

# **Radiations**

**12 - 15 June 2014**

**Institute of Systematic Botany,  
University of Zürich**

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## Friday

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**09:00 - 11:00 Angiosperm Overview** - Elena Conti

09:00 – Susana Magallon - A metacalibrated diversification study of flowering plants

09:30 – Luke Harmon - Progressive Radiations and the Pulse of Angiosperm Diversification

10:00 - Erika Edwards - What is so special about the Miocene?

**10:30 - 11:00 – Coffee**

**11:00 - 12:30 Biotic Interactions** - Peter Linder

11:00 Susanne Renner - Hummingbirds and their plants in time and space

11:30 Steve Johnson - Using ecotypes to reveal the role of niche shifts in plant radiations

12:00 Daniel Kissling - Frugivory and plant radiations

**12:30 - 14:00 – Lunch**

**14:00 - 15:30 Case Studies** - Reto Nyffeler

14:00 - Rick Ree - Causes and consequences of diversification in *Pedicularis*

14:30 – Toby Pennington - *Inga*: a case study for evolutionary radiation in tropical rain forest trees

15:00 - Elena Conti - Processes and outcomes of diversification in Primulaceae: explorations on the functional and evolutionary roles of heterostyly

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**16:00 - 18:00 – Poster session**

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**09:00 - 10:30: Methods** - Colin Hughes

9:00 - Tanja Stadler - A unified analysis of neontological and paleontological data

9:30 - Daniele Silvestro - Opportunities and challenges to investigating plant diversification from the fossil record

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**11:00 - 12:30 Special habitats** - Peter Linder

11:00 - Santiago Madriñán - Patterns and processes of Páramo plant diversification

11:30 - Colin Hughes - Comparative montane plant radiations: from the Andes to the Hengduan Mountains

12:00 - Mark Carine - Island radiations and the evolution of the Macaronesian Island floras

**12:30 - 14:00 – Lunch**

**14:00 - 15:30 Special habitats** - Reto Nyffeler

14:00 - Tony Verboom - Topography as a driver of diversification in the Cape Floristic Region

14:30 - Mike Crisp - Three explanations for mediterranean-climate biodiversity hotspots: small range size, geographic overlap and time for species accumulation

15:00 - Bob Ricklefs - How tree species fill geographic and ecological space in eastern North America

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**16:00 - 17:30 Mixed** - Colin Hughes

16:00 - Peter Linder - Testing the effect of environments and traits on Angiosperm radiations

16:30 - Tim Barraclough - The evolutionary reality of species and higher taxa in plants

17:00 - Christian Lexer - Genomics of the speciation continuum: towards understanding the drivers and limits of radiations

17:30 - Mike Donoghue - Explosive radiations and dying embers in plant phylogeny

**18:00 - 18:10 Close**

**19:00 - 22:00 Boat dinner**

## Sunday

Schynige Platte - Depart 07:30

## Talks

### **A metacalibrated diversification study of flowering plants**

*Susana Magallón (1), Luna Sánchez-Reyes (2), Sandra Gómez-Acevedo (1), and Tania Hernández-Hernández (3)*

- (1) Instituto de Biología, Universidad Nacional Autónoma de México, Mexico;  
(2) Posgrado en Ciencias Biológicas; Universidad Nacional Autónoma de México, Mexico;  
(3) Departamento de Biología Evolutiva; Instituto de Ecología A.C., Xalapa, Veracruz, México.

Angiosperms are characterized by many reproductive and vegetative innovations. However, previous works indicate that the clues to angiosperm success do not lie directly on their innovations, but presumably on further elaborations deployed in particular environments, driving independent radiations. In this study, we investigate angiosperm diversification based on a comprehensive metacalibrated timetree estimated with penalized likelihood and the uncorrelated lognormal method. From a thorough literature-based review of the paleontological record, fossils that reliably represent the oldest members of well-supported clades were selected and implemented as conservative minimum age constraints. The angiosperm crown age was bound within a 95% confidence interval calculated with a method derived from quantitative paleobiology that considers fossil record of the entire group, in the context of a molecular phylogeny. The estimated timetree documents the early rise of many angiosperm families. Using the timetree, we conducted a diversification analysis to identify significant diversification shifts across angiosperms. Our results document that extant angiosperm species-richness and its distribution is the product of several non-synchronous radiations and depletions in independent lineages, which responded to different diversification dynamics in terms of the underlying rates of speciation and extinction; and are associated with a variety of potential intrinsic, ecological and extrinsic drivers.

## **Progressive Radiations and the Pulse of Angiosperm Diversification**

*David Tank (1), Jonathan M. Eastman (1), Matthew W. Pennell (1), Cody E. Hinchliff (2), Pamela S. Soltis (3), Douglas E. Soltis (3), and **Luke J. Harmon** (1)*

Tank, DC, JM Eastman, MW Pennell, CE Hinchliff, PS Soltis, DE Soltis, and LJ Harmon

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(2) Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI

(3) Department of Biology, University of Florida, Gainesville, FL

Most plant species alive today are descended from a common ancestor that lived between 160 and 200 million years ago. Even within this massive radiation of a quarter of a million species, some groups are much more diverse than others. Despite decades of work characterizing angiosperm diversification from both paleontological and phylogenetic perspectives, we still do not have a clear idea of the drivers of differential diversification at broad scales across angiosperms. Our growing understanding of the plant tree of life provides a rare opportunity to investigate angiosperm diversification to try to uncover the major drivers that have led to the diversity of flowering plants. Here we use phylogenetic and taxonomic data to investigate angiosperm diversification dynamics. First, we characterize hot and cold spots of diversification across the angiosperm tree of life. We identify a heterogeneous pattern of rapid radiations nested within other rapid radiations, which we refer to as “progressive radiations.” Second, we show that increases in diversification tend to follow established whole-genome duplication events. Interestingly, these upticks in diversification rates are often not coincident in time with genome duplications, but rather tend to occur on phylogenetic branches that are closer to the present day. These delayed bursts might suggest that genome duplications promote, but are not sufficient, to cause increased diversification. We suggest how such duplications might interact with other biotic and abiotic influences to lead to the progressive pattern of radiations that we see across angiosperm species.

## **What is so special about the Miocene?**

*Erika J Edwards (1)*

(1) Department of Ecology and Evolutionary Biology, Brown University USA

The Miocene spans from 23 ~ 5 million years ago, and while it is a relatively brief period of geological time, a lot happened. It witnessed the birth and expansion of many of our ‘modern-day’ ecosystems, a global transition to a low CO<sub>2</sub> atmosphere, and apparently, a surprisingly large fraction of identified plant radiations- from cycads, to cacti, to tropical rainforest trees. I’ll briefly review studies that have focused on shifts in diversification that occurred during the Miocene, and highlight the commonalities and differences between them. While many radiations occurred within lineages endemic to biomes that were expanding during this time, still others were in contracting biomes- environments which- at least superficially- might have been favored to show higher extinction. If we take analyses at face value, it appears that the Miocene was a truly exceptional time in Earth history, and gave birth to the global plant biodiversity that we now recognize. Alternatively, we may be overestimating Miocene distinctiveness, due to systematic biases in our use of the fossil record and/or our methods of analysis. Or perhaps, we have hit a phylogenetic “sweet spot” – a window of time, not too distant from the present, where the dynamics of speciation and extinction are relatively easier to detect.

## **Hummingbirds and their plants in time and space**

*Susanne S. Renner (1) and Stefan Abrahamczyk (1)*

(1) Institute of Systematic Botany and Mycology, University of Munich, Germany

Hummingbirds and their plants are an example of both *diffuse coevolution*, the evolution of matching traits in interacting guilds, not single interacting species (Janzen 1980), and of *coevolution in the classic sense* of Ehrlich and Raven (1964), i.e., successive radiations, each enabled and followed by new adaptations in one of the partners. Using a chronogram for 221 of the 334 species of hummingbirds and numerous plant chronograms we have investigated three almost-separate bird/plant systems, (i) Caribbean hummingbirds and their plants; (ii) North American hummingbirds and their plants; and (iii) the Andean Sword Bill (*Ensifera ensifera*) and its plants. System iii dates to 11-12 my ago, while systems i and ii date to 7-5 my; all three systems show a gradual build-up of plant species/groups entering the “adaptive zone” of hummingbird pollination; in ii and iii, the oldest plant clade is exactly the age of the oldest local birds, but in the Caribbean, the oldest plant groups is older than the oldest local birds, pointing to possible extinctions and replacements as suggested by Bleiweiss (1998); in all three systems, hummingbird pollination mostly appears to provide the precondition for rapid plant species formation via geographic isolation, rather than drive it by specialization on different bird species.

## **Using ecotypes to reveal the role of niche shifts in plant radiations**

*Steven D. Johnson (1), Jon Ågren (2) and Timo van der Niet (3)*

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(2) Evolutionary Biology Centre, Uppsala University, Sweden;

(3) Naturalis Biodiversity Centre, Leiden University, The Netherlands.

Ecological shifts are considered a major driver of plant diversification as they are associated with functional trait diversification and can promote reproductive isolation. Here we emphasize the value of studying diversification at the ecotype level, where adaptations have spread beyond the population level, but not yet become fixed at the level of species. The ecotype concept was originally applied to plant adaptations to abiotic environments, but is equally useful for studying local adaptations to biotic environments, including pollination niches. Reciprocal translocations remain the fundamental method for quantifying the magnitude of adaptive differentiation among ecotypes. Further experiments are required to identify the key functional traits contributing to adaptive differentiation and the relative importance of abiotic and biotic agents of selection. A review of the existing literature shows that traits that diverge between ecotypes are often also those that characterize the broader radiation of the lineage. Floral adaptation to pollinators can lead to reproductive isolation. However, the reproductive isolation that splits plant lineages is more typically due to geographical factors or habitat specialization.

## **Frugivory and plant radiations**

*W. Daniel Kissling (1)*

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Frugivory (i.e. fruit eating and seed dispersal by vertebrate frugivores) is of key importance for the structure and functioning of tropical ecosystems, but to what extent it has played an important role in plant radiations remains unclear. Frugivore seed dispersal affects gene flow and genetic divergence of plant populations and can therefore have important macroevolutionary consequences for allopatric plant speciation, especially via the frequency of long-distance dispersal events. Here, I provide an overview about the potential role of vertebrate frugivores in plant diversification, especially in relation to plant dispersal mode, fruit size, frugivore specialization, understory adaptation, and dispersal syndromes. Current evidence for a strong role of frugivores in plant radiations is ambiguous, but newly available phylogenies in combination with trait data and ecological networks will allow more rigorous insights in the near future. Further progress can be made by (1) testing the effects of interaction-relevant plant traits on diversification rates of fleshy-fruited plant lineages, (2) quantifying the phylogenetic structure of plant-frugivore assemblages and seed dispersal networks, and (3) analysing co-variation in regional multi-trait combinations of frugivores and plants, especially in the context of generalized coevolution and coevolution through mutualistic networks.

## Causes and consequences of diversification in *Pedicularis*

*Richard Ree (1) and Patrick Kuss (2)*

(1) Field Museum of Natural History, Chicago, USA;

(2) Institute of Systematic Botany, University of Zurich, Switzerland.

*Pedicularis* (Orobanchaceae) is a N Temperate/Boreal clade of hemiparasitic herbs notable for its species richness (~770 spp), especially in the greater Sino-Himalayan region, where species exhibit high endemism, ecological sympatry, and spectacular floral diversity. What processes are responsible for these patterns? Establishing a phylogenetic framework to address this question has proved challenging due to its large size, wide distribution, and incomplete (and often conflicting) taxonomic knowledge, but a large collaborative effort has now yielded near-comprehensive sampling of *Pedicularis* (~420 spp; 2,440 vouchers) throughout its range. While Sanger sequencing of seven nuclear and chloroplast regions fails to resolve the backbone of *Pedicularis* with confidence, the phylogeny nevertheless reveals a trove of insights into the ecological factors potentially driving more recent divergences between – and within – species, as well as broader trends in character evolution and biogeography. Analysis of genomic RAD data not only resolves the backbone of the tree with strong support, but also enables detection of interspecific gene flow, suggesting great potential for improved estimates of phylogeny. As a case study in evolutionary radiation, *Pedicularis* provides much to ponder about the drivers of lineage diversification, especially the nature of general and proximate causes.

## ***Inga*: a case study for evolutionary radiation in tropical rain forest trees**

*Phyllis Coley (1), Thomas Kursar (1), **Toby Pennington** (2), James Nicholls (3), Catherine Kidner (2,3), Graham Stone (3), Kyle Dexter (3), Natasha Wiggins (1), Alexander Weinhold (1), Maria Jose Endara (1), Tiina Särkinen (2), Matt Lavin (4), Alex Twyford (1), James Richardson (1), Ruth Hollands (1), Camilla Drake (1), Tim Baker (5)*

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(5) University of Leeds, UK

Case studies of evolutionary species radiations have not been well developed in the world's most species-rich biome, tropical rain forest. *Inga*, with 300 species, evolved in the last six million years and represents one of the most rapid radiations of neotropical rain forest tree species. It is also one of the most abundant and species-rich genera at any forest site. We evaluate how interactions with herbivores may have been involved in the *Inga* radiation. *Inga* has a diversity of defences to counter herbivores, including patterns of leaf growth, attracting defensive ants, and the deployment of different chemicals. We outline how: (i) *Inga* species with little divergence in morphology or habitat preference have divergent defence strategies; (ii) more closely related species are not more similar chemically; (iii) coexisting species are over-dispersed for chemistry; and (iv) some herbivores choose hosts based on defences and not on phylogenetic similarity. All these factors are consistent with a key role for herbivore pressure in both the *Inga* radiation and the maintenance of local *Inga* community diversity. We show that sympatric communities of *Inga* species have not originated by local or regional speciation, but have been assembled by long-distance dispersal over biogeographic timescales.

**Processes and outcomes of diversification in Primulaceae:  
explorations on the functional and evolutionary roles of heterostyly**

*Elena Conti (1), Barbara Keller (1) and Jurriaan de Vos (1,2)*

(1) Institute of Systematic Botany, University of Zurich, Switzerland;

(2) Department of Ecology and Evolutionary Biology, Brown University, USA.

The spectacular diversity of angiosperms has often been linked to floral evolution. Most flowers are hermaphroditic, thus enabling self-fertilization, which can lead to inbreeding and its disadvantages. Several strategies have therefore evolved to avoid selfing while enforcing outcrossing, and heterostyly is one of the best studied. Occurring in 28 families, heterostyly denotes a floral polymorphism consisting of flowers that differ in the reciprocal positioning of sexual organs and in mating type, ensuring allogamy. Groups characterized by heterostyly are often, but not always, more species-rich than their non-heterostylous relatives, prompting the question of whether this floral polymorphism promotes diversification and how. Primulaceae, with their rich history of biological studies - dating back to Darwin - and wealth of data, represent a prime model to investigate both the mechanisms by which heterostyly might promote diversification and the macro-evolutionary outcomes of this trait. The main questions addressed include: How does heterostyly work within and between species? Does it promote elevated diversification? Does it affect mainly speciation or extinction rates? Are the effects of heterostyly on diversification linked with mechanisms unique to this floral syndrome or not? Do gains and losses of heterostyly have different macro-evolutionary effects at shorter vs. longer temporal scales?

## **A unified analysis of neontological and paleontological data**

*Tanja Stadler (1), Tracey Heath (2) and John Huelsenbeck (2)*

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Molecular (neontological) and fossil (paleontological) data are observations from the same speciation and extinction process. However, when dating (time-calibrating) phylogenies, we typically assume different models for the generation of the extant species phylogeny (obtained from the molecular data) and for the fossil data. While extant species phylogenies might be modelled through a speciation and extinction process, fossil occurrence times are typically modelled through arbitrary calibration densities. I will discuss our new approach assuming a speciation and extinction model simultaneously for both data types. We show in a simulation study the improvement in accuracy of dating phylogenies, while avoiding arbitrary calibration densities. I will end the talk discussing how to further estimate speciation and extinction rates based on both fossil data and molecular data.

This is joint work with Tracy Heath and John Huelsenbeck. The method is implemented in DPPDiv (<http://phylo.bio.ku.edu/content/tracy-heath-dppdiv>) and the manuscript is available on arXiv:1310.2968.

## **Opportunities and challenges to investigating plant diversification from the fossil record**

*Daniele Silvestro (1), Borja Cascales-Miñana (2), Christine D. Bacon (1,3), Alexandre Antonelli (1)*

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(3) Laboratorio de Biología Molecular (CINBIN), Department of Biology, Universidad Industrial de Santander, Bucaramanga, Colombia

The quest for understanding macroevolutionary dynamics through time has boosted a methodological development to estimate speciation (or origination) and extinction rates using fossil and phylogenetic data. While fossil data are generally recognized to provide the most direct information about changes in diversification rates, their use in macroevolutionary analyses is often limited by their incompleteness and inaccessibility. These problems are especially prevalent in plants, since paleobotanical evidence is generally difficult to retrieve from public databases, sparsely sampled, and often not identified to the species level. How extensive is the available plant fossil record and how informative is it to reconstruct speciation and extinction rate dynamics over large time scales? Here we compile a comprehensive plant fossil data set (> 35,000 occurrences) spanning the entire Phanerozoic history of plant life from the Silurian to the present-day from the Paleobiology database ([www.paleobiodb.org](http://www.paleobiodb.org)). We use a novel approach that jointly estimates the preservation process to reconstruct longevity of plant lineages and the underlying diversification process of three main ecological groups of tracheophytes: spore-bearing plants (“ferns and allies”), non-flowering seed-plants (“gymnosperms”), and angiosperms. Our analyses allow us to explore origination and extinction dynamics through large time scales and investigate how each plant group responded to past periods of climate change and mass extinction events.

## **Analysis and visualization of complex macroevolutionary dynamics with BAMM**

*Daniel L. Rabosky (1)*

(1) Department of Ecology and Evolutionary Biology and Museum of Zoology,  
University of Michigan, Ann Arbor, Michigan 48109 USA

Understanding the deep-time dynamics of speciation, extinction, and trait evolution is a central challenge in evolutionary biology. Phylogenetic trees provide an important window into these dynamics, but can be difficult to study on account of the heterogeneous mixtures of processes that have shaped them. I will describe BAMM and BAMMtools, a set of computational tools that we have developed for studying complex mixtures of macroevolutionary processes on phylogenetic trees. BAMM uses reversible jump Markov chain Monte Carlo to explore a vast state space of candidate models and can identify mixtures of time-constant and time-varying diversification processes within single phylogenetic trees. I will present new methods for visualizing diversification dynamics and for assessing model support using output from BAMM analyses. I will apply BAMM to several empirical datasets to illustrate how novel applications of standard Bayesian statistical tools can lead to new insights into the causes of evolutionary rate variation in nature.

## **Patterns and processes of Páramo plant diversification**

*Santiago Madriñán (1)*

(1) Laboratorio de Botánica y Sistemática, Universidad de los Andes, Bogotá, Colombia

Páramos are tropical high elevation ecosystems located above the forest line in the northern region of the Andes. They have a characteristic and unique biota that is the result of complex evolutionary processes. This has produced a high number of endemic plant and animal species, distributed in an archipelago-like environment. Akin to the Galapagos Islands, made famous by Darwin's study on the evolution of finches, and seen as the quintessential laboratory for the study of evolutionary processes, we show that the Neotropical Páramos, a continental island system, offer a host of examples of comparable biological diversifications. We compared diversification rates of lineages in fast evolving biomes using 73 dated molecular phylogenies. We demonstrate that average diversification rates of Páramo plant lineages are faster than those of other reportedly fast evolving hotspots and that the faster evolving lineages are more likely to be found in Páramos than in the other hotspots. Páramos therefore represent the ideal model system for studying diversification processes. Additionally, we present the 'Páramo Plants Online' project, a web-based relational database of the flora of the Páramos.

## **Comparative montane plant radiations: from the Andes to the Hengduan Mountains**

*Guy Atchison (1), Nicolai M. Nürk (2), Marcus Koch (2), Florian Jabbour (3), Florian C. Boucher (1), **Colin E. Hughes (1)***

(1) Institute of Systematic Botany, University of Zurich, Switzerland;

(2) Centre for Organismal Studies, COS, Ruprecht Karls Universität Heidelberg, Germany;

(3) Département Systématique et Évolution, Muséum National d'Histoire Naturelle, Paris, France

Plant radiations have been documented for all the major mountain ranges of the world, and the world's mountains offer an excellent comparative island-like system for investigating predictors of radiation. These radiations are generally considered to be young and fast, driven by ecological opportunities afforded by the recent emergence of islands of high elevation alpine and sub-alpine habitats resulting from the most recent phases of mountain uplift. However, there have been few attempts to globally compare the extents and rates of diversification for plant radiations across different mountain systems. Here we explore species diversification trajectories, associated trait shifts and rates of trait evolution, for a set of montane plant radiations (*Lupinus*, *Hypericum*, Delphinieae, Arabideae, *Androsace*) spanning different mountain ranges. We highlight a syndrome of shifts to longer life histories associated with shifts to higher rates of species and life form diversification, and lack of evidence for diversification rate slowdowns, as the hallmarks of montane plant radiations. This suggests that many of these radiations are still in the early explosive phase of adaptive radiation. Our results also suggest that the shift from annual to longer life histories acted as a possible key evolutionary innovation facilitating ecological release and radiation associated with expanding ecological opportunities, especially in the Pliocene and Pleistocene, across the world's mountains.

## **Island radiations and the evolution of the Macaronesian Island floras**

*Mark Carine (1)*

(1) Department of Life Sciences, The Natural History Museum, London, UK.

Volcanic oceanic archipelagos have long been considered natural laboratories for the study of evolution, serving as model systems for understanding speciation processes. The Macaronesian region, comprising the volcanic oceanic archipelagos of the Cape Verdes, Canaries, Madeira, Selvagens and Azores, hosts a rich endemic flora including notable examples of evolutionary radiations. However, radiations in the flora are restricted to a relatively small number of groups (all angiosperms) which typically exhibit insular woodiness and occupy a range of habitat types. Across the region, there are marked differences in the extent of radiations in the archipelago floras. Notably, whilst the Canaries forms the hub for large radiations such as the *Aeonium* alliance (> 60 endemic taxa), diversification in the Azores has been much more limited with the orchid genus *Platanthera* currently constituting the largest Azorean ‘radiation’ with three endemic species. Explanations for the marked differences in the extent of diversification observed across the region include the ages of the islands or of the lineages, differences in palaeoclimatic conditions or in the extent of habitat diversity and the lack of a consistent taxonomic framework. This talk considers these hypotheses in light of recent work to characterize morphological and molecular patterns in the endemic flora.

## **Topography as a driver of diversification in the Cape Floristic Region**

**G. Anthony Verboom** (1), *Vera Hoffmann* (1), *Nicola G. Bergh* (2), *Sarah Haiden* (1) and *Matthew N. Britton* (1)

(1) Bolus Herbarium and Department of Biological Sciences, University of Cape Town, South Africa;

(2) Compton Herbarium, South African National Biodiversity Institute, South Africa.

Many plant radiations, including that of the flora of the Cape Floristic Region (CFR), have taken place in the context of topographically complex landscapes. Where past authors have emphasized the importance of elevational gradients as stimuli for ecological speciation in the CFR, the archipelagic configuration of the Cape Fold Mountains provides ample scope for non-ecological speciation process, especially at high elevations. Using six montane plant lineages, we demonstrate a general pattern of elevational niche conservatism, suggesting that speciation in the CFR occurs largely within elevation zones rather than along elevational gradients. We also demonstrate a general tendency for high-elevation species to have smaller distribution ranges than do lower-elevation species, potentially explaining why high-elevation sister pairs more often show strong allopatry. Along with evidence for weaker climatic- and edaphic-niche differentiation, and weaker morphometric differentiation, in high-elevation sister pairs, these results suggest a diminished role for adaptive divergence in the radiation of the high-elevation flora of the CFR. The archipelagic distribution of this flora may be a product of either climatically- and erosionally-forced fragmentation of a once-continuous high-elevation flora, as envisaged by Adamson, or dispersal, the latter potentially facilitated by Miocene-Pleistocene climate fluctuations.

## **Three explanations for mediterranean-climate biodiversity hotspots: small range size, geographic overlap and time for species accumulation**

*Lyn G. Cook (1), Nate B. Hardy (2) and Michael D. Crisp (3)*

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To understand the generation and maintenance of biodiversity hotspots, we test three major hypotheses: time for species accumulation (TSA), rates of diversification, and ecological limits to diversity (ELD). We compare the Southwest Australia Floristic Region (SWAFR, a global biodiversity hotspot) with a latitudinally equivalent non-hotspot, southeast Australia (SEA) using dated molecular phylogenies, measures of species' range size and geographic clade overlap, niche modelling, and lineages-through-time plots of Australian Fabaceae. Ranges of species (real and simulated) are about one-third smaller in SWAFR than in SEA. Geographic overlap of clades is significantly greater for *Daviesia* in SWAFR than in SEA, but the reverse for *Bossiaea*. Lineage diversification rates over the past 10 Myr do not differ between SWAFR and SEA in either genus. Interaction of multiple factors probably explains the differences in measured diversity between the two regions. Steeper climatic gradients in SWAFR likely explain the smaller geographic ranges of both genera, and simulated ranges, there. Greater geographic overlap of clades in SWAFR, combined with a longer time in the region, can explain why *Daviesia* is far more species rich there than in SEA. Our results suggest that both the TSA and ELD hypotheses, in concert, might explain the differences in biodiversity.

## **How tree species fill geographic and ecological space in eastern North America**

***Robert E. Ricklefs (1)***

(1) Department of Biology, University of Missouri-St. Louis, St. Louis, USA

Diversification occurs within large regions. Recent interest has focused on whether regions become 'saturated' with species, causing diversification to slow as ecological space is filled. Focusing on the deciduous trees of eastern North America, I test predictions from competition theory concerning the distribution and abundance of species, particularly that more closely related species compete more intensely. The absence of a relationship between species abundance and the number of close relatives suggests that the influence of competition does not dominate the distribution and abundance of individual species. The concentration of variance in these population traits among closely related species suggests a central role for specialized interactions, particularly with pathogens. Differences in diversity between regions with similar environments, as well as the frequent success of invasive species, suggest that regions do not become ecologically saturated. Accordingly, the long-term stability of species richness often observed in the fossil record might reflect regional clade-level processes other than competition.

## Testing the effect of environments and traits on Angiosperm radiations

*H. Peter Linder (1), Renske E. Onstein (1), Yanis Bouchenak-Khelladi (1), Yaowu Xing (1) and Orlando Schwery (1)*

(1) Institute of Systematic Botany, University of Zurich, Switzerland.

Three questions might be central to understanding radiations: firstly, the environment in which the radiations took place (Simpson's "adaptive zone"); secondly, the character syndrome that allows the lineage to survive in this environment ("key innovations"); and finally the mechanism(s) that drive(s) diversification in this lineage. There seems to be no clarity in which of these provides the context of the radiation, and which the trigger that initiates the radiation. Here we develop a protocol for identifying environmental attributes that might define suitable adaptive zones and traits that might define character syndromes associated with radiations, and to determine which provide the context, and which triggered, the radiations. We apply this protocol to four large plant clades: Ericaceae, Fagales, Poales and Rhamnaceae. In Ericaceae and Fagales, the traits evolved first, with the environment acting as a trigger; in Rhamnaceae traits and environments co-varied as triggers, and in Poales at least one radiation was triggered by the evolution of C4 photosynthesis. We extend and generalize our results with a literature survey, which reveals a complex interaction between environments, traits and diversification mechanisms.

## **The evolutionary reality of species and higher taxa in plants**

*Timothy G. Barraclough* (1), *Aelys M. Humphreys* (1,2)

(1) Department of Life Sciences, Imperial College London, UK;

(2) Department of Ecology, Environment and Plant Sciences, Stockholm University, Sweden.

Species are regarded as the fundamental unit of diversity. Species evolve independently from one another and define the transition from microevolution to macroevolution. But are species real evolutionary entities of key mechanistic importance or merely a convenient focus for classification in a continuous hierarchy from populations to whole clades? A classical view has been that genera are more natural units in plants. Revisiting a survey of botanists by Edgar Anderson in 1940, we confirm that opinions have shifted towards perceiving species as the most ‘evolutionarily real’ unit of plant diversity, although alternative views remain. We then discuss processes that generate discrete units of diversity and evolutionary independence, and how those might operate, not only at the species level, but on higher clades as well. We review evidence that reproductive isolation generates discrete units of diversity and whether those coincide with the taxonomic level of species. We then show how independent evolution can result from species turnover within ecologically or geographically separated clades, and present new evidence for such units in land plants, around the level of genera or families. Some processes that cause coherence and divergence can operate across multiple scales of diversity, bridging the distinction between microevolution and macroevolution.

## **Genomics of the speciation continuum: towards understanding the drivers and limits of radiations**

*Christian Lexer (1)*

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Rapid recent progress in ecological & evolutionary genomics is imparting fresh perspectives to the study of population divergence and speciation, i.e. the origin and maintenance of biological diversity. My group's research interests revolve around the use of novel laboratory and computational tools for studying adaptive evolutionary responses, speciation, and species radiations in plants. To achieve these goals, we make use of Northern hemisphere 'model' taxa for which extensive genomic and biological resources are available, and we transfer knowledge and 'know-how' gained from this work to other plant radiations in highly structured and species-rich environments, including mountains in the continental New World tropics and the Cape of southern Africa. In my talk, I will briefly introduce the basic concepts underlying our work, I will highlight recent progress by my group using Eurasian *Populus* spp. (Salicaceae) and African Restiads (Restionaceae) as examples, and I will sketch how population and speciation genomics may help identify the drivers and limits of radiations within trans-disciplinary research.

## **Explosive radiations and dying embers in plant phylogeny**

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Much attention has focused on identifying upward shifts in the rate of diversification in phylogenies and connecting these to potential key innovations or opportunities. This has spawned a host of clever methods, which have, in turn, yielded insights into evolutionary dynamics across plants. Often, however, it has proven difficult to pin down the one true point at which something interesting happened. Rather than searching for the true point, it may be more productive to identify phylogenetic regions within which a series of events yielded an outcome. From this perspective it is natural to consider sequences of events, such as alternation of decreases in extinction rate followed by increases in speciation rate. This fits with the observation of shifts nested within shifts, with the notion of precursor enabling traits, and with what appear to be delayed evolutionary responses to a trait of interest. It may also help us focus on the shape of phylogenetic trees more generally. The existence of ancient depauperate lineages also needs to be explained. What sequence of diversification-related factors can account for what appear to be “dying embers” in the tree of life? We will highlight relevant examples and potentially productive avenues of research.

## Posters

### Role of pollinators in the diversification of *Passiflora* supersection *Tacsonia*

Stefan Abrahamczyk (1), Daniel Souto (2) and Susanne S. Renner (2)

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A striking example of plant/pollinator trait matching is found in Andean passion flowers, many of which have 6-14 cm-long nectar tubes and depend for the reproduction on the Sword-Billed Hummingbird, *Ensifera ensifera*, which has a bill up to 11 cm long. Because of their self-incompatibility and position of anthers and stigmas, the long-tubed passionflower species depend on this single bird species for pollination. We have used a multi-locus dated DNA phylogeny to investigate how often and when these mutualisms evolved and under which conditions, if ever, they were lost. The phylogeny includes four of the seven bat-pollinated species of the relevant group (supersection *Tacsonia*, 62-64 species in total), 13 (68%) of the 19 species with tubes too short for *Ensifera*, and 26 (70%) of the 37 extremely long-tubed flowers, for a total sampling of 43 (69%) of all *Tacsonia* species (plus 11 outgroups). Results show that *Tacsonia* is monophyletic and that its stem group dates to 12.6 mya, matching the divergence at 11.6 mya of *E. ensifera* from its short-billed sister species. Pollination by *Ensifera* is the ancestral condition, and there is statistical support for six losses of *Ensifera* dependence between 6.4 and 1.5 mya, three involving shifts to bat pollination and three shifts to short-billed birds. Besides being extremely asymmetric – a single bird species coevolving with a large plant clade – the *Ensifera/Passiflora* system is a prime example of a specialized pollinator not driving plant speciation, but instead being the precondition for the maintenance of isolated populations (through reliable seed set) that then undergo allopatric speciation.

## **Diversification and Biogeography of Neotropical Costaceae (Zingiberales)**

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Nearly half of Costaceae's species richness belongs to Neotropical *Costus*. Ornithophily has evolved several times from melithophylous ancestrals and this shift has been suggested as fundamental to Neotropical diversification. However, reversals to bee pollination from ornithophilous ancestral also occurred, and major clades have both pollination types. Furthermore, comprehensive and current chronological and biogeographic analyses of Costaceae diversification have not yet been considered. Here, we elucidate phylogenetic relationships within Costaceae, with special focus on Neotropical clades, by presenting a robust fossil-dated molecular phylogeny with most extant species. We also analyzed species' spatial distribution in the context of their phylogenetic relationships. Divergence time analysis indicates that the origin of the Neotropical *Costus* lineage happened around 10 Ma ( $\pm 3$  Ma). Most early-divergent lineages are currently endemic to Central America and Northwestern South America, and allopatric and sympatric distributions between sister lineages are found within clades. Miocene is known as a key period for modern Neotropical diversity, specially due to Andean uplift, ocean level upraise and incursions to the South American continent, and Central America geomorphological dynamics. Spatio-temporal congruence between environmental changes and diversification reveal that, additionally to pollination shifts, orogenic processes might have played an important role in speciation bursts in Neotropical Costaceae.

## **Harnessing the power of genome-wide RAD data for resolving rapidly evolving clades - a case study in *Lupinus* (Leguminosae)**

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There are many examples of rapid episodes of species diversification, or species radiations across the tree of life, yet fundamental questions about how and why radiations happen remain largely unanswered. This is mostly due to the difficulties and challenges associated with reconstructing well-resolved and robustly-supported phylogenies for very rapidly evolving clades. We are investigating these questions for the genus *Lupinus* (Leguminosae, Papilionoideae) which comprises c.275 species of annuals and perennials spanning the Mediterranean, North and South America. The unifoliate Floridian clade of *Lupinus* is thought to comprise five species, yet recent studies have found evidence for a morphologically distinct entity. However, lack of phylogenetic resolution hampers our understanding of relationships within the clade and our ability to confidently delimit species. To tackle this issue we are exploring the utility of genome-wide nextRAD data to infer species level relationships within rapidly evolving clades. We have generated nextRAD data for 92 accessions of Floridian *Lupinus* with multiple accessions for all species. Here we present preliminary results from this dataset which show the potential utility of genome-wide RAD data to provide phylogenetic resolution for rapidly evolving species radiations and to delimit species within an integrative taxonomic framework.

## Evolution of the widely distributed endoparasites Apodanthaceae

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Apodanthaceae (Cucurbitales) are non-photosynthetic parasitic plants growing inside the stems of their hosts (Fabaceae and Salicaceae), from which they emerge once a year to form tiny flowers and fruits. Using the most comprehensive morphological and molecular data so far, we showed that the family comprises 10 species divided in the two genera, *Apodanthes* and *Pilostyles*, and is distributed in Central and South America (5 species), East-Africa (one species), Middle-east (one species) and Western Australia (3 species). No fossils are known from Apodanthaceae and since the clade has a different substitution rate compared to other Cucurbitales, we compared the performances in estimating divergence times of the Uncorrelated Lognormal (UCLN) and Relaxed Local Clocks (RLC) models of rate heterogeneity implemented in BEAST. In an unusual move, we modified the prior on the number of permitted rate jumps in the RLC model, leaving it either at the default Poisson distribution (RLCp) or using a uniform prior (RLCu). The models gave very different ages, yet Bayes factors indicated that the RLCu and UCLN models did not differ significantly, while the RLCp model fit poorly. This case sheds a warning light on simple-minded reliance on the UCLN model for each and any rate-heterogeneous data set.

## **The staggered evolution of ant-plant symbioses in the World's intertropical regions during the last 15 million years**

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Symbioses between ants and plants involve an intricate mix of obligate and facultative mutualisms. Because ant/plant interactions are ubiquitous, especially in the tropics, and since ants and plants have coexisted for at least 160 million years, it has been hypothesized that ant-plant symbioses are old and first arose in the Cretaceous. To infer the ages and degree of species-richness in these symbioses, we analyzed the relevant literature of the past 150 years, which revealed ~700 ant-plant species, way above previous estimates. We then generated a large phylogeny including ant-plants and their close relatives to reconstruct ancestral states and determine the absolute age by molecular-clock dating of local phylogenies. Our analysis reveals 60-100 origins of domatia in plant lineages, staggered over the last 15 million years, with no extant ant-plant radiation predating the Miocene. Younger ages of African symbioses, compared to American and Australasian ones, suggest that Miocene and Pleistocene climate oscillation delayed or increased the turnover in ant/plant symbioses. Within ant-housing lineages, numerous losses and gains of structurally equivalent domatia pinpoint the evolutionary plasticity of these structures. Although plant lineage extinction and domatium losses are insufficiently addressed by our data, such frequent and recent evolution of ant plants is puzzling and may reflect changes in diet and behavior in ants, as postulated in Wilson and Hölldobler dynastic-succession hypothesis.

## **Epidermal micromorphology as a tool to understand early cycads evolution**

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Recent studies based on molecular dating techniques suggested that extant cycad diversity resulted from speciation events during the Miocene-Pliocene. However, the relationships between extant genera and fossil cycads from the Mesozoic and Cenozoic are still poorly understood. To get more insight into cycad evolution, we are investigating cuticle and epidermal micromorphology in all extant genera of the Cycadales, integrating electron microscopy (SEM, TEM), Confocal Microscopy and Light Microscopy. Our results suggest that all cycad genera can be quite well defined by sets of epidermal characters. A preliminary comparison of extant epidermal morphology with fossil cycads reveals that no fossil cycad from the Mesozoic can be easily fitted in any modern genus. The repeated evolution of some characters (overprotection of stomata, thick cuticle, trichomes or papillae) in extant and fossil taxa could indicate the presence of similar ecological pressures (aridity, volcanism). An analysis of disparity through time and a tentative phylogenetic analysis of extant cycads fossil could help to have more rigorous quantitative tests of the hypotheses that are emerging from the analysis of micromorphology.

## **Branching process prior influences Bayesian molecular dating: an empirical assessment with cycads (Cycadales)**

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Understanding the timeline of plant evolution has been significantly influenced by Bayesian relaxed-clock molecular dating. This approach relies on the use of branching process priors, yet little is known about the impact of different priors on divergence time estimates. We investigated the effect of prior choice on the dating of an iconic plant clade: the cycads (Cycadales). We conducted a series of phylogenetic reconstructions with BEAST, using four fossil constraints and a thorough calibration jackknifing procedure. For each combination of calibrations we compared results obtained using Yule versus birth-death priors. We found striking differences in divergence time estimates depending on prior choice. Dating with the Yule prior suggests that most extant cycad genera began to diversify in the Late Cretaceous or Early Cenozoic, while use of the birth-death prior suggests the onset of within genus diversification in the Miocene: estimated within genus crown ages were on average ~50 million years older when using the Yule prior, with an extreme difference of 71 Myrs in the *Cycas*. These results suggest that much more attention needs to be given to the choice of branching process prior in molecular dating, and that we need to revisit the age of the living cycad species.

## **A link between the woody habit and speciation on the Canary Islands.**

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Oceanic islands are characterized by a high proportion of woody species. Often, these woody island species have evolved from herbaceous relatives, a phenomenon known as insular woodiness. On the Canary Islands, there is a striking pattern between insular woodiness and species radiation. Our recent review paper on the Canary Islands indicates that 34 genera developed into 220 insular woody shrubs on the archipelago, accounting for 20% of the native non-monocot angiosperms (40% of endemics). Of these 34 genera, 8 genera include more than 10 species, giving rise to 144 out of 220 species. Surprisingly, there are three times as more native herbaceous non-monocot angiosperms than insular woody ones, but these herbaceous groups do not radiate. We have experimental evidence that woody stems may increase the ability to avoid air bubbles in the water conducting cells due to drought stress. This enables woody shrubs to survive easier in drier environments than their herbaceous relatives, and may facilitate speciation.

We are using a global approach to identify a pattern in niche usage within and between plant genera. Special focus will be drawn on the intra-genus niche differentiation in insular woody genera compared to herbaceous and primarily woody genera.

## **Evolution of correlated traits and the diversification of inflorescences among *Lewisia* spp. (Montiaceae)**

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Understanding of factors and processes affecting the diversification of inflorescences lags far behind understanding of the evolution of floral traits. Flower number - flower size trade-offs as a consequence of finite investment in reproduction are widely documented, but how they constrain evolutionary trajectories of reproductive diversification is poorly understood, especially in the face of pervasive evolution of plant body size and resource investment. These issues are explored using Montiaceae (Portulacineae, Caryophyllales), for which a hyb-seq based phylogeny is being estimated.

Comparative analyses demonstrated that rates of diversification of number- and size-traits of flowers is much higher in *Lewisia* than in related genera. In *Lewisia*, floral traits evolve among species in a positively-correlated fashion. Thus, I find evidence for an overall trade-off in flower number per plant and flower "size", pertaining to various aspects of sepaloids, petaloids, androecium and gynoecium. Deviations are well explained by evolution of body size: bigger plants make both "bigger" and more flowers.

The nature of evolution along (or away from) trade-off axes is interpreted through analysis of ecological correlates (patterns of precipitation and temperature), and through field experiments aimed to uncover differences in flowering phenology and consequences for pollen transfer dynamics.

## **Detecting diversity dependent speciation using a birth-death model in BEAST 2**

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The amazing biodiversity of life on earth emerges through the constant evolution of new species. Although diversification is a constantly ongoing process, the rates at which new species arise and others die out are far from constant. Adaptive radiations are a major proposed mechanism for diversification. Adaptive radiations occur when a species evolves a key innovation or disperses to a new environment, opening up many empty niches. Filling these niches leads to an increase in the speciation rate, followed by a slowdown as available niches become filled with novel species.

We quantify diversity-dependent speciation by modeling diversification as a birth-death process with an explicit dependence between the number of available niches and the speciation rate. By decoupling the intrinsic speciation rate and the clade-level carrying capacity we can shed light on whether diversity dependence provides an explanation for observed bursts in speciation, or if other mechanisms are responsible [1]. Furthermore, as the method is implemented in BEAST 2, it can be used as a tree-prior in conjunction with a model of molecular evolution to directly infer new phylogenies.

[1] Moen D, Morlon, H, “Why does diversification slow down?” Trends Ecol Evol (2014)

## **Patterns of lineage diversification in the genus *Solanum* L.**

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With more than 1400 species, *Solanum* L. (Solanaceae) is one of the largest genera of angiosperms. Its greatest diversity occurs in the neotropics, especially in the Andes. The variety of traits and occupied niches makes this genus an interesting case study to understand the diversification dynamics of the neotropical flora. Using MEDUSA to analyse a time-calibrated phylogeny and the species richness of 37 major clades within *Solanum* L, we detected four major shifts in diversification rates. The most significant shift was found within the clade composed exclusively of taxa from the Old World. This radiation includes the majority of the Old World spiny *Solanum* with a wide variety of phenotypes. Further work is needed in order to identify the drivers of this significant radiation of Old World clade.

## **The palms of Madagascar: unraveling the eco-evolutionary assembly of an exceptional island flora**

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The island of Madagascar harbours biotas with exceptionally high levels of endemism. Much of this endemic diversity stems from in situ diversification following a few colonization events, resulting in few hyper-diverse endemic lineages. Other diversification events, however, were followed by little or no diversification. Madagascan palms (198 spp., 195 endemic) are representative of this pattern, with excessive diversification following just one of at least seven colonisation events. To unravel the eco-evolutionary assembly of this exceptional flora, we will reconstruct the phylogeny of all Madagascan palms, and analyse it together with information on species distributions, traits, and niches. First, we will investigate why some clades have diversified excessively while others have not? Second, we will study the diversification of two larger clades in detail and test hypotheses regarding the roles of traits, niches, and environmental change. Third, we will conduct a population-level study to test the role of adaptation in Madagascan palm diversification. Finally, we will integrate the phylogenetic information with distribution data and IUCN Red List assessments to derive new conservation priorities for species and regions. The results will both improve our understanding of palm evolution and systematics, and provide general insights into biodiversity dynamics.

## **Radiative evolution and polyploidy in *Knautia* (Caprifoliaceae)**

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The genus *Knautia* comprises ca. 60, mostly European species. Whereas the species-poor diploid sections *Knautia* and *Tricheroides* are centred in the eastern Mediterranean and comprise mostly annuals, the section *Trichera* includes mainly perennials, with centres of diversity on the Balkan and Iberian Peninsulas, as well as the Alps and Apennines. The three sections represent independent evolutionary lineages and whereas the early diverging annual sections remained species poor, radiative evolution took place in sect. *Trichera* after transition from annuality to perennity. The main diversification mechanism in this lineage was polyploidisation to the tetra- and hexaploid levels. Twenty-four species are diploid, 16 tetraploid and two hexaploid, whereas ten species possess two, and two species three ploidy levels. Di- and tetraploids are distributed across most of the distribution area of *Knautia*, whereas hexaploids are limited to the Balkan and Iberian Peninsulas and the Alps. Molecular phylogenies of the ribosomal nuclear ITS and plastid *ycf6-psbM* regions as well as of amplified fragment length polymorphisms (AFLP) are poorly resolved and do not follow the taxonomic boundaries. We suggest that the group diversified recently and that both hybridisation and recurrent polyploidisation are blurring the relationships among the morphologically and ecologically very diverse taxa.

## Geographical radiation in the *Pentameris pallida* (Poaceae) complex

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*Pentameris pallida* (Poaceae) is a variable and widespread lineage in the Cape Floristic Region of South Africa. We use molecular, morphological, and anatomical variation of 44 populations covering the entire distribution area to explore the phylogeographical pattern in the complex. Chloroplast data suggests four geographically separated groups in *P. pallida*: one along the coast, one west of the Hottentots Holland mountains, one in the southern Cape, and one on the Swartberg and east of the Knysna forests. ITS data corroborates the coastal and eastern groups, but combines the southern and western groups. These ITS groups also differ in leaf anatomy, leaf width and spikelet morphology. This pattern suggests incomplete divergence within this species, but it is not clear whether the primary driver is allopatry, or ecological adaptation. The latter is possible, as the four plastid groups significantly differ in rainfall and temperature. Further, the coastal form is restricted to calcareous sand dunes along the coastline. The genetic patterns are consistent with hybridization between the coastal and southern forms resulting in the western form. Such parapatric, ecologically supported, differentiation has been reported among sister species in several Cape clades, and may be a common form of divergence in this rich flora.

## **Orchid phylogenomics, historical biogeography, and drivers of exceptional species richness**

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Orchids form the largest family of flowering plants, including ca. 900 genera and 25,000 species. Previous studies based on one to five plastid genes failed to resolve relationships among tribes within subfamilies, especially Epidendroideae, which includes roughly 80% of all orchid species. We use plastome sequence data for 39 taxa representing all but one tribe to produce the first well-resolved, strongly supported phylogeny for the family. Reconstruction of historical biogeography using BioGeoBears suggests that orchids arose in Australia and/or South America ca. 112 Mya, with later dispersal into Southeast Asia, Eurasia, Japan, and Pacific Islands. Orchidoids arose in South America or Africa, with subsequent spread of Orchideae into Eurasia and North America, of Diurideae into Australia and nearby areas, and of Cranichidae back into South America. Epidendroids, containing 80% of orchid species, arose 64 Mya, with rapid-fire divergence of the upper epidendroid clades between 38 and 31 Mya, including radiations in South America, Southeast Asia, and Africa/Madagascar. Four significant accelerations of net diversification occurred within Asparagales, all within the orchids, and three within the upper epidendroids. As predicted, pollinia, epiphytism, CAM photosynthesis, tropical distribution, and pollination via deceit, euglossine bees, or Lepidoptera are significantly correlated with rates of net diversification.

## Speciation in the high-altitude Páramo ecosystem

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Páramo is a unique Neotropical high altitude ecosystem with an island-like distribution along the mountaintops of the northern Andes Mountain Range. Its likely young geological age and extremely high plant diversity makes it a good model for studying plant phylogeography so as to elucidate the patterns and processes behind speciation. The five species within the American clade of *Oreobolus* (*O. cleefii*, *O. ecuadorensis*, *O. goeppingeri*, *O. obtusangulus* and *O. venezuelensis*) were selected as a study group based on their distribution patterns and the fact that a dated phylogeny exists. Sequences from three plastid markers (*rpl32-trnL*, *trnH-psbA* and *trnL-trnL-trnF*) and nuclear ribosomal ITS were obtained covering the full extent of the geographical distribution for each of the five species. We present preliminary results of the phylogenetic reconstruction and genetic structure within the clade.

## **A tale of two morphs: Modeling pollen transfer, magic traits, and reproductive isolation in heterostyly**

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The remarkably high diversity of angiosperms has been attributed to co-evolution with pollinators. We hypothesize that reproductive traits promoting ‘precise’ pollen transfer from anthers to pollinators to stigmas might promote diversification. In particular we test, using an individual-based model, whether spatial mismatch of reproductive organs between species might reduce interspecific pollen movement and thus increase reproductive isolation. We use the outcrossing floral polymorphism ‘heterostyly’ as model system. Populations of heterostylous species consist of two/three sets of plants with flowers differing in the reciprocal placement of reproductive organs. Outcrossing is facilitated by a close inter-morph spatial fit of reciprocal organs, ensuring precise inter-morph pollen movement, and a pollen incompatibility system. Our model shows that between species, when precise enough, pollen transfer can cause sexual selection leading to divergence in reproductive organ positions between populations served by different pollinators, pleiotropically causing partial reproductive isolation through a ‘magic trait’ mechanism. A different set of pollinators, however, reduced the adaptive divergence, resulting in asymmetric interspecific pollen flow, indicating that magic traits in speciation are not ‘magic’ in isolation, but depend on ecological opportunities. Overall, we show that close morphological fit of pollinators and flowers may cause partial reproductive isolation facilitating adaptive divergence.

## **New insights into the evolutionary history of *Gnetum* (Gnetales)**

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*Gnetum* is a woody genus with a disjunctive pantropical distribution. Evolutionary relationships and biogeographic history of *Gnetum* are not fully understood despite previous efforts. We performed a new study of phylogenetic relationships, divergence times of clades, and ancestral area reconstruction in *Gnetum*, using an extended ingroup and outgroup sampling compared to previous studies. The estimated age of extant *Gnetum* is 81 Mya, and the earliest split within the genus resulted in a South American clade sister to the remaining taxa. A subsequent split, resulting in a sister relationship between an African clade and an Asian clade, took place around 74 Mya. Within the Asian clade the arborescent species of *Gnetum* diverged from the lianoid taxa around the K-Pg boundary (ca. 65 Mya). After the K-Pg boundary, diversification processes continued in all these clades and contributed to present-day biodiversity of *Gnetum*. The estimated ages are much older than those of previous studies and may indicate the correlation between diversification processes in *Gnetum* and major plate tectonic events, such as the breakup of the Gondwana continent. Results of ancestral area reconstruction vary depending on how the distribution of its sister-group (*Welwitschia*) is scored. Central Gondwana (South America and Africa) is resolved as the ancestral area of *Gnetum* when former distribution of the *Welwitschia* lineage is taken into consideration.

## **Evolution of gymnosperms into independently evolving higher clades**

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Identifying biodiversity units is fundamental to studying how diversity evolves. Species are widely accepted as discrete, evolutionary units and the processes by which species are formed are well known from a rich body of theoretical literature. In contrast, and despite their historical status as natural entities, higher taxa (e.g. families and genera) tend not to be considered real, evolutionary units in the same way; processes that cause evolution of discreteness above the species tend not to be considered. A simulation study has recently shown that processes that cause evolution of discrete species, namely geographical isolation and ecological divergence, can cause evolution of discrete, independently evolving units above the species as well. Analyses of densely sampled phylogenies revealed strong support for the existence of such units in mammals, generally corresponding to the family level in traditional taxonomy, and there is evidence to suggest that their formation followed occupation of distinct ecological zones (“adaptive zones”). In this poster we present results for ancient seed plants: gymnosperms. We find strong evidence that gymnosperms have evolved into independently evolving higher units and that the striking phylogenetic patterns so characteristic of several gymnosperm clades cannot be explained by a constant-rates birth-death process. In contrast to mammals, gymnosperm hESUs tend to correspond to genus-level taxa. The analytical framework and the findings we present offer a new realm for studying diversity at broad scales and provide a crossroads between taxonomy and evolution currently lacking above the species.

## **Recent radiation of *Senecio* L. (Asteraceae)**

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*Senecio* s.str., with about 1000 species, is among the most species-rich angiosperm genera. *Senecio* has a cosmopolitan distribution, and ancestral area reconstructions show that it originated in southern Africa. To determine the times of origin and diversification of the genus we used a fossil and ITS substitution rates to calibrate a molecular phylogeny based on Pelsner et al. (2007; *Taxon* 56:1077-1104) and expanded it to represent more than 250 species of *Senecio*. Furthermore, diversification rates and shifts were calculated. We inferred a stem age of 10 Million years before present. This makes *Senecio* an almost unparalleled recent radiation with a worldwide distribution. Other recently radiated plant groups with comparable diversification rates have much more restricted distribution ranges. Long-distance dispersal events from southern Africa to the Northern Hemisphere and Australia, and from South America to the Juan Fernandez Islands, have resulted in increased diversification rates. Our analyses indicate that in clades originating from long-distance dispersal and showing elevated diversification rates extinction is negligible. In contrast to this, extinction seems to play a major role in the regions where these clades originated, i.e., in southern Africa and South America.

## **Phylogenetic structure and source sink dynamics along a latitudinal and elevational gradient**

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A promising way to understand global patterns of plant diversity is to incorporate phylogenetic data to add a long-term evolutionary perspective to biodiversity research. Advances in resolving phylogenetic relationships have triggered recent progress in community ecology but studies of phylogenetic patterns at macro-scales have been so far mostly descriptive and focused on terrestrial vertebrates. Disentangling the processes generating phylogenetic diversity patterns is therefore at the forefront of macroecological and macroevolutionary research. Aside from environmental filtering, and species interactions, source sink dynamics might influence the phylogenetic structure of communities. Here we investigate the relative importance of source sink dynamics for the phylogenetic structure along an elevational and latitudinal gradient in Asia using a unique data set of the fertility status of 445,471 individual records of ferns species. We used a time-calibrated global fern phylogeny pruned to genus level to calculate phylogenetic distance metrics for source and sink communities and compared their relative patterns along the elevational and latitudinal gradient. Our results indicate a significant influence of source sink dynamics along the elevational gradient while along the latitudinal gradient the influence is negligible.

## **Habitat shifts to and higher diversification rates in tropical rainforest reject the museum model of rainforest diversity for the Mahogany family (Meliaceae)**

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Tropical rainforests are the ecosystems with the highest diversity on the planet. Two competing hypotheses for rainforest hyperdiversity have been proposed: 1) the "museum" hypothesis, which suggests that diversity has accumulated over a long time, and 2) the "cradle" hypothesis, which suggests that much of the diversity is recent and is caused by higher diversification rates. We evaluate these competing hypotheses with the Mahogany family (Meliaceae) as our study group. We use available and newly generated DNA sequence data to infer a large time-calibrated phylogeny for the family, with complete sampling of genera. We reconstructed presence/absence in rainforest habitats and deciduous vs. evergreen leaves over the phylogeny and use a recently developed model averaging approach of the BiSSE model to estimate trait-dependent diversification rates. Our results suggest that the ancestral Meliaceae was a deciduous species that inhabited seasonal tropical habitats in the late Cretaceous or early Paleocene. The two main rainforest clades date back to late Paleocene, suggesting that most of the rainforest diversity arose during the Miocene and after. We also find that rainforest lineages have experienced significantly higher diversification rates. Taken together, our results lend support to the cradle hypothesis, and reject the museum hypothesis for the Mahogenies.

## **Effects of polyploidisation upon plant lineage diversification**

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The importance of polyploidisation on the evolution of angiosperms has long been recognized. Countless examples of plant genus exhibiting different ploidy levels exist, but thanks to the advance of sequencing, paleopolyploidisation events are now dated with increasing precision. Hypothesis linking paleopolyploidy and diversification or survival to mass extinction events have been made by authors but evidence using recent phylogeny-based methods is highly debated. Thus, we discuss the importance of choosing appropriate dataset to test this association: recent polyploid events should be treated with caution as diversification is studied through longer evolutionary scales. Moreover, we will address the need of choosing diversification estimation methods enabling to fit complex diversification scenarios for the comparison of sister clades differing in ploidy levels. Finally, we present the reanalysis and generation of phylogenies that will enable the comparison of diversification patterns of polyploids and diploid species. So far, results do not show increased diversification for the few polyploids lineages examined. Aggregating bigger dataset, encompassing paleopolyploid events in other kingdoms of the tree of life, will enable us to give a definite answer regarding the effects of genome duplication in diversification.

## **Disentangling the evolutionary history of extrafloral nectaries in deserts**

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Desert plants face great challenges to growth and survival from herbivorous insects. Many reward aggressive ants with carbohydrate-rich, liquid secretions from extrafloral nectaries (EFNs), and the ants in turn attack the plants' enemies. Such ant-plant mutualisms are well studied in tropical and savanna-like habitats. In deserts, it is not clear how plants can manage their limited water budget to produce a water-based reward. Therefore, we investigated morphology and evolution of EFNs focusing on characteristic elements of the northern Sonoran Desert (USA) vegetation. In Leguminosae (15 EFN-bearing genera), most EFNs are on leaves and tend to have less secretory cell layers and tissue area than EFNs from wetter habitats. In Cactaceae (eight EFN-bearing genera), EFNs occur as modified areolar spines or on floral bud scales, which are already highly xerophytic. Dated phylogenies indicate that desert EFN-bearing species derived from ancestors with EFNs. Desert EFNs, therefore, were retained, and remained functional, through the relatively recent transition to desert habitats. However, while in extant cacti EFNs are still central in protective mutualisms with desert ants, in legumes, such mutualisms await verification. The most reduced EFNs might still be functional because of phylogenetic inertia and the low cost of retaining EFNs.

**The strategy of the marathon runner: ancestral resilience drove the evolution of the species-rich, age-old genus *Hypericum* (St John's wort, Hypericaceae)**

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With nearly 500 spp. *Hypericum* is one of the 100 largest angiosperm genera. Today, it is distributed in the temperate Holarctic regions, but biogeographic reconstructions indicate that *Hypericum* probably originated in the Early Cenozoic from tropical African ancestors. We use fossil-based ecological niche models, ancestral state reconstruction and birth-death models to infer how *Hypericum* diversified through the major climatic changes of the Cenozoic and which mechanisms generated its large extant diversity. We found a change of ecological tolerances from tropical to temperate climates, coincident with its initial diversification and the dramatic climate cooling of the end of the Eocene, after which climatic preferences remained stable for the last 35 million years. Diversification rates did not support a correlation with the appearance of ecological key innovations, but a model in which steady accumulation of species through time explains the high diversity today. Like a marathon runner, *Hypericum* has been able to keep a steady diversification pace through time by developing new characters and bouncing back to previous states. Although adaptive radiations and key innovations have been a major focus of biodiversity studies, ancient lineages like *Hypericum* emphasize the role of resilience and plasticity in coping with climate extinction.

## **Exploring large-scale phylogenetic imprints to get insight on the emergence of Mediterranean biodiversity hotspots**

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Understanding the historical and ecological mechanisms that shape large-scale distribution of lineages is a challenging task for integrative biogeography. Many of the macroevolutionary episodes giving rise to the present phylogenies were caused by geological events such as intermittent connections between continents, and thus phylogenetic trees can provide information on such events. Focusing on a western Mediterranean plant biodiversity hotspot divided between two land masses separated by the Mediterranean Sea, we explored the spatial structure of phylogenetic relationships within and among large-scale plant assemblages of the hotspot, and related them to the current climatic conditions. We found significant turnover among deep lineages trends to occur between plant assemblages within land masses, following a general west to east precipitation gradient. We suggest that niche conservatism at high levels of the phylogeny together with differential diversification rates of spatially restricted lineages could give rise to this phylogenetic pattern. In contrast, significant turnover of terminal lineages trend to occur between plant assemblages across land masses. This suggests a common scenario of allopatric speciation on disparate angiosperms lineages that could be facilitated by the intermittent connections between both continents, thus constituting an important stimulus for diversification and the emergence of Mediterranean hotspots.

## **Does the interaction between Mediterranean-type ecosystems (MTEs) and typical MTE-traits affect diversification rates in Rhamnaceae?**

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Species diversification is thought to be linked to a lineage's intrinsic innovations and the extrinsic events it is exposed to over evolutionary time. However, the temporal sequence of these diversification 'triggers', and their additive or interactive effects on speciation and extinction rates is unclear. We assembled trait and biome data for 759 Rhamnaceae species (70% of total species), built a phylogenetic tree for 280 Rhamnaceae species and estimated divergence times by using eight fossil calibrations to test (1) if lineage diversification within Mediterranean-type ecosystems (MTEs) is faster than in other biomes, (2) if typical MTE-traits (low specific leaf area, small leaves, revolute margins) are exaptations or adaptations to MTEs and (3) if the interaction between these traits and occurring in MTEs affects diversification rates. Our results indicate that diversification rates within MTEs are generally faster than in other biomes, and that this is driven by low extinction rates in the Cape and Western Australia. Typical MTE-traits evolved after the transition to MTEs (or their ancient equivalents), but prior to the onset of summer-dry climates in these regions. Interestingly, a decreased speciation rate was detected for the interaction between occurring in MTEs and having any of the MTE-traits, suggesting that specialised lineages in Mediterranean shrublands may reach evolutionary dead ends.

## The spectacular radiation of *Erica* in the Cape Floristic Region and beyond

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Of the extraordinary plant species diversity found in South Africa's Cape Floristic Region (CFR), 7% is represented by a single genus: *Erica*. Although regarded as the largest of the 'Cape clades' (c. 690 spp. in the CFR), *Erica* is also distributed more widely, from Central and Western Europe, Macaronesia, the Mediterranean and the Middle East (21 spp.); south across the high mountains of Africa (74 spp., including South African Drakensberg); and on Madagascar and the Mascarene islands (41 spp.). We infer a phylogeny of over 60% of the 800+ species of *Erica* using both nuclear ribosomal ITS and multiple chloroplast DNA sequence markers. Two major clades together represent almost all Afrotropical species, the larger of which includes all those of the CFR and none from outside South Africa. Biogeographic models representing the Drakensberg as a meeting point, but not as a springboard either to or from the CFR, fit the data better than either southerly stepping stone or 'Cape to Cairo' dispersal routes. Given the general rarity of dispersal between areas the immense radiation of *Erica* must be explained by processes acting within regions of the Afrotropical - most notably the CFR - and not recruitment between them.

## **Floral key innovations in angiosperms: the case of floral symmetry**

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The appearance of flowers is generally agreed to be one of the key innovations that made angiosperms more diverse than any other living plant group, despite their relatively recent origin. However, diversity within the angiosperms is unevenly distributed, with families ranging from 1 species to more than 20,000 species. Two main types of perianth symmetry are found in flowers: radial symmetry (actinomorphy) and bilateral symmetry (zygomorphy). Several studies have shown zygomorphy to be characteristic of several clades that hold more diversity than their respective sister clades. However, these studies have been conducted thoroughly only on a limited number of clades and have neglected larger clades in which zygomorphy does not appear at all. As a first step towards testing whether zygomorphy may be considered a key innovation across all angiosperms, we investigated the evolution of perianth symmetry in monocots and superrosids, which together cover more than half of angiosperm species. Using a backbone consensus phylogeny of the angiosperms, parsimony reconstructions suggest at least 25 independent origins of zygomorphy in each clade and a number of reversals towards actinomorphy. The next step will be to refine our results using maximum likelihood methods, and to test the impact of this trait on species diversification rates.

## **Evolution of the mega-diverse genus *Crotalaria* (Fabaceae) – first results**

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*Crotalaria* L. includes an estimated 600 species of which c. 500 occur in Africa and Madagascar, 159 in tropical and temperate Asia and Australasia, 31 in North and Central America, and 64 in South America. Some of these species are now distributed pantropically due to their economic importance as fiber crops, green manure and cattle fodder. Along with 10 other genera *Crotalaria* belongs to the Crotalarieae, and two small African genera appear to be its closest relatives. The current infrageneric classification largely stems from the characteristics of the 500 African species. So far we have compiled a matrix of 192 ITS sequences representing 120 species (20% of the total), mainly from Africa and India, plus nine representing five genera of Crotalarieae and one representing Genisteeae, the sister tribe. With the current sampling, the genus *Crotalaria* appears monophyletic. We plan to add sequences of as many species as possible, and with this poster would like to encourage anybody who has specimens they want identified or samples they might share to contact us. Questions that we want to address concern the arrival and diversification of *Crotalaria* in the different regions where it occurs today as well as trait change, especially of leaf morphology.

## Settling down of seasonal migrants promotes bird diversification

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How seasonal migration originated in birds, and how it impacted diversification, remain largely unknown. Although migratory behaviour is likely to affect bird diversification in various ways, previous studies have not detected any significant effect. For example migration can potentially enhance speciation, because different populations within the same species can have different migratory flyways or strategies, which can lead to genetic divergence between populations. Conversely, migration could reduce opportunities for speciation as it may increase gene flow between breeding populations, thereby reducing genetic divergence between populations. Seasonal migration can potentially also have effects on extinction. During past glaciation cycles in particular, migratory species were more likely than sedentary ones to escape from changing environmental conditions and to avoid extinction. Here, we infer ancestral migratory behaviour and the effect of seasonal migration on speciation and extinction using an almost complete bird tree of life.

Our analyses infer that the sedentary behaviour is ancestral, and that the migratory behavior originated repeatedly and independently during birds evolution. The speciation of a sedentary species into two sedentary daughter species is more frequent than that of a migratory species into two migratory daughter species. However, migratory species often diversify by generating a sedentary daughter species in addition to the ancestral migratory one. This leads to an overall higher migratory speciation rate. Migratory species also experience lower extinction rates. Hence, although migratory species represent a minority of all extant birds, they have a higher net diversification rate than sedentary species. These results suggest that the evolution of seasonal migration in birds has facilitated diversification through the divergence of migratory subpopulations that become sedentary, and illustrate asymmetrical diversification as a potentially under-recognized mechanism by which diversification rates are decoupled from species richness.

## **Fire intensity influences diversification rates in *Pinus***

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Plants have been exposed to fire throughout their whole evolutionary history and the role of fire in driving natural selection and therefore its effects on the evolution of adaptation strategies in fire-prone areas has been widely examined and confirmed. Plants have evolved a range of different strategies to successfully colonize fire-prone areas. The role of the different strategies on plants' diversification rate has been assessed in several studies either at specific fire-prone sites or in global studies based on few species belonging to different taxonomic groups. However, the role of fire as a driver of diversification in plants remains controversial. Therefore, we investigated in a globally and taxonomically comprehensive assessment using *Pinus* the impact of fire on diversification rates, and we compared the effect of the different plant functional strategies on diversification. We demonstrate that it is likely not only the change in life histories that influences diversification rates but rather the evolution of environmental specialization to tolerate fire regimes, the associated degree of pleiotropic investment costs and its effects on life histories. Our results provide a basis for understanding the role of disturbances on species diversification rate linked to the degree of their environmental specialization and the associated costs.

## **Multiple shifts in diversification and rate of origin of higher clades might explain species richness heterogeneity in angiosperms**

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Underpinning the causes of species richness heterogeneity among clades is a long standing challenge in evolutionary biology. Some of the main difficulties are the inability to disentangle effects of factors, establish correlations confidently and assign causality. It has been pointed out recently that assuming particular models of diversification greatly influence the results of statistical tests of correlation and thus the causal relationships inferred. Therefore, considering the true underlying model of diversification of clades is crucial. Model fitting approaches with maximum likelihood or Bayesian statistics are able to find the best model based on phylogenetic and/or taxonomic data of clades. However, they can sometimes infer a best model that is not necessarily the true model. This can in turn be evaluated with simulations and comparisons between statistical properties from the empirical data and the ones expected from simulations. In this work we apply a simulation method that takes into account phylogenetic and taxonomic structure, to evaluate statistic properties such as gamma statistic, age-richness correlation, and variance of clade richness from angiosperm families, to evaluate the model of diversification that might have generated the huge species richness heterogeneity we can see in this group nowadays.

## **eFLOWER: A framework for understanding the evolution and diversification of flowers**

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Understanding the global patterns of floral evolution in angiosperms has been limited so far by the availability of a morphological data set representing all lineages. Using a new flexible and innovative approach, centered on a multi-user database (PROTEUS), we are building this data set. Unlike most other studies of character evolution at the scale of angiosperms so far, we are only recording exemplar species, allowing explicit reconstructions without assumptions on ancestral states or monophyly of supraspecific taxa and, most importantly, direct matching with the species sampled in molecular phylogenetic trees, offering the possibility of taking branch lengths into account. Here we demonstrate the approach with a pilot study based on a new data set of 710 species and a matching fossil-calibrated timetree. We reconstruct ancestral states with parsimony as well as with several maximum likelihood models of character evolution. Our inferences for key nodes of the phylogeny show that the gigantic data set that will eventually provide the answers can realistically be built by multiple researchers in a relatively short time, and that the results obtained are likely to challenge current hypotheses on large-scale floral evolution. Importantly, all data from the eFLOWER project will be made public upon publication ([www.eflower.org](http://www.eflower.org)).

## **Speciation and sex determination in the dioecious carnivorous *Nepenthes* pitcher plants**

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All *Nepenthes* (Nepenthaceae, Caryophyllales; > 140 spp.) are dioecious and produce conspicuous traps, special jug-shaped leaves, that serve to acquire additional nutrients, usually by attracting, killing and digesting insects. These sophisticated organs are among the most highly derived laminae of all plants. In a species radiation in Southeast Asia, pitcher traps have greatly diversified in shape and function. An intriguing hypothesis is that selection on trap function may drive ecological divergence and speciation - especially in sympatric species that can form natural hybrids.

We investigate the population genetics and introgression among seven common *Nepenthes* spp. from northwestern Borneo and Singapore, using genome-wide SNP markers (RAD-seq). In a study of specific traits involved in carnivory, we focus on digestive protein adaptation towards different prey spectra, applying a combined proteome-transcriptome approach. Preliminary results confirm that RAD-seq detects thousands of SNPs within and among species with large and previously unstudied genomes and reveals first insights into the genetic basis of sex determination in Nepenthaceae. First results from a proteomics approach identify a diversity of digestive proteins in *Nepenthes* pitchers. We will combine proteomics with RAD-seq and RNA-sequencing with the goal to unravel evolutionary forces underlying the radiation of *Nepenthes*.

## Pollinator-driven genic ecological speciation in sexually deceptive orchids

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Mediterranean orchids of the genus *Ophrys* are well known for cheating their pollinators, mimicking sexual signals of insects to achieve highly specific pollination. In particular, chemical mimicry of the insect sex pheromone is suspected to have enabled species radiations within the genus, because its nature as a blend of several substances may easily be affected by change in any of its constituent compounds. To better understand speciation in *Ophrys*, we studied the reproductive barriers, phenotypic differences and population genomics of four closely related species that occur in sympatry in southern Italy: *O. exaltata*, *O. garganica*, *O. incubacea*, and *O. sphegodes*. These species effectively lack post-pollination barriers, but are strongly isolated by their different pollinators, and to a smaller extent, by flowering time shifts. Differences in several floral characters were found, including size, shape, morphology, coloration and odour, many of which may be linked to pollinator differences. Genotyping by sequencing (GBS) revealed very little population genetic structure between species, indicating shared polymorphism throughout the *Ophrys* genome. Few markers that are highly differentiated between species and repeatable in several populations were identified in  $F_{ST}$  outlier scans. Among these, one previous candidate gene putatively involved in pseudo-pheromone biosynthesis was identified. Overall, our data indicate that pollinators mediate reproductive isolation between phenotypically different *Ophrys* species, even though very little population genetic structure and only few divergent loci are evident in the genome. These data therefore suggest that ecological speciation associated with different pollinators in *Ophrys* has a genic rather than genomic basis, thereby enabling potentially rapid speciation.

## **Leaf Traits and Mountain Association influence Diversification in Ericaceae**

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Angiosperm diversity is unevenly distributed across lineages, but the factors that affect changes in a lineage's diversification rate are not well understood. Here, we hypothesize that the interaction between functional leaf traits and habitat can influence diversification rates. We investigate this question in the family Ericaceae, which has a worldwide distribution with around 4000 species occurring in various habitats from sea level to >5000 m elevation. We predict that the interaction of low specific leaf area (SLA) and the environmental conditions of mountain habitats will be correlated to accelerated diversification rates. A molecular phylogeny based on *rbcL* and *matK* sequence data was built and dated using 18 fossil calibrations and divergence time estimates, resulting in the largest dated phylogeny of Ericaceae. We sought correlates of changing diversification rate, and using BiSSE showed that lineages in mountains diversified faster than non-mountain lineages (higher speciation rate, but no difference in extinction rate). Similarly, lineages with low SLA diversified faster than high SLA lineages. MuSSE further showed that habitat and trait had an interactive effect on diversification. Using the newly developed method BAMM, we revealed six diversification rate shifts. Our results suggest that ecological opportunity and phenotypic adaptation are important drivers of diversity.

## **Diversification rate-shifts and trait correlates of the Gesnerioideae subfamily in the Neotropical region**

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Angiosperms are well known for their striking species diversity. Disparities in species richness may be linked to a variety of factors including the evolution of particular traits, environmental differences or the colonization of new habitats. Here, we investigated the shifts in the rates of species diversification occurred during the evolution of the Gesnerioideae lineage (*Gesneriaceae* family), and the correlation of specific morpho-ecological traits with the speciation and extinction probabilities. This lineage is widely distributed over the Neotropical region, with large disparities in species richness across clades and a high morphological diversity. The evolution of different characters as fruit morphologies, pollination systems and growth habitat types have been previously documented in the Gesnerioideae, but their contribution to this richness imbalance by influencing the diversification rates has been narrowly tested. Based on four nuclear and chloroplastic DNA regions we reconstructed a phylogenetic tree with 600 species and examined for shifts in diversification rates and trait correlates (BAMM and BiSSE-BMA models). Our results suggested multiple rate shifts across branches in the phylogeny, and a correlation of epiphytism, fleshy-fruits and hummingbird pollination syndrome with increased net diversification in the lineage.

## **Estimating shifts in diversification rates based on higher-level phylogenies**

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Macroevolutionary studies recently shifted from only reconstructing the past state, i.e. the species phylogeny, to also infer the past diversification dynamics which gave rise to the phylogeny. Methods for estimating diversification dynamics are sensitive towards incomplete species sampling. We introduce a method to estimate time-dependent diversification rates accounting for sampling species of a clade such that the sampled species are as different as possible. A popular example of this type of data are phylogenies on the genus or family level, i.e. phylogenies where one species per genus or family is included. We conduct a simulation study to validate our method. An analysis of higher-level ant and angiosperm phylogenies indicates that the diversification of the two clades is linked.

**Drivers of plant diversification in Madagascar:  
Evolutionary history, biogeography and ecological patterns**

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Madagascar is recognized as one of the most important biodiversity hotspots because of its extremely high levels of species richness and endemism. This island's limited size, geographical isolation and ecological differentiation make it an ideal model region for understanding the ecological and evolutionary processes underlying species diversification. A study of the drivers of plant diversification in Madagascar was undertaken to explore the dynamics of this process in selected endemic lineages. This involved an integrated approach using phylogenies, trait evolution and niche analyses on nearly a dozen endemic plant groups that comprise a representative sample of the Malagasy flora. The major goals are to: i) elucidate the dynamics of plant diversification in Madagascar; ii) understand niche evolution of the selected clades and explore the potential role of selected ecological parameters in diversification; and iii) identify adaptive trends and explore possible links between diversification events.

## **C<sub>4</sub> photosynthesis promoted species diversification during the Miocene grassland expansion**

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C<sub>4</sub> photosynthesis, an adaptation that maintains photosynthetic efficiency under conditions of drought, high temperature, and low atmospheric CO<sub>2</sub>, has evolved multiple times in the PACMAD grass clade. Here, we assemble the largest phylogeny yet compiled for grasses and present evidence that the evolution of C<sub>4</sub> photosynthesis was a key physiological innovation that promoted high rates of diversification in several lineages. In most cases there was a significant lag time between the origin of the pathway and subsequent radiations, suggesting that the ‘C<sub>4</sub> effect’ is complex and derives from the interplay of the C<sub>4</sub> syndrome with other factors. We also identified comparable radiations occurring during the same time period in C<sub>3</sub> Pooid grasses, a diverse, cold-adapted grassland lineage that has never evolved C<sub>4</sub> photosynthesis. The mid to late Miocene was an especially important period of both C<sub>3</sub> and C<sub>4</sub> grass diversification, coincident with the global development of extensive, open biomes in both warm and cool climates. As is likely true for most “key innovations”, the C<sub>4</sub> effect is context dependent, and only relevant within a particular organismal background and when particular ecological opportunities became available.

## **Balancing supply and demand: diversification depends on the rate of niche formation**

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How a single species can give rise to multiple new taxa in the presence of gene flow has been a controversial question. Differential selection associated with different habitats is one way in which populations of a single species may eventually become reproductively isolated and lead to new species. Here, I test whether diversification rates vary more with the rate at which new adaptations or niches arise. I consider the potential for multiple niches to arise simultaneously (“novel invader” scenario), gradually (“geological building” scenario), and through repeated expansion and contraction (“climate change” scenario). My approach is to incorporate multiple multidimensional niches into a widely-used mathematical model of adaptive radiations and track individual plants over thousands of generations. The model links reproductive and ecological traits to their underlying genetic signatures, and incorporates spatial heterogeneity in niche-dependent selection, reproduction and dispersal. My findings generate new mechanistic-based hypotheses that can help inform future directions of biodiversity change in a world increasingly transformed by human activities.

## **The origin of diversity in a Southeast Asian biodiversity hotspot: Testing hypotheses on drivers of diversification of Sulawesi *Begonia***

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Hypotheses advanced to explain the exceptional diversity in the Malay Archipelago (MA), whose islands form three of 34 global biodiversity hotspots, have highlighted either present-day environmental factors or historical processes such as mountain uplift, and frequent climate and sea-level changes as drivers of diversification. This project seeks to inject new data into the problem by investigating the diversification of the mega-diverse flowering plant genus *Begonia* on Sulawesi, an island located in the heart of the MA. Dated non-coding plastid DNA phylogenies (ca. 3.4 kb, 112 accessions) indicate three independent colonization of the island in the late Miocene and Pleio- to Pleistocene, only the first of which resulted in a larger radiation (> 42 species). Preliminary climate niche comparisons of sister species pairs (principal component analysis, Bioclim data) show substantial niche overlap in allopatry, and only few cases of conspicuous climate niche differentiation. These results are consistent with the hypothesis that mountain uplift and associated formation of topographical heterogeneity coinciding with the Sulawesi *Begonia* radiation were major drivers of speciation by the facilitation of microallopatry. Data from reduced genome representation methods and analyses of microniche parameters will be used to further explore the role of ecological differentiation in this radiation.

**Explaining the differences in African and South American species richness by comparing diversification rates: The Andean orogeny hypothesis.**

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The Neotropics are considered as one of the most diverse regions of the already diverse tropical forests. I aim to test whether high neotropical species richness can be explained by higher (relative to other regions) phylogenetic diversification rates associated with speciation during uplift of the tropical Andes over the last ca. 25 my, and particularly the last 10 my. We aim to estimate and compare diversification rates of the Andean-centred genus *Renealmia* in the Neotropics and Africa using a multi-locus phylogeny, and address the uncertainty inherent to estimation of diversification rates.

## **Biogeography and diversification patterns of the Andean plant genus *Macrocarpaea* (Gentianaceae).**

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The tropical Andes encompass three biomes, the Seasonally dry tropical forests (SDTF), the High- elevation grasslands (HEG), and the Mid-elevation montane forests (MMF). Studies have revealed island-like process of diversification in plants for the first two biomes. In contrast, MMF is unlikely to show island-like patterns of diversification because of a more continuous distribution. We used the plant genus *Macrocarpaea* to address the patterns of diversification of plant species from the MMF. *Macrocarpaea* is composed of 114 species, 91 of which are endemics to the MMF. We sampled 76 species that were sequenced for 6 markers. This dataset was used to reconstruct a dated phylogeny, which was subsequently used to infer a biogeographical hypothesis for the genus, with a probabilistic approach implementing a model testing procedure. We also used the dated phylogeny to estimate *Macrocarpaea* diversification rate and its variation through time and among lineages in a Bayesian framework.

We found that founder-event speciation is the dominant process structuring the biogeography of *Macrocarpaea* in the Andes. Range expansion has proceeded from north to south, starting around 7Ma and attaining its actual most southward range area in less than 3My. This period of rapid range expansion coincides with a massive increase in the diversification rate.

Our results suggest that the uplift intensification in the northern Andes have initiated range expansion and diversification in *Macrocarpaea* by providing a launch pad to the already raised central and southern Andes. Dispersion and diversification patterns we infer advocate in favor of an island-like model for the MMF plant assembly.

## **Cichlid species-area curves are shaped by adaptive radiations that scale with area**

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A positive relationship between species richness and island size is thought to emerge from an equilibrium between immigration and extinction rates, but the influence of species diversification on the form of this relationship is poorly understood. Here, we show that within-lake adaptive radiation strongly modifies the species-area relationship for African cichlid fishes. The total number of species derived from in situ speciation increases with lake size, resulting in faunas orders of magnitude higher in species richness than faunas assembled by immigration alone. Multivariate models provide evidence for added influence of lake depth on the species-area relationship. Diversity of clades representing within-lake radiations show responses to lake area, depth and energy consistent with limitation by these factors, suggesting that ecological factors influence the species richness of radiating clades within these ecosystems. Together, these processes produce lake fish faunas with highly variable composition, but with diversities that are well-predicted by environmental variables.

## **Fossils and a large molecular phylogeny show that the evolution of species richness, generic diversity and turn-over rates are disconnected**

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The magnitude and extent of global change during the Cenozoic are remarkable, yet the impacts of these changes on biodiversity and the evolutionary dynamics of species diversification remain poorly understood. To investigate this question we combine palaeontological and neontological data for the angiosperm order Fagales, an ecologically important clade of c. 1370 species of trees with an exceptional fossil record. We show differences in patterns of accumulation of generic diversity, species richness, and turnover rates for Fagales. Generic diversity evolved rapidly from the Late Cretaceous and peaked in the Eocene or Oligocene. Turnover rates were high during periods of extreme global climate change, but relatively low when the climate remained stable. Species richness accumulated gradually throughout the Cenozoic, possibly at an accelerated pace after the Middle Miocene. Species diversification was into new environments: Quercoids radiating in Oligocene subtropical seasonally arid habitats, Casuarinaceae in Australian pyrophytic biomes, and *Betula* into late Neogene holarctic habitats. These radiations were counterbalanced by regional extinctions in late-Neogene mesic warm-temperate forests. Thus overall diversification at species level is linked to regional radiations of clades with appropriate ecologies exploiting newly available habitats.

## **Climate-change induced shifts in leaf-out times**

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A well-timed phenology is essential for plant growth and reproduction, but species-specific phenological strategies are still poorly understood. Under widely accepted climate change scenarios, by 2075 the Munich region will change from its current cold, fully humid climate with warm summers to a more seasonal climate, most likely leading to changes in the flora. Here, we demonstrate how a common-garden approach can be used to compare leaf-out data for woody species from different native climates and thus to forecast how climate-induced shifts in the floristic composition might affect community phenology. In addition, we are presenting a new approach, namely using herbarium specimens to infer past leaf-out times. In combination, the two approaches allow (i) to study species-specific effects of climate change on leaf-out and (ii) to study ecotypic phenological variation across latitudinal gradients. Southern-climate-adapted species flush later than Munich natives, and photoperiod- and chilling- sensitive species all flush late. The herbarium method, with data for the past 140 years, revealed that species unfold their leaves 5-7 days later per 1°C increase in spring temperature and that photoperiod- and chilling-sensitive species show smaller interannual variation in budburst than do entirely temperature-dependent species. These results forecast that (i) a northward expansion of southern species due to climate warming will increase the number of late flushing woody species in the north, counteracting documented and expected flushing-time advances, and (ii) photoperiod- and chilling-sensitive woody species cannot rapidly track climate warming.

Reference: C. M. Zohner & S. S. Renner, *Ecology Letters*, doi: 10.1111/ele.12308