may result in local reduction of the pollinator wasps and may transform this obligate interaction between figs and fig wasps into a parasitoid/ host system. In addition, the consequences may lead to local reduction and in some extreme cases to local extinction of *F. thonningii*, which is a keystone species in tropical ecosystems. This may achieve diversity displacements and extinction of rain forest animals.

The effects of different densities of invasive plant on native plant pollination

Dara Stanley

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Invasive plants compete with native species for both abiotic and biotic resources. However, the nature of this competition is very variable. Previous studies have rarely looked at the impact of density of invasive plant stand on this interaction. This study aims to investigate the effect of invasive plant density on native plant pollination. The results would have implications in the study of invasive plant mechanisms, conservation and management. Two invasive species, *Rhododendron ponticum* and *Impatiens glandulifera* were used, compared respectively to the native species *Digitalis purpurea* and *Epilobium hirsutum*. Four variables were tested - Visitation rate, Nectar standing crop, Stigma analysis and Seed set- in natural sites to investigate overall pollination of 3 different densities of both invasive species. Although no statistically significant difference between any of the variables was found in both the *R. ponticum* and *I. glandulifera* sites when analysed using ANOVA, a number of interesting trends were observed. It may be that there is no difference in the effects of different densities of these invasive plants on native plant pollination, or perhaps there are a number of factors that can explain these results.

ABSTRACTS - Talks

The ecology of “special” rewards in the tropics: plant-pollinator co-specialisation and web symmetry.

W. Scott Armbruster

School of Biological Sciences, University of Portsmouth, United Kingdom.

Most plants reward pollinators with nectar or pollen. In the tropics and subtropics, however, a significant proportion of plants offer alternative rewards. These include nutritive rewards, such as oils used by bees for larval provisioning, brood sites for rearing larvae, and non-nutritive rewards, such as fragrances and resin or waxes used by bees for mate attraction or nest construction, respectively. Studies of pollination webs and specialization have focused on nectar and pollen reward systems, largely concluding that generalization is common and that pollination webs may often be asymmetrical (specialist flowers are pollinated by generalist animals and specialist animals visit generalist flowers). This may lead to plants with specialized pollination systems being at no more risk to disturbance-induced extinction than plants with generalized pollination systems. Here I ask: does this pattern also hold for plants with special rewards? The answer seems to be no. Special rewards involve fewer kinds of animals and may lead to specialization; e.g. brood-site systems attract only a few taxa of wasps, moths, or beetles; floral oils attract a few genera of apid bees in the New World and melittid bees in the Old and New Worlds; floral fragrances attract only male euglossine bees (Apidae); floral resins and waxes attract only a few genera of megachilid and/or apid bees. Use of these special rewards by small sets of insect species engenders a degree of specialization in plant-pollinator relationships not seen in most nectar- /pollen-reward systems. There is ample evidence that, despite pre-adaptive origins, most of these systems are co-evolved, at least diffusely. In contrast to nectar and pollen systems, special rewards may often generate symmetrical pollination webs, leading to mutual dependency and possibly greater risk of secondary extinction as a result of disturbance.

Stamen mimicry and pollen eating insects

Klaus Lunau

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Many flowers that are pollinated by pollen-eating insects such as syrphid flies and pollen-collecting insects such as bees visually display yellow anthers and yellow pollen. However, some flowers conceal their stamens and replace visual stamen signals by colourful floral guides that are mimicking visual properties of anthers. Naive hoverflies, *Eristalis tenax*, innately respond towards visual signals of anthers and extend their proboscis towards yellow colour patches. The ultraviolet reflection properties are involved in the fine-tuning triggering the proboscis reaction. Yellow pollen absorbs ultraviolet light. The innate proboscis extension in *Eristalis tenax* is strongly inhibited by admixing small quantities of ultraviolet towards a yellow colour stimulus. Moreover, the hoverflies did not learn to extend their proboscis towards other colour stimuli than UV-absorbing yellow colours despite intense training with coloured sugarwater. Naïve bumblebees, *Bombus terrestris*, innately target at visual stamen signals in a manner that brings the tips of their antennae into contact with the visual stimulus. Chemical cues of pollen control subsequent reactions in hoverflies and bumblebees. Remarkably, the flowers of some diclinous, dichogamous and heterostylous plants visually display both stamens as well as stamen-mimicking yellow, UV-absorbing floral guides. Our hypothesis assumes that additional floral guides hamper bumblebees to discriminate between the flowers of different flowering phases in dichogamous and of different morphs in diclinous and

heterostylous plants. Dichogamous plants need flower-visitors shuttling between the flowering phases to carry pollen from pollen-donating male to pollen-accepting female flowers. Since male- and female-phase flowers differ in the amount of pollen reward, optimally foraging flower-visitors are expected to preferably visit more rewarding male-phase flowers. Diclinous and heterostylous plants need pollen transport between different morphs that differ in properties of stamens and pollen reward. Using naïve bumblebees and dummy flowers simulating the flowering phases, resp. floral morphs, we tested, whether bumblebees discriminate better between the types of dummy flowers in the absence of an additional uniform floral guide. We set up experiments in which 2 types of blue dummy flowers simulated the two flowering phases: T1 dummy flowers offered 7 μ l of 50% sugar solution and displayed a small yellow spot simulating available yellow pollen; T2 dummy flowers offered 7 μ l of 10% sugar solution and displayed a small brown spot simulating emptied stamens; both types displayed an additional small yellow spot simulating a floral guide. After 300 approaches of bumblebees towards dummy flowers, still 51% of the approaches towards the less rewarding T2 ended up with a landing reaction, and 76 % of the approaches towards T1. In a control experiment with dummy flowers without additional floral guide, only 15% of the approaches towards the less rewarding T2 ended up with a landing reaction, and 75% of the approaches towards T1. The proportion of bumblebees that landed on less rewarding dummy flowers was significantly different at dummy flowers with and without an additional floral guide (ANOVA, $p = 0.002$, $n = 25$). Additional experiments show, that the position of the floral guide affects discrimination learning, and that bumblebees preferably associate reward with a pollen-yellow colour. We conclude that visual anther signals have a negative effect upon discrimination learning concerning floral guides in bumblebees. We discuss that diclinous, dichogamous and heterostylous plants exhibiting distinguishable flowering phases or floral morphs benefit from the presentation of a floral guide in terms of pollination success.

Specialized pollination of orchids by euglossine bees in Mexico

Charlotte Skov

Copenhagen, Denmark.

Specialization is less common than generalization in pollination systems, yet, in a few cases plants and pollinators appear to have 1:1 relationships. In the American tropics, andro-euglossophilous orchids rely exclusively on male euglossine bees for pollination. The only reward is floral scent, which the male bees collect and store in their hind legs. Each orchid species produces a unique floral scent and each bee species has particular scent preferences. Due to chemical specificity, each orchid species rarely is visited by more than a few species of the available bees. I studied scent source use in a community of euglossine bees in the tropical dry forest of Pacific Mexico. I used 21 chemical compounds to attract male bees and scored the number of males with orchid pollinaria for each species. Of 1,535 males from 11 species, 27 males from four species carried pollinaria from five orchid genera. Each bee species carried pollinaria from a distinct orchid genus; one bee species carried pollinaria from two genera. Three of the orchid genera are unknown from the coastal study area and imply that male bees undertake altitudinal migrations further inland to find their scent sources. Four of the seven species that did not carry pollinaria are known to visit orchids elsewhere. Comparative data from southern Mexico revealed that this apparent case of highly specialized pollination is partly an artifact from the distributional range of both bees and orchids, which in my study area are close to their northern limit.

The parallel evolution of plant-pollinator interactions in African Marantaceae

Alexandra Ley and Regine Claßen-Bockhoff.

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The Marantaceae (ca. 550/31) are a pantropically distributed family of herbs and lianas from the order Zingiberales renown for their irreversible explosive pollination mechanism with secondary pollen presentation. The complexity and uniqueness of this mechanism within the Zingiberales arises the hypothesis that it might be an evolutionary key innovation. Extensive field investigations in Gabon (34 ssp.) including different morphological types in the pollination mechanism in two phylogenetically unrelated clades have elucidated a remarkable even higher floral diversity within these different morphological types and clades. This is correlated with flower ecological parameters (e.g. nectar sugar concentration and volume) and four guilds of specialised plant-pollinator interactions. The latter include pollinators such as *Amegilla*, Halictidae, *Xylocopa*, nectarbirds. Independent of clades two ecological strategies become apparent: competition avoidance for pollinators through short but intensive consecutive flowering of species and pollinator sharing between morphologically similar species by sparsely parallel flowering over a long time. Furthermore, pollination and bagging experiments have shown that all species are self-fertile including two autogamous species. Pollen is densely packed with a P/O-ratio of (2,2 -) 35 to 140 which might be a hint to a precise pollen transfer mechanism during the single pollination chance of each flower. Considering the phylogenetic background, a strong parallel evolution in floral morphology and plant-pollinator interactions becomes apparent among the two African clades. This obviously indicates similar selection pressures in the course of evolution which act independently on different morphological pollination mechanisms.

Andromonoecy and architectural effects in the wild olive

Granado-Yela, C.1,2; Balaguer, L. 1; García-Verdugo, C. 1,2; Vargas, P. 2; Pérez Corona, M.E. 3; Manrique-Reol, E. 4 and Méndez, M. 5.

1. Department of Plant Biology I. Complutense University of Madrid. Spain.
2. Royal Botanical Garden of Madrid, CSIC. Spain.
3. Department of Ecology, Complutense University of Madrid. Spain.
4. Center of Environmental Sciences, CSIC. Madrid. Spain.
5. Area of Biodiversity and Conservation. Rey Juan Carlos University. Madrid. Spain.

All the representatives of the genus *Olea*, including the wild relatives, are andromonoecious. Andromonoecy is a breeding system in which an individual plant produces both male and hermaphroditic flowers. Male flowers result from gynoeceum abortion at varying stages of gynoeceum development, often to complete resorption, and possess a non-functional pistil.

The aim of this study was to analyze which environmental and morphological variables are related to sexual expression in *Olea europaea* L. subsp. *guanchica*, an endemism from the Canary Islands. We studied a xeric and a mesic population in each of three of the occidental islands in the archipelago (Tenerife, La Gomera and La Palma). We also analyzed the structure of the inflorescence (a panicle) in *Olea europaea* L. subsp. *europaea* (Iberian peninsula wild olive) in a population in its limit of distribution, near Madrid. Inflorescences, bearing between 3 and 15 flowers, had a main axis and, in some cases (panicles with 11 or more flowers), two secondary axes at the base of the main one.

The variability found in the intensity of flowering and in the frequency of male and hermaphrodite flowers depended on the year, population, individual, branch, and even inflorescences inside the same branch. This variability is interpreted as part of an overall reproductive strategy that adjusts maternal investment in response to available resources and environmental conditions.

The phenotypic femaleness (measured by the G index) was positively correlated with SLA (Specific Leaf Area) and with the size of the canopy, so individuals living in more favourable environments are expected to grow more and express more femaleness.

Male and hermafrodite flowers developed simultaneously within the same panicle. The structure analysis of the inflorescences showed that these flowers were not distributed at random within the inflorescence. An architectural effect was detected, namely a higher probability of developing hermaphrodite flowers at the apex of the inflorescence axes (both principal and secondary) compared to lower nodes. No significant differences in the probability of developing hermaphrodite flowers at the apex of the principal axis and at the apexes of the secondary ones were found.

This apical dominance was stronger in the secondary axes, having the middle regions of these branches the lowest probability of developing hermaphrodite flowers.

The probability of developing hermaphrodite flowers at each position increased with an increase in the number of flowers per inflorescence.

Effects of population size and co-flowering species on reproductive success in a common and an endangered orchid (*Spiranthes spiralis* and *S. romanzoffiana*)

Karl Duffy

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Plant population size and density can affect plant-pollinator interactions and subsequent reproductive success in outcrossing plant species such as orchids. Due to a shortage of conspecific mates and pollinator attention, low reproductive success is expected in small and sparse populations (Allee effects). Therefore, local density may be particularly important for the reproductive success of rare species. Here we present the results of an investigation of the effects of population size and density on reproductive success on two congeneric, nectar-rewarding orchid species in Ireland: *Spiranthes romanzoffiana* and *S. spiralis*. Both species are self-compatible but require pollinators for fruit set. *S. romanzoffiana* flowers approximately one month earlier than *S. spiralis*, is very rare and is listed as 'endangered' in Ireland (Red Data Book, 1988), while *S. spiralis* is more abundant. We selected two relatively large and two relatively small populations of each species and quantified reproductive success by estimating pollinia removal and deposition and fruit and seed set. In addition, within populations, we examined the role of small scale density effects in dense and sparse patches. Furthermore, we examined visitation rates to common co-flowering species over the flowering season to examine the role of co-flowerers and their density on potential competitive/facilitative interactions. Results indicate population size affects reproductive success in *S. romanzoffiana*, with higher levels of pollinia removal and deposition in large populations. Fruit set did not occur in *S. romanzoffiana* despite pollinator attention, but fruit set was high in *S. spiralis*. Implications of findings for the future conservation and management of these species will be discussed.

Positional effects on fruit mass of *Tragopogon porrifolius* L.

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Positional effects entail a variation along an inflorescence in the probability of setting fruits, seeds or in the seed mass of the fruits produced. These positional effects have been attributed to competition for resources among the fruits in the inflorescence, or to architectural effects. They have been mostly studied for elongated inflorescences, where flowers in upper positions show lower

fruit set, seed set or seed mass than flowers in lower positions. We present results of a study on *Tragopogon porrifolius* L. showing a strong positional effect on fruit mass in a capitate inflorescence.

Fruit mass decreased from peripheral to central positions in the capitulum. This decrease was gradual and did not involve a heteromorphism in fruit mass. A flower removal experiment showed that removal of inner flowers increased the fruit size of the remaining, outer flowers; and that removal of outer flowers increased the fruit size of the remaining, inner flowers. This supports the hypothesis that this positional effect is due to competition for resources among fruits of the same capitulum. A germination experiment did not show differences in germination between seeds produced in different positions of the capitulum.

Positional effects such as the one studied here are widespread in Asteraceae. Consistent production of small fruits in the center of capitula could be one evolutionary reason why gynodioecy (outer female flowers, inner bisexual flowers) has often evolved in this family.

Floral size and female reproductive success in three poppy species (poster)

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Floral attractive structures are considered to benefit mainly flowers through increasing pollen export (male function). However, the female function also gets benefits from attraction of pollinators. In addition, benefits for the male and the female function could change as flower size changes, depending of the overall floral display, maintenance costs of large flowers and self-compatibility. In particular, producing a bigger flower could involve not only changes in size but also changes in the relative allocation to attractive, male or female structures, depending on the net benefit for pollen export or receipt of a bigger flower. Such allometric variation in allocation to floral structures should be more important for species producing only one or a few flowers. These ideas were tested for three *Papaver* species differing in the number and size of flowers produced. *P. rhoeas* produced many flowers and was self-incompatible, while *P. hybridum* produced a few flowers and was self-compatible. *P. dubium* produced mostly one flower and literature data indicate that was also self-compatible. *P. rhoeas* and *P. dubium* allocated ca. 40% of dry mass to the corolla, while *P. hybridum* allocated > 50% of dry mass to the gynoecium. A petal removal experiment showed no effect of corolla size reduction in any of the species, although in *P. hybridum* a positive relationship was found between floral size and seed set. The only species showing significant allometric changes in allocation to floral structures was *P. hybridum*, for which an increase in flower size entailed a disproportionate increase in stamen compared to gynoecium mass. Overall, flower size showed little or no correlation to seed set in these species and the allometric changes in allocation to floral structures were not consistent with the data on self-compatibility.

Pollen limitation within a plant community

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The difficulties in attracting pollinators with various behaviours and stochastic fluctuations in abundance in time and space frequently result in pollen limitation in plants (in 62-73% of all biotic pollinated species studied). Pollen limitation occurs when plants achieve a lower female reproductive success compared to their potential, due to inadequate pollen deposition. Reduced pollen availability in plants may be a consequence of smaller pollinator populations, loss of

pollinator species or competitive interactions with other species for pollination. Based on several recent reviews the main expectations are that plant species receiving few visits and/or species that specialised on few flower visitors most likely will experience pollen limited reproduction. Furthermore it is expected that pollen limitation may cause reduced seed and fruit production or quality, which subsequently may affect the germination and survival of young plants and hence influences plant demography and population dynamics.

With this background we examined:

- 1) How common is pollen limitation among a subsample of eleven species within the same plant community?
- 2) Do pollinator specialisation levels or visitation rates explain the variation in the magnitude of pollen limitation among species?
- 3) Using a focal species, *Ranunculus acris*, we ask how increased pollen availability affects reproductive output and subsequent recruitment into the population.

It appears that relatively few species within the community experience pollen limitation. The magnitude of pollen limitation is not related to pollinator specialisation level of plant species, but interestingly it seems that the most attractive species are also the most pollen limited. *R. acris* responds to increased pollen availability by producing heavier seeds that germinates better. Implications of these findings will be proposed.

Based on:

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

Hegland, S. J. and Totland, Ø. 2007. Is the magnitude of pollen limitation in a plant community affected by pollinator visitation and plant species specialisation levels? *Submitted to Oikos*.

Pollen donor efficiency in *Silene acaulis*

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Within the genus *Silene* a diverse array of reproductive systems are found, ranging from dioecy and gynodioecy to hermaphroditism. A large number of studies have been undertaken in order to elucidate the functioning and evolution of the reproductive systems in this genus especially in species showing gynodioecy, gynomonoeicy or dioecy.

In *Silene acaulis* two or three morphs (female, hermaphrodites and males) are found in the populations. A number of studies have looked at several aspects of the reproductive system including sex distribution, fruit set, seed traits, seedling survival, deposition of pollen, effect of relatedness of pollen donors.

To get a more full knowledge of evolution in the reproductive system we decided to look at the pollen competition between hermaphrodite-like individuals against more male-like individuals. Simultaneously pollination with pollen from the two morphs with subsequent determination of the "lucky pollen donor" to the offspring showed that the two morphs sired the expected number of progeny in relation to their number of well-developed pollen grains in the pollen mixture. Male-like pollen donors had, however, more well-developed pollen grains per anther than most hermaphrodites and consequently sired more offspring.

Whether the reproductive system is stable or is developing towards dioecy or hermaphroditism will be discussed.

Spatio-temporal variations in plant-pollinator systems

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Several important structural properties of plant-pollinator networks have been recognized that might be important for the stability, evolution and persistence of these networks. In particular, mutualistic networks have been showed to be very heterogenic, to display a nested structure and to be highly asymmetric. I identified these structural properties in the plant-pollinator networks under study, and showed that these structural patterns prevail also in habitats disturbed by forest management operations.

Studies of ecological interaction systems seek to illustrate the species present and how they interact at a particular point in time. A major problem with studies of multi species interaction systems is that they base their analysis on data cumulated over extended time periods. I have showed that within the plant-pollinator system under study there is a high within season temporal dynamic that is hidden when analysing cumulative data only. I have also showed that the nested structure and the degree-strength relationship prevailed also in networks based temporarily constrained data. However, the number and identity of species, number of links and the connectance value of the networks showed unrealistic values when based on cumulative data, compared to values obtained from networks based on data from shorter time periods.

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Plant-pollinator networks: adding the pollinator's perspective

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Plant-pollinator interactions surveys are typically plant-centered: Pollinators visiting a number of surveyed plants are recorded. This sampling may affect perceived community patterns, such as the disproportionately long tail of specialist pollinators found in most pollination networks. One way to avoid this bias is to include an animal-centered sampling in the study, for example by examining the pollen attached to the bodies of pollinators. Pollen grains may remain on the body of pollinators for several days, and thus pollen analysis provides a reliable record of previous visits. We have studied the pollination community of a Mediterranean scrubland in Northeast Spain combining both methodologies. We recorded 4382 plant-pollinator contacts involving 124 pollinator and 20 plant species, and representing 356 specific interactions. Compared to similar studies, the sampling effort employed in our field survey should be considered satisfactory. Yet, the addition of pollen analyses revealed a very significant number of otherwise undetected interactions (1.45-fold increase), significantly increasing overall connectance. The addition of pollen analysis information revealed two important facts: (1) The level of generalization was much higher than previously thought. The number of hiperspecialists was reduced to almost one half; (2) Pollen analysis was particularly useful to reveal interactions involving rare species, but also infrequent interactions by generalist species. As a result, an increase in both centralization and relative nestedness occurred.

Regional spatial-scale patterns in bee species composition in Kakamega Forest area, Kenya

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Local habitat structure and resource configuration as well as matrix structure appear of great importance to the behaviour and survival of bees. We examined the contribution of three different habitat types (farmland, forest edge, forest interior) to regional diversity in the tropics, and established the differences and overlap in plant-bee community interactions between the nearby habitats. We identified the key species in the three different webs and used network properties, like connectance, nestedness, quantified network to describe temporal and spatial variation. The study was carried out on 18 study sites (6 in each habitat type) in the Kakamega Forest area in Kenya. In total we found a number of 121 bee and 89 plant species involved in the interactions. The highest number of bee species as well as flowering plant species was found at the forest edge. Consequently, in this habitat type the network ($M = 9384$) showed almost double the size of the networks in the farmland ($M = 4958$) and inside the forest ($M = 5049$). Connectance was significantly highest in the farmland (farmland: $C = 3.41$, forest edge: $C = 2.12$, forest: $C = 1.56$). The pollination webs in all three habitat types were highly asymmetric, with the three most involved plant species building 54 – 84% of the network. *Apis mellifera* was the most abundant bee species, and was involved in 60 – 80% of the interactions in the networks. Besides the spatial variation in plant-pollinator interactions, we also found high seasonal variation, with seasons of high flower abundance showing the highest bee species richness. This pattern was found especially inside the forest. There was notable overlap in the communities of different habitat types and habitat types closely resembled each other in terms of their most important plant and bee species.

Modules in pollination networks

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In natural communities, species and their interactions are often organized as non-random networks, showing distinct and repeated complex patterns. A prevalent, but poorly explored pattern is modularity, with weakly inter-linked subsets of species (modules), which, however, internally consist of strongly connected species. The importance of modularity has been discussed for long but no consensus on its prevalence in ecological networks has yet been reached. Progress is hampered by inadequate methods and a lack of large datasets. We analyzed 51 pollination networks including almost 10000 species and 20000 links, and tested for modularity using a recently developed simulated annealing algorithm. All networks with more than 150 plant and pollinator species were modular, whereas networks with less than 50 species were never modular. Both module number and size increased with species number. Each module includes one or a few species groups with convergent trait sets that may be considered as coevolutionary units. Species played different roles with respect to modularity. However, only 15% of all species were structurally important to their network. They were either hubs (i.e. highly linked species within their own module), connectors linking different modules, or both. If these key species go extinct, modules and networks may break apart and initiate cascades of extinction. Thus species serving as hubs and connectors should receive high conservation priorities.

Modularity of pollination networks: Do modules reflect “syndromes”?

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Pollination syndromes are a classification of flowers according to floral characteristics, e.g. morphology and colour, which are thought to be associated with certain groups of pollinators, e.g. bees, flies, beetles etc. The concept of syndromes has been heatedly debated (also at SCAPE!). The main concerns have been the prevalence of generalization of pollination interactions, and that even specialized plants may attract several visitor groups. In the present study, we use a network approach to assess the presence of pollination syndromes. The idea is to detect modules, i.e. groups of species interacting more with each other than with species outside the module. Modules were identified by the algorithm simulated annealing (SA1) using the software recently developed by Guimerá and Amaral (2006). We used a large and well-resolved dataset of plant-pollinator interactions from two heath sites in different landscape contexts. The plant communities of the two study sites are almost identical, while the insect assemblages differ in species composition (about half of the species are shared between sites). All interactions between flowers and flower-visitors were recorded during the entire field season. Insect species were grouped in functional groups and weighted by visitation frequency. Both networks were significantly modular, and module composition was similar at the two sites. Modules typically contained one-two highly connected plant species (hubs) and were dominated by certain functional insect groups. Our results add support to the conclusion that plant-visitor associations are not formed at random, and that certain species interact more strongly than others, forming distinct groups within the network.

Are modules explained by floral properties?

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The substructure of a pollination network from a ruderal plant locality (22 plant species; 363 pollinator species; 695 links) was analysed looking for explanatory patterns. We detected a significant modularity, which provided us nine well defined modules, i.e. solid subgroups well connected internally and less connected externally to each other. Modules consisted of one to five plant species in the same module, and a varying number of insect species. Nine main floral characteristics were considered here to explore the underlying classification of plants into different modules. Only two of these variables were able to explain the module classification: flower depth and flower accessibility. On the other hand, analyses revealed that main pollinator groups were distributed according to their relative species richness in different modules. Some physical characteristics of the pollinators were considered to look for their relationship with the modules, but no significant results were found.

Further analyses should be performed to study the relationship between more detailed functional groups of pollinators not only with the modules they belong to, but also with respect to the roles the plants they visit play in the entire network.

The structure of nectar bird communities in Wallacea

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The biogeographic region of Wallacea comprises a complex combination of nectar bird species. It is the contact zone of sunbirds and honeyeaters and at least three more, true flower-bird families, are resident in the region. The Indonesian distribution of these species was analyzed in order to achieve a biogeographical overview. The analysis produced six distinct species/island modules, four of which were true Wallacean. Further investigation within these modules suggested spatial separation of species by island or altitudinal range and a presumed functional separation reflected in body size.

Bird-flower interactions in the Canary Islands

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Most of Macaronesian island avifauna has an Western Palearctic origin, a region characterized by the absence of current specialist nectar-feeding birds, although the discovery of hummingbird fossil from Oligocene with morphological adaptations to nectarivory has been recently confirmed, suggesting Old World bird-flower interactions in the past. Despite there have been many observations of non specialised nectarivorous birds (mainly *Sylvia*, *Phylloscopus* and *Parus*) as mutualistic agents visiting both introduced and native flowers in Europe, even pollinating them, these species confine the opportunistic use of floral resources to their winter zones related to the scarcity of arthropods at this time of the year. In contrast with mainland populations, the phenomenon of generalist nectar feeding vertebrates as potential pollinators of insular flora has been proposed to have an insular biogeographical distribution according to reported evidences during last decade, explained by the high bird densities (density compensation) combined with lower predation risk they experience, both insular ecological conditions that promote the expansion of their diet including unusual food resources such as nectar or pollen compared to continental relatives.

To test this hypothesis in the Macaronesian Region for the first time, the relative contribution of passerine birds as effective pollinators in the endemic Canarian ornithophilous species *Isoplexis canariensis* (Scrophulariaceae) was examined by three main objectives: (1) identification of flower visitors and their visit frequency; (2) study of the breeding system of *Isoplexis canariensis* (3) evaluation of their role as pollen vectors by specific exclusion experiments. Even though the plant is self-compatible, the great differences found in both fruit and seed set in those flowers that were visited by generalist passerines than in the rest, concluding that there is a need for vertebrate pollinator involvement in this plant species.

Bumblebee foraging behaviour on alien *Impatiens glandulifera*: implications for native plant pollination

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Alien plants constitute 44% of the Irish flora and can negatively affect native plant communities by altering ecosystem processes and community interactions and physically damaging, competing and hybridising with native species. Our knowledge of the interactions between alien flowering plants and native bumblebees is limited and it is not known whether pollinator switching to aliens affects native plant pollination and hence reproductive success.

We investigated whether bumblebees (*Bombus hortorum* and *Bombus pascuorum*) readily switch between the alien (*Impatiens glandulifera*) and two native co-flowering plants (*Lythrum salicaria* and *Stachys palustris*) and assessed the proportion of alien and native plants utilised during foraging bouts in a site located in County Galway, Ireland where *I. glandulifera* has established along river banks. Individual bumblebees were randomly selected and followed while foraging and all plant species, the number of flowers and inflorescences visited, their feeding behaviour (nectar feeding and/or pollen collecting), time spent on each flower and total time elapsed were recorded. In addition, we examined the effect of alien plant density on bumblebee visitation to and seed set of the two native plants. This was done by assessing the transfer of alien pollen to native plant stigmas and subsequent seed set at three *I. glandulifera* densities (low, medium and high). Preliminary results will be discussed.

Comparison of floral visitors between the invasive *Senecio inaequidens* and the native *S. jacobaea*.

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At the end of the 19th century, *Senecio inaequidens* (Asteraceae) was introduced from South-Africa into Europe by wool transport and became invasive about 40 years ago. Very few studies are published about its reproductive biology and its interactions with insect pollinators. The native congener *S. jacobaea* is pollinated by generalist insects. This pair of species allows to disentangle the role of insect pollination in invasion process. Visitor guild, visitation rate, phenology and floral display of the two *Senecio* were compared in two natural invaded sites and in experimental garden in Belgium (over 2 years). Reproductive success was compared in the invaded sites.

S. inaequidens and *S. jacobaea* shared the same visitor guild, though some differences have been detected, due to seasonal effect, as the flowering period of *S. inaequidens* is two or three fold longer than that of *S. jacobaea*. *S. inaequidens* had two-fold higher visitation rate and reproductive success. These results could be linked to the distinct floral displays of the two species, measured as the open capitula density on an individual.

Effects of alien invasive *Rhododendron ponticum* on survival and resource sharing in Irish bumble bees

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The increase in biological invasions and associated threats for biodiversity have been a major concern in recent years. Alien invasive species alter the structure of ecosystems and can modify native ecosystem processes such as plant-animal interactions.

Plant-pollinator mutualisms may be particularly vulnerable to alien invasive species as native outcrossing plant species and their pollinators are already in decline. To date, most research has been focussed on the influences of alien invasive plant species on native plant species' pollination. These studies revealed mainly disruptive or neutral effects on visitation and reproduction of natives. However, invasive flowering plants can also affect native pollinators. They may increase population densities and pollinator diversity by offering valuable floral resources or providing a substitute for a lack of native foraging plants. Contrarily, they may harm pollinators by producing toxic secondary compounds in floral rewards and plant tissues, or displacing native host plants.

Using traditional feeding experiments and molecular methods we investigated these possible effects of an alien plant species, *Rhododendron ponticum*, which is severely invasive in Ireland.

Irish *R. ponticum* is mainly visited by native bumble bee species, in particular by *Bombus lucorum*, *B. pascuorum*, *B. pratorum* and *B. hortorum*. Flowering early in the season, the alien provides required resources at a period when bumble bee queens establish their colonies. Beside its large display of highly rewarding flowers, *R. ponticum* is known to produce nectar and vegetative tissue that contain grayanotoxins, i.e. neurotoxins that interfere with action potentials.

To examine the suitability of *R. ponticum* nectar and pollen as a bumble bee aliment we individually caged workers of *B. lucorum* in a climate chamber and kept them under six different feeding regimes. Neither nectar and/or pollen of *R. ponticum* nor sucrose solution containing neurotoxin significantly reduced the survival rate of bumble bee workers in comparison to nectar and pollen of native *Digitalis purpurea* or commercial bee food.

Furthermore, we estimated and compared the number of bumble bee colonies utilizing invaded and uninvaded field sites by genotyping workers of *B. lucorum* and *B. pascuorum* at six polymorphic microsatellite DNA loci and reconstructing sisterhoods among the individuals. Results and implications for conservation will be discussed.

Pollination and herbivory in fragmented populations of a perennial forest herb: Balancing effects on plant reproductive success?

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In fragmented landscapes, many plant species are confined to remnants of formerly more widespread habitats, with their populations often being small and isolated. Such populations may experience reductions in fitness and viability and become locally extinct in response to a number of factors, including the disturbance of mutualistic plant-animal interactions such as pollination. Habitat fragmentation, however, may have beneficial effects on fitness when also disrupting antagonistic interactions, releasing plants from their herbivores or pathogens. In this study, I investigate fragmentation effects on mutualistic and antagonistic plant-animal interactions, using the non-clonal perennial forest herb *Phyteuma spicatum* (Campanulaceae) as model species. The species is self-incompatible and insect pollinated and also suffers grazing damage through herbivory by roe deer. Using an experimental approach, I specifically examine how population size and isolation affect both pollination and herbivory and how these influence net plant reproductive success.

Spatial variation in the interaction between *Vincetoxicum hirundinaria* and its specialist herbivores: leaf chemistry, plant fitness and herbivore damage

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As stated by the geographic mosaic theory of coevolution, variation in species interactions is the raw material for the coevolutionary process, which takes place over a large geographic scale. One key assumption underlying the process of coevolution is that natural enemies exert selection on plant populations. In this study I examined if herbivores cause phenotypic selection for resistance in their host plant and whether the selection pressure varies among populations. As study system I used populations of a perennial herb, *Vincetoxicum hirundinaria* (Asclepiadaceae), and its three specialist herbivores. The study was conducted in the southwestern archipelago of Finland where

the distribution of the host plant is highly fragmented. Selection imposed on host plants by herbivores was examined by analysing the associations between levels of herbivory, plant fitness and concentrations of a number of secondary chemicals. I found out that in the study area levels of herbivory and plant's reproductive output varied extensively among populations. There was also both quantitative and qualitative variation in leaf chemistry among populations, which means that there is potential variation in plant quality as food for the herbivores. From previous studies we know that herbivores have effect on plant's fitness. On the basis of this study we know that there is spatial variation in the strength of the interaction between *Vincetoxicum hirundinaria* and its specialist herbivores indicating potential for coevolution to occur.

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