



3rd UK PLANT EVOLUTION MEETING

Lisa Sainsbury Lecture Theatre

Jodrell Laboratory

Royal Botanic Gardens, Kew

3-5 April 2019

ABSTRACTS

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TALK ABSTRACTS

Monography: where are we and where are we going?

Monographs are the 21st century's cornerstone for sustainable development

Alexandre Antonelli

Royal Botanic Gardens, Kew

Taxonomic monographs originated from our early desire to identify and classify nature, but today they play a role that extends far beyond human curiosity: they provide the fundament upon which to understand the health and functioning of our ecosystems. This is reflected by the fact that two out of the 17 Sustainable Development Goals – the biggest of all societal challenges – focus on biodiversity. However, surprisingly few people outside academia realise that monographs are pre-requisites for assessing and protecting biodiversity. Without them, it may be impossible to confidently understand species' boundaries, their distributions and ecological requirements. Monographs are also crucial for exploring our Natural Capital, such as bio-medical properties and other uses confined to particular species. In this talk I will argue that the need of monographs has never been as acute and relevant as today. To advance monographs at a pace and volume that are commensurable with their need, I propose that we i) re-evaluate the concept of a monograph, updating its contents, presentation and rationale; ii) integrate monographic work and taxonomy across all biodiversity-related research, in particular phylogenomics which hold the potential to increase objectivity and reproducibility in species identifications and delimitations; iii) embrace the potential of citizen science and machine learning to accelerate the identification of collections, mapping of species distributions and phenology; iv) increase the accessibility to, and standardisation of, monographic data; and v) ensure the training of taxonomists and transfer of expertise across generations. Assuming that taxonomists are prepared to embrace such developments, I believe that integrative taxonomic monographs are at the dawn of a renaissance.

Monographing monsters – challenges and opportunities

Sandra Knapp¹ and Tiina Särkinen^{1,2}

¹Natural History Museum, ²Royal Botanic Garden Edinburgh

Large plant genera – those with species numbers exceeding 1,000 – have tended to be “where angels fear to tread”; their sheer size and difficulty of biting off doable chunks means that many have not been treated monographically in their entirety since the 19th century. Today's focus on projects with three- to five-year time spans can lead botanists to focus on smaller, more tractable groups – leaving the “monsters” to languish in confusion and without a globally unified view. Many different methods have been suggested to overcome the challenges posed in treating large genera on a global scale – we will explore some of these through our own experience with the genus *Solanum* (Solanaceae). Working in larger teams, using phylogenetic methods to define doable chunks for study, taking advantage of the burgeoning new digital resources available – all these have helped to overcome, at least in part, the challenges of working with large genera. But no one of them is the silver bullet! Even though they present challenges, these large genera also represent golden opportunities for investigating evolutionary and ecological questions, such as nature of species and speciation, genome evolution, evolution of rarity, niche axis and traits, host-pathogen and plant-insect co-evolution. Globally integrated views of plant diversity are diverse in their scope and composition, but can be seen as an iterative enterprise, with small parts building a unified whole. Monographs are also essential for the conservation of plant diversity, if we are really committed to understanding the patterns and processes generating diversity - monographs of monsters can help this understanding in unique ways.

Grass monography on different planets: in Madagascar and in Britain

Maria S. Vorontsova

Royal Botanic Gardens, Kew

Grasses are the only large and well known family of plants which is equally diverse, and equally significant, in tropical and temperate parts of the world. This presents an opportunity for a comparison between monographic work in a poor megadiverse country with that in a wealthy country with the world's best known flora. Maria's recently published *Identification Guide to Grasses and Bamboos of Madagascar* (541 grass species in 144 genera) was published in 2018, nine years after the *Grasses of the British Isles: BSBI Handbook 13* by Tom Cope and Alan Gray (220 species in 67 genera). This presentation will compare the history, scientific process, and perspectives for grass taxonomy in Madagascar and in the UK. In both countries every child knows the word *grass*, or *bozaka*. But in spite of Madagascar's greater diversity there are fewer collections and a lower level of interest in herbaceous plants. The majority of Malagasy Poaceae specimens are held outside the country and the majority of monographic work also takes place outside, with just a fraction of UK's citizen scientist contributions. The quality of species knowledge is lower, the species descriptions are shorter with poorer accuracy, and there are fewer opportunities for genomics work. Working across multiple languages and the lack of specialised molecular laboratories present barriers for career development. Recent studies suggest the internet has the effect of increasing global inequality. Greater mutual understanding between scientists would enable everyone to better understand their field of study in a global context.

The value of a dot on a map: how monographs are helping deliver conservation targets

Peter Wilkie

Royal Botanic Garden Edinburgh

Using the tropical tree family Sapotaceae as an example this presentation will explore how information held in monographs, floras and related databases is fundamental to delivering global biodiversity priorities such as the Aichi Biodiversity and the Global Strategy for Plant Conservation targets, in particular delivering conservation status of species. It will provide an overview of how the data included in these publications are used, their limitations and gaps and how advances in digital technologies and bioinformatics has allowed us to do so much more than was possible only a few years ago. It will also investigate ways in which information traditionally held in monographs can be made more accessible and produced more quickly so that meaningful assessment of threat to species can be made, used to prioritise conservation actions and ultimately protect species from extinction.

The world without monography

Eve Lucas

Royal Botanic Gardens, Kew

The proportion of the world's flora that has been monographed is unknown. This proportion is estimated using appropriate criteria and examined in historical and future terms. The consequences of a complete halt to global monography will be considered, as well as the likely increase in in-situ monography. Consequences linked to using incomplete taxonomies and knowledge of relationships will be considered using case studies from the perspectives of ecology, evolution and conservation, as well as for our ability to reliably identify plant species.

Re-appraising the catch-all genus *Caesalpinia*: preparation, pit-falls and pay-back

Gwilym Lewis

Royal Botanic Gardens, Kew

With 770 genera and close to 20,000 species the Leguminosae (Fabaceae) is the third largest angiosperm family after the Asteraceae and Orchidaceae, and economically the second in importance after the Poaceae. Legumes have been the focus of many recent phylogenetic analyses at the family, subfamily, tribe, clade and genus levels. Much of the research underpinning these studies is taxonomic, floristic and monographic, ensuring that we know what species grow where and what are their correct identities. In 2017 the international legume community, under the umbrella name of the Legume Phylogeny Working Group (LPWG), published a new six subfamily classification of the legumes which, for the first time, renders subfamily Caesalpinioideae as monophyletic. Within this subfamily the type genus *Caesalpinia* has varied in content from 140 to 9 species during the past 150 years, based largely on regional flora accounts and morphological study. Since the late 1980s an international collaboration between Brazil, Canada, the UK, the USA and Switzerland have been gathering data towards the goal of resolving the genus and species level taxonomy of the pantropical “*Caesalpinia* group”. A new generic system for the group was published in 2016. This “mini monograph” recognised 26 genera, of which four were described as new, two old genus names were reinstated and the circumscriptions of six other genera were emended. Seventy-five new species combinations were proposed. The talk will discuss the route from initial selection of *Caesalpinia* as a taxonomic challenge needing attention, through some of the challenges met on the way, to final publication, and the powerful advantages of having a robust phylogeny and new taxonomic system which permits new questions to be asked and answered.

Unleashing the power of global natural history collections

Robert W. Scotland

University of Oxford

As a prelude to writing *On the Origin of Species*, Darwin spent nine years researching a taxonomic monograph of barnacles. Such comprehensive monographs that facilitate significant biological progress are now rare as they are considered too daunting to tackle in a realistic time frame, given the information overload associated with the world’s natural history collections. Here, we report a novel global-scale monographic study of morning glories (*Ipomoea* and allies) integrating DNA barcodes, high-throughput sequencing and the morphological study of herbarium specimens. This approach overhauled the taxonomy of the group and generated significant discoveries in relation to food security, crop domestication, conservation, evolutionary radiations and the description of many new species and country records. This integrated approach demonstrates how the most severe taxonomic problems can be addressed at world and continental scales to realize the potency of the world’s natural history collections to contribute to global challenges of the Anthropocene.

Opportunities for the future in monography

Olwen M. Grace

Royal Botanic Gardens, Kew

Monography is widely regarded as the foundational discipline for many other facets of botanical research, with far-reaching applications in fields concerned with the use and conservation of plant diversity. In a time of biodiversity in crisis and environmental change, a pragmatic approach to monography is required, so that Earth’s plant diversity may be documented, conserved and sustainably used where possible. Priority setting must necessarily take a long view to draw upon past strengths, take advantage of existing resources, and identify the plant groups in most urgent need of monographic

attention. I argue that the substantial volume of novel data generated is an idiosyncrasy of the contemporary monographic process, and that these important stand-alone contributions become more valuable when synthesised in the monograph itself. I use the leaf-succulent genus *Aloe* L. (Asphodelaceae), native to Africa and the Arabian Peninsula, to illustrate the process and highlight challenges to be confronted when monographing ecologically and economically important plant groups.

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How to solve Darwin's abominable mystery

Richard J. A. Buggs

Royal Botanic Gardens, Kew

The term "Darwin's abominable mystery" has been widely used to describe uncertainties in almost every imaginable aspect of the origin and diversification of the angiosperms. Suggested solutions have therefore included: better-resolved molecular phylogenies, putative pre-Cretaceous angiosperm fossils, detection of ancestral whole genome duplications, floral evo-devo models, and the proposal of almost every angiosperm-specific trait as a possible key innovation. This is reasonable, given that Darwin described the mystery as "the rapid development ... of all the higher plants within recent geological times". However, it has been widely forgotten that Darwin and his contemporaries believed that a few monocot fossils were present in the fossil record from the Carboniferous to the Cretaceous, and these provided a stem lineage for the rest of the angiosperms. Thus, the abominable mystery as we see it today involves a larger transition and a bigger radiation than Darwin thought it did. It would not be solved in Darwin's eyes simply by the discovery of a few pre-Cretaceous angiosperms, or the identification of a sister lineage to the angiosperms. As well as these, Darwin would seek a diverse assemblage of pre-Cretaceous angiosperms or a mechanism for rapid diversification.

The Leverhulme Lecture

The wondrous cycles of polyploidy in plants

Jonathan F. Wendel

Iowa State University

One of the signal realizations of the genomics era is that all flowering plants are multiply polyploid, varying in the number and relative antiquity of their episodic, whole-genome doubling events. *Gossypium*, the cotton genus, exemplifies this recurrent, episodic polyploidization, with both ancient polyploidy and more recent neoallopolyploids that originated following a biological reunion 1-2 MYA of divergent diploids from different hemispheres. This most recent serendipitous merger between diploid genomes that vary two-fold in size generated myriad genomic and transcriptomic responses, which serve as illustrative models for understanding evolutionary processes following allopolyploidy. Genomic processes include homoeologous exchange, gene silencing, intergenomic gene conversion, and novel cytonuclear interactions. Allopolyploid formation also induces complex transcriptomic responses, including genome-wide modification of gene expression and co-expression patterns and variable *cis*- and *trans*-controls governing duplicate gene expression. Cyclical, recurring polyploidy occurring over time scales ranging from hundreds to millions of years sets in motion processes that lead to genome downsizing, genomic fractionation, and chromosomal diploidization. This polyploidy-induced dynamism, observed in *Gossypium*, is episodically and variably reiterated throughout the angiosperms. A major challenge is to connect these long and short-term processes to our understanding of the genotype-to-phenotype

equation, and hence the adaptive role of polyploidy and its importance to the generation of biodiversity and to agriculture.

Evolution and development of the earliest land plant rooting systems

Liam Dolan

University of Oxford

The evolution of the first rooting systems some time before 400 million years was a key innovation that occurred when the first complex multicellular eukaryotic photosynthetic organisms – plants – colonized the land. Rooting systems are important for land plants because they facilitate the uptake of most chemical elements that are required for growth, water uptake and anchorage. The rooting systems of the earliest diverging group of extant land plants comprised unicellular tip-growing filaments called rhizoids and are morphologically similar to cells that develop at the interface between the plant and the soil in vascular plants – root hairs. Subsequently specialized axes – multicellular structures that develop from self-renewing populations of cells called meristems – with evolved that carry out rooting function. A major aim of our research is to use fossils and genes to understand key events in the evolution of land plant rooting systems. Fossils demonstrate the variety of forms that existed and how these forms developed. We have identified the oldest rooting structures with meristems. Genetics has allowed us to define the regulatory mechanisms that controlled the development of the first land plant root system and demonstrate how these mechanisms changed during the course of evolution. This positive regulatory mechanism is preserved in most land extant plant lineages. By contrast, negative regulatory components of the mechanism evolved independently in different lineages and some are more than 300 million years old. By combining evidence from paleontology, genetics and development we can construct a picture for the evolution of rooting systems in the 100 million years after plants colonized the land and radiated across the continental surfaces.

Painting a bullseye: understanding the evo-devo mechanisms of petal patterning

May Yeo, Stefano Gatti, Alice Fairnie, Valentina Travaglia, Joseph Walker, Lucie Riglet and

Edwige Moyroud

University of Cambridge

Patterning mechanisms are essential to produce functional organs from undifferentiated cells in both plants and animals. Evolution acts on these mechanisms to generate morphological diversity. The patterns on the petals of flowering plants are striking examples of evolutionary diversification by natural selection and play a crucial role in pollinator attraction. These patterns are often highly elaborated and combine differences in pigmentation, cell shape and ornamentation of the cuticle (a waxy layer that protects plant surfaces) to generate neighbouring tissues with very distinct appearances. However, the mechanisms that permit the set-up of such patterns across the angiosperms are not well understood. Our group has recently started to investigate the mechanisms that regulate pattern formation and diversification in petals, using Venice mallow, a small hibiscus species with a striking bullseye pattern, as a model system. We combine genetic and phylogenomic approaches with imaging and modelling to dissect the processes underlying pattern acquisition and evolution in Venice mallow and its close relatives. Our results should help us understand how plants can set-up boundaries within their petal epidermis to shape their corolla and how evolution tinkers with these processes to generate the diversity of petal patterns observed in nature.

Ejaculation in moss: morphomechanical Innovation for gamete dispersal in early land plants

Bo Xu, Xiaolong Lyu and Samuel Brockington
University of Cambridge

Dispersal refers to the movement of a variety of dispersal units derived from different life stages of plants, including the dispersal of gametes, spores, and seeds. Plants are sessile, and so survival through movement to new habitats and ecological niches depends on the dispersal mechanisms. Consequently, land plants have developed elegant innovations to split tissues for release of gametes, spores, and seeds. Recent studies on release mechanisms in angiosperms reveal that a group of NAC domain transcription factors, NAC SECONDARY WALL THICKENING PROMOTING FACTOR (NST)/SECONDARY WALL ASSOCIATED NAC DOMAIN PROTEIN (SND), are crucial for tissue opening by inducing deposition of secondary cell wall in specified tissues, providing the mechanical tension for dispersal. However, little is known about how these mechanisms have evolved, and there is little data on release mechanisms in early diverging plant lineages. Taking advantage of the moss *Physcomitrella patens*, we revisited this issue. By studying the *PpVNS* proteins homologous to NST/SND in higher land plants, our research resolves the biomechanical mechanism underlying sperm release in mosses, revealing convergent evolution of morphomechanical innovations between bryophytes and angiosperms.

Space matters: how spatial constraints affect the floral development of Caryophyllaceae

Louis Ronse De Craene
Royal Botanic Garden Edinburgh

Flowers of Caryophyllaceae are constructed on the widespread pentamerous pentacyclic Bauplan of Pentapetalae, consisting of five imbricate sepals, five narrow petals, two whorls of five stamens, and five carpels. However, there is a strong tendency for petals to become reduced or lost, positions of whorls to shift, stamen numbers to fluctuate between ten and one, and the gynoecium to become reduced to three or two carpels. A selection of developmental stages of different species show that four developmental processes are independently responsible for the changes occurring in Caryophyllaceae flowers. (1) Petal initiation is strongly delayed and petals become absorbed in stamen-petal primordia, eventually leading to the loss of the petals. (2) A concerted delay in initiation of petals and antepetalous stamens leads to obdiplostemony and a shift in carpel positions. (3) Strong pressure of the quincuncially initiated calyx, coupled with a delayed initiation of the petals is responsible for an inversed developmental sequence of antesepalous stamens and their upward shift. (4) Carpels create a spatial constraint on the androecium and loss of carpels induces a loss of stamens in a predicted sequence. The occurrence of heterochrony and spatially induced pressure of the calyx and ovary establish a predictive pattern for a progressive reduction of the androecium, where antepetalous stamens are affected differently from antesepalous stamens. It is demonstrated that subtle changes in timing of initiation as well as pressures of pre-established organs are the causes for the morphological diversity in the flowers of Caryophyllaceae beyond any genetic predisposition.

The Evolution and Development of Nectar Spurs

Erin Cullen and Beverley Glover
University of Cambridge

Nectar spurs (tubular outgrowths of the petal) are hypothesized to be a 'key innovation' which can lead to rapid speciation within a lineage and are important for pollinator specificity. However, there is still much to learn about nectar spur development. This project aims to probe both the morphological and molecular basis of nectar spur outgrowth. We have investigated the control of variation in nectar spur length, in a clade of eight Iberian toadflaxes, focusing on *Linaria becerrae* and *Linaria clementei*, two closely related species which have extremely long and short spurs respectively. We undertook a morphological characterisation (recording cell number and cell length across a range of developmental stages) to determine whether the difference is due to cell expansion or cell division. We found that primarily cell number and therefore cell division drives an increase in spur length. This contrasts with previous studies in *Aquilegia* which have found that variation of nectar spur length is due to directed cell expansion (anisotropy) over a longer timeframe. To probe the basis of spur outgrowth, the same approach has been applied to the species *Linaria vulgaris* (which has a nectar spur) and *Antirrhinum majus* (possesses only a nectar pouch, called a gibba). This morphological framework has been used to inform a comparative transcriptome based on *A. majus* and *L. vulgaris* at three developmental stages which provides a global view of the genes involved in nectar spur and gibba development.

Dynamic histories of adaptation and deterioration in plant domestication revealed through archaeogenomics

Robin Allaby
Warwick University

The forces of selection involved in cereal domestication have varied over time in both strength and nature. It is becoming apparent that these forces of selection stretch back deep in time far beyond the onset of widespread cultivation. Using archaeogenomics it has become possible to gain insights into the way in which plants transitioned into domestication and the consequent impacts of that on their adaptive plasticity. A picture is emergent of domestication as a landscape scale process in which diversity was successfully brought wholesale in from wild populations. Adaptive episodes can be resolved which sequentially reveal the selection on fundamental domestication syndrome genes, environmental adaptations and later domestication improvement genes. The damage accrued in domesticated genomes through mutation load is not particularly associated with initial domestication, but with subsequent founder events and adaptive episodes reaching critically high levels in recent history. These insights both underline the importance of wild genetic diversity in rescuing core genomic functions of cultivars as well as improvement traits, and in some cases highlight how long-term agricultural practices might be revised to support future sustainability.

CAM and capacitance in *Clusia*: dissecting two adaptations to drought in tropical trees

Alastair P Leveret and Anne Borland
Newcastle University

When thinking of leaf succulents, one often considers taxa from semi-arid desert environments, such as *Agave* and *Aloe*. However, a variety of leaf succulent syndromes exist in tropical tree species, particularly those that experience seasonal dry periods. Tropical tree species within the genus *Clusia* have evolved succulence in different ways; by increasing the depth of specialised water-storage hydrenchyma tissue, increasing the size of photosynthetic chlorenchyma cells, or some combination of the two. In addition, *Clusia* species with larger chlorenchyma cells often evolve crassulacean acid metabolism (CAM). CAM is a photosynthetic adaptation which improves water use efficiency roughly 10-fold compared to other types of photosynthesis by enabling CO₂ uptake through open stomata at night, when transpiration is reduced, and its photosynthetic re-fixation behind closed stomata during the day. Thus, in *Clusia* a diversity of succulent syndromes exists, due to the evolution of the aforementioned anatomical and metabolic adaptations. Our aim is to understand how these functional traits each affect the hydraulic and photosynthetic physiology of *Clusia* trees during drought. We used Newcastle University's *Clusia* collection, the largest in Europe, to test: a) which form of succulence (specialised hydrenchyma or enlarged chlorenchyma cells) is better at buffering leaves against water loss; b) does the presence of CAM photosynthesis affect a species' ability to withstand low water potentials?; and c) what affect does CAM have on metabolic activity during drought? Results show that hydrenchyma buffers leaves against water loss by deflating and releasing water to the photosynthetic tissue. Enlarged chlorenchyma cells, on the other hand, appear to function as a hydraulic 'source'. CAM photosynthesis does not appear to be a good predictor of species' ability to tolerate low water potentials, but rather functions to allow higher rates of photosynthesis and respiration during exposure to stress. These findings dissect the nuances of different aspects of the succulent syndrome in tropical trees and the role they play during drought.

Tyrosine-rich metabolism and the evolution of betalain pigmentation

Samuel Brockington
University of Cambridge

Unlike animals, plants are sessile, and produce a diverse range of specialised metabolites in order to adapt to their environment. Specialised plant metabolites, by definition, contribute to plant fitness in specific ecological niches, and occur in a taxon-specific and niche-specific manner. The lineage specificity of specialised metabolites, coupled with the quasi-linear nature of metabolic pathways, enhances comparative approaches across phylogenetic hierarchies, enabling the step-wise dissection of metabolic trait assembly. One of the best examples of a taxonomically-restricted metabolic trait are the tyrosine-derived betalain pigments, which are unique to the order Caryophyllales, and responsible for the deep purple colour of beetroot. Over the past five years we have assembled a dataset of transcriptomes for over 350 species across Caryophyllales, which together with over 10 sequenced genomes, covers 32/39 families and over 30% of the 752 genera in the order. We have utilised this dataset to identify lineage-specific gene radiations, step-wise gene duplications, neo-functionalisation, and syntenic rearrangements that underpin the emergence of the betalain pathway. More recently we have described a previously unknown novel isoform of the enzyme Arogenate Dehydrogenase that is driving the unusual phenomenon of tyrosine-rich metabolism in Caryophyllales. Here we argue that tyrosine-derived betalain pigmentation is one of many metabolic innovations that have arisen in the context of a novel tyrosine-

enriched adaptive landscape, which has had a profound impact of the patterns of trait evolution in Caryophyllales.

Role of storage roots in sweet potato domestication.

Pablo Muñoz-Rodríguez

University of Oxford

Ipomoea batatas (L.) Lam., the sweet potato, is among the most consumed crops worldwide and a staple in many developing countries. This crop of American origin is now cultivated in all tropical and subtropical regions of the Globe for its edible storage roots, which are able to grow in poor dry soils with minimum labour. In my talk, I will present the results of a comprehensive phylogenomic study on the origin and evolution of the sweet potato and its storage root. I will first show how a comprehensive taxon and data sampling allowed us to investigate the origin of the crop; to identify the wild species that is sweet potato closest relative; and to reveal the dual role of this wild species in the origin of the crop through an ancient hybridisation event. Next, I will present a timeframe of the evolution of the crop and its storage root. The phylogenetic framework in place allowed us to investigate two assumptions that had never been critically assessed: 1) that sweet potato storage roots are the result of human domestication and 2) that sweet potato demonstrates the existence of human contacts across the Pacific in pre-European times. Despite the limited taxon and data sampling in previous studies, important conclusions have been drawn from dubious information —including the multiple origin of sweet potato and the existence of human contacts across the Pacific Ocean in pre-European times. This talk aims to clarify the widespread confusion that surrounds sweet potato research by providing a new, robust phylogenetic framework of the evolution of the crop and its storage roots. Our results have important implications for our understanding of sweet potato evolution and domestication, as well as for the interpretation of archaeological remains in the context of human migrations and crop exchanges in ancient times.

Selective sweeps during domestication and adaptation of rice subpopulations within a diverse collection of Vietnamese Rice

Janet Higgins¹, Bruno Santos², Tran Dang Khanh³, Khat Huu Trung³, Le Huy Ham³, Mario Caccamo² and Jose De Vega¹

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Rice in Vietnam is important both for export and for providing a staple food for 100 million people. Vietnam's national seedbank holds over 9,000 samples which represent the rich diversity of rice germplasm grown in Vietnam. This includes native and local landraces and varieties adapted to growing in the low-lying rice deltas. These regions are particularly vulnerable to the effects of climate change, meaning that there is an urgent need to understand the local diversity and accelerate the breeding of new climate-resilient rice varieties. We have sequenced 616 rice varieties from Vietnam, these represent 202 Japonica and 379 Indica subtypes with the remaining 35 being classified as admixed. We have added 107 accessions from Vietnam and nearby East Asian countries from the 3,000 Rice Genomes Project, which represent all twelve Asian rice subpopulations. We have classified the Vietnamese Indica subtypes into five subpopulations and the Japonica subtypes into four subpopulations. Using the Cross-population composite likelihood ratio method (XP-CLR), we have detected signatures of selection between these subpopulations during the breeding of rice within Vietnam. We have related these regions, which span around 5% of the genome, to QTLs detected by our group and in published studies using a subset of Vietnamese samples. Selected regions in Japonica have been related to the adaptation of subpopulations to lowland (irrigated and rainfed) and upland (drought) environments. One of the Indica subpopulations shows a high signature of selection and contains diversity unique to Vietnam. This subpopulation is mainly located in North Vietnam around the Red River Delta, whereas the widely distributed elite Indica varieties show a much lower signature of selection. Our analysis provides evidence of novel diversity in Vietnamese

native rice that can be used to improve the global rice gene-pool tolerance to the demands of a changing climate and growing population.

Molecular trajectories of pollination strategy shifts: the evolution of sexual deception in *Gorteria diffusa* (Asteraceae)

Roman Kellenberger

University of Cambridge

The astonishing diversity of flowering plants is linked to interactions with their animal pollinators. In the last decades, genetic pathways have been identified which control the development of pollinator-relevant floral traits. However, it remains challenging to trace back variation in pollinator behaviour to alterations in genetic pathways. Here, we explore the developmental genetic basis of a shift in pollination strategy from nutrition advertisement to sexual deception in the South African daisy *Gorteria diffusa*. Within its native range, ca. 16 *G. diffusa* morphotypes have been described, which differ mainly in number and morphology of dark, raised spots on the petals. Interestingly, the behaviour of their main pollinator, the bee-fly *Megapalpus capensis*, varies between morphotypes: While morphotypes with simple spots elicit normal feeding behaviour, morphotypes with complex spots that contain large cellular papillae trick *M. capensis* males into copulation attempts with the flower. To find genes responsible for papillae development, we have sequenced the transcriptome of a normal and a sexually deceptive morphotype, and compared gene expression levels (1) between spotted and plain petals, and (2) between petals with simple and papillate spots. This approach has yielded promising candidate genes from gene families known to be involved in plant cell growth. A combination of genetic, phylogenetic, morphological, and pollinator behavioural assays will enable us to further clarify the role of these genes in papillae development, and to reconstruct the evolutionary pattern of sexual deception among the *G. diffusa* morphotypes.

Evolution of floral shape in *Pelargonium* (Geraniaceae)

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Floral evolution in the 6th largest Cape Floristic Region clade *Pelargonium* clade (Geraniaceae) has resulted in a broad spectrum of shapes and syndromes, reflecting the use of several groups of pollinators. *Pelargonium* displays spur pollination with spur lengths probably reflecting pollinator proboscis lengths. Pollinator switches may have driven actual speciation and hence clade size differences in this group, as judged by studies using nectar spur lengths optimisation on phylogenetic trees. The overall trend was found to be towards longer spurs. In this study, I focus on the evolution of floral shape and its relation to clade size and speciation in *Pelargonium*. Floral morphological differences among *Pelargonium* species are quantified using geometric morphometrics in order to infer trends in *Pelargonium* corolla-, spur-, and stamen shape. This enables testing whether different aspects of floral shape have evolved in concert or independently, and whether selection works on each aspect separately. Exploring the relation between phylogenetic placement and floral shape, we find instances of both convergent and divergent evolution and can, unsurprisingly, conclude that floral shape is not constrained by phylogenetic signal. We find the relation between phylogenetic and morphological distance to be random, which underlines the finding that similar shapes have evolved multiple times and large switches in shape between sister-species are possible. In addition, we can infer possible 'avoided shapes' in corolla, spur, and stamens, and explore structural (and possibly biological) boundaries to shapes as they are realised in the *Pelargonium* clade. We can then identify potential explanations why these shapes did not form. Structural boundaries are for

instance petiole length which, as expected, determines spur length and may therefore have ultimate consequences for speciation in *Pelargonium*.

Genes for resistance to an insect pest in *Fraxinus* (Oleaceae) identified via comparative genomics

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Genome-wide discovery of candidate genes for functional traits within a species typically involves the sequencing of a large number of phenotyped individuals, or linkage analysis through multiple generations. When a trait occurs repeatedly among phylogenetically independent lineages within a genus, an alternative approach may be to identify candidate genes via detection of amino acid residues shared by species possessing that trait. Here, we took this approach to identify loci in the genus *Fraxinus* (ash trees) that may be involved in resistance to the emerald ash borer beetle (EAB; *Agrilus planipennis*), a naturally rarely occurring inhabitant of ash within its native East Asian range that has become a highly destructive invasive forest pest in North America. Vulnerability to EAB varies across *Fraxinus*, with North American species typically showing very high levels of susceptibility and those from Asia, within the native range of *A. planipennis*, much lower susceptibility (or resistance). Using data from whole genome assemblies, we compared protein-coding sequences to seek significant evidence of convergent amino acid evolution between resistant ash tree lineages, which share a co-evolutionary history with the beetle. We identified 53 candidate genes via this approach, each with one or more amino acid residues with evidence of convergence. Predicted function of these candidate genes, as well as analysis of their impact at the protein structure level, provides support for significant differences between susceptible and resistant species of *Fraxinus* that may be related to defence response against EAB.

Floral humidity: it's diversity and role within floral displays

Michael Harrap

University of Bristol

The floral displays of angiosperms produce many different signalling components to influence the behaviours of their pollinators. Some floral signals are salient to humans and well-known, such as visual and scent cues. Others are hidden to humans without use of modern technology. One such 'hidden' signal is floral humidity, an area of elevated humidity about the flower. Hawkmoth, *Hyles lineata*, have been shown to prefer flowers of primrose *Oenothera caespitosa* with elevated floral humidity. However, little is known about the wider occurrence of floral humidity in flowering plants. Furthermore, it is unknown whether floral humidity functions as a flower signal to other more widespread pollinators outside of the *O. caespitosa* - *H. lineata* pollination system. Using new robotic tools, the floral humidity about 42 flower species, from 21 widespread families, is sampled. We reveal humidity about many flower species to be elevated and various flower species differ in humidity intensity and structure. Using captive bumblebees and artificial flowers that differ in floral humidity in a way comparable to real flowers, we demonstrate that flower naïve bumblebees can learn to distinguish artificial flower based on floral humidity differences. Furthermore, bumblebees show a similar preference for humid flowers as shown by hawkmoths. These results suggest that floral humidity is more diverse and widespread than previously known. Furthermore, it can be utilized by more widespread and generalist pollinators as a flower learning signal. This expands our understanding of how flowering plants may be influencing pollinators but also our understanding of what aspects of the floral display may be subject to selection based on pollinator foraging choice.

Paleogenomic annotation of historical *Cinchona* bark samples across time and space

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Museum collections are a valuable source of biodiversity for evolution, authentication, drug discovery, and other studies. With the advent of high-throughput sequencing techniques of ancient DNA (paleogenomics), new opportunities for exploring and using natural history collections have emerged. *Cinchona* bark, the source of quinine for treatment of malaria, is an outstanding time referenced model system. Using modern samples, we are building a phylogeny for the genus across the geographical range, which will then be used to annotate unrivalled historical collections of about 1000 specimens documenting distribution of *Cinchona* forests and collecting and breeding experiments over 200 years. Additionally, Howard & Sons chemically annotated hundreds of these historical samples. However, botanical and geographical origin of the historical samples were poorly recorded until now. Annotating these samples based on the modern phylogeny, will allow us to trace the alkaloid content dynamics over time and through species.

Diversification of the Macaronesian endemic genus *Argyranthemum* (Asteraceae; Anthemideae)

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Argyranthemum (Asteraceae; Anthemideae) is a genus of flowering plants that is endemic to archipelagos of the North Atlantic Ocean, collectively known as Macaronesia. With a total of 24 species, it is the largest endemic genus found on these islands and has occupied the wide variety of habitat types available. In addition, *Argyranthemum* is known for a rare example of homoploid hybrid speciation, the origin of a hybrid species without a change in chromosome number. As such, *Argyranthemum* is an excellent example of an evolutionary radiation that we can investigate to try and understand the drivers of plant diversity. In this study we investigate the relative roles of geographic isolation, habitat shifts and hybridisation in the diversification of *Argyranthemum*. To do this, we used Next Generation Sequencing, specifically Genotyping-By-Sequencing (GBS), to identify thousands of single nucleotide polymorphisms (SNPs) across the genome and resolve evolutionary relationships within the group. Ancestral state reconstruction demonstrates that habitat shifts are a more important driver of speciation than previously thought and D-statistics show that hybridisation between lineages co-occurring on the same island has been widespread. However, hybridisation does not explain the occurrence of non-monophyletic species as previously hypothesised, which is more likely due to morphological convergence. Our findings have revealed the evolutionary processes responsible for generating the endemic diversity in *Argyranthemum* and highlighted the value of Next Generation Sequencing (NGS) for future studies. In particular, we identified an important role for habitat shifts in generating plant diversity, which in turn may have been facilitated by hybridisation.

Divergent selection on multiple genomic regions allows physiological divergence despite gene flow

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Over large evolutionary scales, complex multigenic adaptations emerge via the repeated fixation of adaptive mutations within populations. The efficiency of the process is determined by the interplay between demographic and selective forces but over time, the accumulation of mutations will blur the genomic traces of these processes. However, species where complex and contrasted phenotypes co-exist offer an opportunity to disentangle the importance of demographic and evolutionary forces on the build-up of genomic differentiation linked to the trait. We address the genomic drivers of phenotypic divergence by studying the grass *Alloteropsis semialata* in Africa, where individuals possessing the complex, multigenic trait C4 photosynthesis co-occur with populations lacking the adaptive anatomical and biochemical modifications. Using genome-wide data from 80 populations with contrasted phenotypes, we reconstruct the history of divergence and gene flow and identify genomic regions that represent peaks of differentiation linked to the phenotypic diversification. Despite recurring gene flow, the two photosynthetic phenotypes form distinct genetic groups, which are associated with large genomic blocks of increased differentiation spread across the genome. These divergence peaks are mostly localized around regions of low recombination, which we propose increase the efficiency of divergent selection on C4-related genes. The maintenance of the two phenotypes is furthermore reinforced by repeated polyploidization, reducing gene flow between locally co-occurring photosynthetic types. The resulting partial isolation coupled with strong selection resulted in phenotypic divergence despite gene flow, in this geographically limited region

DNA methylation during plant sexual reproduction: contrasting patterns of gene-targeted and global reprogramming

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DNA methylation is observed across the genomic landscape of mammals and is important for transposon repression and developmental gene expression. It is vastly reprogrammed during germline development, in part to maintain silencing of retrotransposons and for the purposes of imprinting. DNA methylation in plants is more tightly associated with transposons and hence transposon repression. This tight association and other evidence have suggested that complete loss or gain of methylation does not occur in plant germlines. Recently, we identified a previously unseen *de novo* gene-targeted methylation phenomenon in the male germline of the model plant *Arabidopsis* and demonstrated that this methylation is important for gene regulation and meiotic function. Here, we show that the gene-targeted methylation signature is present in the meiotic and germ cells of multiple species across the plant kingdom, establishing a common mechanism for sexual *de novo* methylation in plants. However, we have also identified a more radical and unique methylation reprogramming event in the sperm of the plant *Marchantia polymorpha*, with the majority of cytosines across the genome being *de novo* methylated in a manner that is similar yet distinguishable to plant transposon methylation. Notably, promoters and transcriptional start sites of genes expressed during *Marchantia* sperm development remain unmethylated in a comparable fashion to mammals. Despite this widespread methylation, it is largely absent outside of transposons following fertilisation and in somatic tissues, highlighting this phenomenon as an interesting parallel of the large-

scale DNA methylation reprogramming observed in mammalian systems and establishing an important plant model for studying the conflicts between methylation reprogramming and transposon suppression.

Phylogenomic analyses reveal the genomic novelties accompanying the major transitions of plant life

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Identifying the genomic changes that have accompanied the origin of distinct plant groups is key to unravelling the molecular basis of biological innovations. In the last decade, the quantity and quality of complete genomes has dramatically increased, allowing for large-scale phylogenomic comparisons. Approaches that utilise a phylogenetic framework to perform comparative genomics will inform our understanding of the influences of speciation and duplication on gene family innovation, expansion and reduction. Using a phylogenomics pipeline incorporating data for 208 species, evolutionarily conserved gene innovations across the plant phylogeny were identified. Analyses have revealed large numbers of core gene novelties in the ancestors of Embryophyta and Streptophyta, likely involved in the transition of plants from water to land and the evolution of multicellularity. Gene Ontology analysis has identified the functional changes that have accompanied major plant developments. These results will help us to understand the influence of genomic innovations on plant diversification.

Hybrid speciation in *Brassica*

Annaliese Mason

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Hybridization (where two species come together to form a new species) has played a major role in evolution and speciation, particularly in the flowering plants. Many crops grown today are hybrid species, including wheat, canola, sugarcane and cotton. However, exactly how hybrid species form is still a mystery in almost all genera. New hybrids face a number of challenges to establishment, the most serious of which may be regulating meiosis. In most newly-formed hybrids, two sets of chromosomes from each of the progenitor species will be present. These sets of chromosomes not only contain competing genomic information, but almost always share regions of genomic similarity that can hinder homologous chromosome pairing and segregation. Failure of meiosis to correctly segregate chromosomes belonging to different genomes usually results in loss of chromosomes and genomic information from one generation to the next, and subsequently loss of fertility and true-breeding in offspring. Hence, hybrids must regulate meiosis to establish as new species. But how? In the *Brassica* genus (cabbages, turnips, canola, mustards), cultivated species share combinations of the A, B, and C genomes: A, B, C, AB, AC and BC genome-types all exist as established crops. Via production and investigation of *Brassica* hybrids of different types with different genome combinations, our research aims to answer the question of how hybrid species form, and to potentially build new crop species through novel interspecific hybridization events.

The extraordinary evolution of eyebrights (*Euphrasia*): parasitism, polyploidy and phenotypic plasticity

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Many biologists have questioned the existence of clear-cut plant species and have instead suggested that species are largely an arbitrary human construct. The question of the discreteness or objectivity of plant species has largely been driven by a handful of taxonomically complex groups where species discrimination is particularly challenging. Here we tackle the nature of species differences in one such 'nightmare' group, British eyebrights (*Euphrasia*), a genus characterised by recent postglacial divergence, parasitism, polyploidy, phenotypic plasticity and self-fertilisation. We use growth experiments with different hosts to understand species differences and to characterise life-history traits, and a diversity of genomic approaches (whole genome sequencing, transcriptome sequencing, population genomics, plastid sequencing) to understand how the transition to parasitism has shaped genomic diversity. We show that amongst the mess is a suite of definable genetic units that have evolved in response to the parasitic lifestyle. Our results highlight the need to study evolutionary processes in neglected taxonomically complex groups.

Genome size and dynamics of DNA repeats in palms (Arecaceae) with focus on *Pinanga*

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Interactions between genome size and ecological factors such as soil nutrients, climate and pollution influence the distribution of species while in return genome size variation may influence the diversification of lineages, and adaptation to new ecological niches. The balance between the accumulation and removal rates of repetitive DNA is known to play a significant role in genome size variation, but the dynamics of repetitive elements and their influence on genome structure and function remain unclear. Given the 2,400-fold range of genome sizes encountered across angiosperms, in palms (Arecaceae) there is little variation between species of the same genus. The genus *Pinanga* is a notable exception, as genome sizes have been shown to vary from 6.7 to 15.8 pg even though the number of chromosomes is the same ($2n = 32$). *Pinanga* comprises ca. 140 species occurring in South-East Asian rainforests, with high levels of endemism in Borneo, the Philippines, and Sumatra, and is thus a good model to investigate the link between the dynamics of repetitive DNA, genome size variation and speciation. We generated new genome size data for 38 *Pinanga* species, used target sequence capture to produce the first comprehensive phylogeny of *Pinanga*, and genome skimming data to analyse the repetitive DNA content of species with different genome sizes. Our results show a high turn-over and heterogeneity in the repeats between species, and suggest that a variety of mechanisms have been involved in generating genome size diversity in *Pinanga*. We will discuss these results in relation to a newly resolved phylogeny and biogeographic history of the genus.

The African rainforest during the Ice Ages

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The rainforests of West and Central Africa have experienced fluctuations over time. Today the forest cover is continuous in Central Africa but the fossil record indicates forest fragmentation due to the arid conditions dominant during the Ice Ages. In this study we sequenced reduced representation libraries of 150 samples representing five Legume tree species that have widespread distributions in African rainforests, in order to investigate the genetic signal of the rainforest fluctuation. Overall 475 GBS libraries from 792 DNA extractions from 150 individuals were run on four Illumina lanes. Phylogenetic analysis on the datasets clearly identified that the population of each species was comprised of an early divergent lineage in West Africa (Upper Guinea), and two reciprocally monophyletic clades in Central Africa: Lower Guinea-North and Lower Guinea-South. As the structure separating the Northern and Southern clades cannot be explained by geographic barriers such as rivers or mountain chains, we used demographic model testing to test other hypotheses for explaining the structure. The best estimates recovered using dadi indicate that the two clades split between the Upper Miocene and the Pleistocene, a date compatible with forest fragmentation during Ice-Age climatic oscillations. Furthermore, we found that the fragmentation dates were older for the species with limited seed dispersal than those capable of long-distance dispersal, as would be expected given their relative potentials for gene flow. We also traced the spatial signal of recolonisation from forest refugia. We show that the genetic diversity significantly declines with the distance from refugia in the two long-distance dispersed species only.

Macro- and microevolutionary drivers of allopolyploid evolution in European marsh orchids

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Whole genome doubling (WGD) is a central force shaping plant evolution. Early-generation allopolyploids need to quickly accommodate divergent genomes into one nucleus by adjusting organization and function, with ecological consequences. The orchid genus *Dactylorhiza*, with its diverse array of polyploids constitutes an excellent system to investigate allopolyploid evolution. With phylogenomic methods applied to RADseq data, we document the parentage and times of origins for as many as 14 established *Dactylorhiza* allopolyploids of four main parentage groups. Whereas NW Europe is dominated by allopolyploids of postglacial origins, comparatively older allopolyploids are distributed further south. We bring evidence for frequent gene flow between sibling polyploids in contact zones. This process enriches their genetic pools, but some genomic regions appear resilient to admixture, suggesting a strong divergent selection maintaining the observed phenotypic divergence. We further investigate in detail the molecular basis of ecological distinctiveness between two of these sibling allopolyploids (*D. majalis* and *D. traunsteineri*). Their diploid parents have diverged six MYA and feature at present highly divergent transcriptomes and TE landscapes, indicating a significant shock on allopolyploid formation. By using complementary physiological, ecological and transcriptomic investigations we reveal webbed differences between the two polyploids at the level of nutrient transport, chlorophyll abundance, energy harvesting and use, together with photoprotection, which permit occupation of distinct ecological niches. Alternative parental dominance (in *trans*) is confirmed to largely trigger the ecophysiological divergence, whereas homoeolog expression bias (in *cis*) appears to be under strict constraints. We conclude that the significant divergence observed between diploids became reconciled in different ways in sibling *Dactylorhiza* polyploids, as a result of an interplay

between stochastic genomic alterations and distinct selection pressures. This ultimately drives distinct adaptations to specific environments and renders evolutionary independence through a pervasive resilience to gene flow.

Flower microevolution under stable and changing pollinator environments

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Floral trait variation at the macroevolutionary level is often believed to be the result of adaptations to pollinators. Yet studies measuring pollinator-mediated natural selection on floral traits frequently find little evidence for strong evolutionary change taking place in wild populations. A possible reason for this is the prevalence of periods of stasis, when pollinator-mediated directional selection on flowers is relaxed under stable conditions, followed by more unstable periods where pollinator changes provide innovative selection. I will present results of two studies that examine floral trait evolution under opposite pollination situations. In one case, the Mediterranean gorse (*Ulex parviflorus*) has a stable pollination environment dominated by a single pollinator, *Apis mellifera*. The common foxglove, bumblebee-pollinated *Digitalis purpurea*, is native to Europe but introduced and naturalised in many areas of the world, including neotropical mountains where hummingbirds are added to the visitor spectrum. In wild populations of both systems we study the pollination ecology and measure natural selection along with marker-based field heritability to explore the role of pollinators in current and potential evolution of flowers. In *Ulex*, we find evidence of low heritability constraining evolution of floral size. In turn, a floral attraction trait harbours significant heritable variation but is not under selection when pollinators are stable. This trait, however, has the potential to respond to novel selection. This is consistent with what we find in *Digitalis*, whose tropical populations present changes in corolla traits that are consistent with selection by hummingbirds and bumblebees with longer tongues. These studies highlight the importance of drastic pollination changes in the evolution of floral morphologies.

Grass diversification sheds light on the origin of Madagascar's biomes

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Madagascar has a striking diversity of plants, which occur in contrasting biomes. To understand the origin of these biomes, looking at plant groups that diversified on the island can be informative. We studied grasses (Poaceae), one of Madagascar's most widespread and species-rich families. A large phylogenetic analysis suggests that repeated immigration and endemic radiation of C4 grasses, characteristic of open habitats, occurred since the Late Miocene. This supports an ancient, pre-human origin of some of Madagascar's grasslands. C3 forest grasses comprise two large endemic groups that diversified since the Miocene. Further work is in progress to relate forest grass diversification to potential drivers like uplift and forest fragmentation, and thus reveal factors underlying the high rate of endemism in Madagascar's forests.

Do dynamic genomes drive speciation in the fastest-growing genus *Begonia*?

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Begonia is the fastest growing and one of the most species-rich angiosperm genera with c.1900 pantropically distributed species currently identified and many new ones being described every year. Recent taxonomic studies on *Begonia* provide a robust phylogenetic background for the analysis of evolutionary patterns across the group and confirm niche specificity cannot be the only factor driving speciation. Besides the wide phenotypic variation found in this genus, previous studies have also shown that *Begonia* species have very variable and dynamic genomes. Their genome sizes vary from 1C=244Mbp to 1C=1427Mbp, chromosome numbers go from n=8 to n=52 and repetitive elements can take up from 50% to 70% of their genomes. To better understand the role of genome dynamics in the evolution of this genus, Whole Genome Sequencing (WGS) strategies have been used to identify repeat content and variation among *Begonia* species. In order to also comprehend if intra-specific genome structure variation drives speciation by introducing crossing barriers between populations, different *Begonia heracleifolia* populations showing variable genome sizes have also been sequenced. In addition, the genome of the only *Begonia* sister species *Hillebrandia sandwicensis* has been included in our study in order to compare these two genera at a genomic level and better understand the specific factors involved in the repeated radiation events described in *Begonia*. Our results suggest that *Begonia* species show more complex, repetitive and dynamic genomes overall than *Hillebrandia*. We have found a wide variation in both content and types of DNA repeats across most *Begonia* species radiations. We have been able to identify different Long-Terminal Repeat (LTR) expansions of both gypsy and copia types throughout the phylogeny. Future analyses and transposon-dating results will allow us associate these expansions to speciation patterns across the genus.

Ecological Speciation of *Senecio* Species on Mount Etna, Sicily

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Senecio aethnensis and *Senecio chrysanthemifolius* are sister species inhabiting contrasting environments of high (above 2000m) and low altitude (below 1000m), respectively, on Mount Etna, Sicily. They form a hybrid zone at intermediate altitudes between their respective ranges. Previous work demonstrated that speciation of these *Senecio* species was likely parapatric, with gene flow continuing ever since their divergence around 100-150 thousand years ago, that coincided with the rise of Mount Etna. Despite their recent divergence, some hybrid breakdown was observed in F2 hybrids, indicating that these species have already evolved some degree of postzygotic isolation. This project aims to reveal the evolutionary forces during on-going ecological speciation driven by adaptation to contrasting conditions at high and low altitudes. Using a combination of phenotypic, genetic and genomic data, we first carried out demographic modelling and inferred key demographic features in the speciation of this system. We compared clines of phenotypic traits and genomic markers, and identified markers under diversifying selection, some of which are promising candidates to test for adaptation on the mountain. Selection is also estimated to be strong in the hybrid zone. Future analyses will allow us to further investigate the selective pressures keeping the two species distinct while maintaining a hybrid zone.

Shifting patterns of plant dominance in Earth history determined by interplay between atmospheric change and photosynthetic physiology

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The photosynthetic rate (P_n), water use efficiency (WUE) and photosynthetic nitrogen use efficiency (PNUE) are crucial factors in the ecological success of plants and are largely governed by the relative abundances of $[O_2]$ and $[CO_2]$. Interestingly, the fossil record and models of palaeo- $[O_2]$ and $[CO_2]$ suggest that past shifts in plant ecological dominance often coincided with dramatic changes in Earth's atmospheric composition. However, the potential role of fluctuating $[O_2]$ and $[CO_2]$ in shaping patterns of plant macroevolution lacks a mechanistic basis. To assess the impact of atmospheric change on the photosynthetic physiology of angiosperms, gymnosperms and monilophytes, we carried out 5 highly novel 'miniworld' experiments. Early diverging species belonging to the 3 plant groups were grown under different O_2 and CO_2 concentrations and their responses were assessed using physiological methods. Our results showed major group-level differences in the magnitude and, in some cases, the trend of the observed responses. Empirical relationships describing the responses of all major photosynthetic parameters to changing atmospheric composition were constructed for each group and their P_n , WUE and PNUE were modelled throughout the Phanerozoic. The deep-time simulations demonstrated that past fluctuations in $[O_2]$ and $[CO_2]$ had a significant impact on the relative competitiveness of angiosperms, gymnosperms and monilophytes. Accordingly, our results provide a mechanistic understanding for the broad temporal correlation between atmospheric change and shifts in plant evolutionary group-level richness and highlight the role of group-level physiological differences in shaping past and modern geographical distribution patterns.

Multilevel modularity and integration of floral traits: adaptive cordilleras versus adaptive ridges of pollination success

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Although the canalization and modularity (decoupling) of floral traits relative to vegetative traits has been well demonstrated in a diversity of taxa, floral-trait integration is less well understood both theoretically and empirically. Selection for covariation is expected when traits interact functionally ("functional integration"), but the organizational level at which functional integration is expressed in plants is often unclear. We suggest that detailed consideration of the shapes of adaptive landscapes will allow better understanding of the functional basis of trait covariation and the level at which it should be expressed. Here we focus on the distinction between adaptive ridges and adaptive cordilleras (aligned chains of adaptive peaks). We consider two pairs of functionally interacting traits in *Dalechampia* vines (Euphorbiaceae): i) sizes of upper and lower involucral bracts, ii) reward-to-stigma distance and reward-to-anther distance. Because the upper and lower bracts work together to protect flowers and fruits in species with nocturnal bract closure, we hypothesized that this pair of traits is governed by an adaptive ridge. We predicted and found covariation between upper bract-size and lower bract-size within and among plants (within populations), among populations, and among species. Only species lacking nocturnal bract closure lay far off the 1:1 regression line. In contrast, adaptive accuracy theory predicts that the optimal value of the reward-stigma distance should be the population mean value of the reward-anther distance, and vice versa; i.e. we do not expect selection for integration of these two traits within

populations. If this is correct, then each population is governed by a single adaptive peak. Across populations, however, these peaks are expected to form a diagonal cordillera. Hence we predicted, and found, weak within-population correlations, but strong among-population and among-species correlations.

The topology, divergence times, and evolution of land plants

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The evolutionary emergence of land plant body plans transformed the planet. However, our understanding of this formative episode is mired in the uncertainty associated with the phylogenetic relationships among bryophytes (hornworts, liverworts, and mosses) and tracheophytes (vascular plants). Here we attempt to clarify this problem by analysing a sizeable transcriptomic dataset with models that allow for compositional heterogeneity between sites. We find Zygnematophyceae as sister to land plants, but we obtain several distinct relationships between bryophytes and tracheophytes. Concatenated sequence analyses that can explicitly accommodate site-specific compositional heterogeneity give more support for a mosses-liverworts clade Setaphyta as the sister to all other land plants, and weak support for hornworts as the sister to all other land plants. We also find support for Bryophyte monophyly in gene concatenation analyses using models explicitly accommodating lineage-specific compositional heterogeneity and gene tree analyses. Finally, we show support for bryophyte monophyly using maximum-likelihood tests that compare the fit of each gene tree to proposed species trees and Bayesian supertree estimation. Of the 15 distinct rooted relationships for embryophytes, we reject all but three hypotheses, which differ only in the position of hornworts. We also find support for these results through the analysis of morphological data and also estimate the location of fossils given these extant taxa relationships. Our results imply that the ancestral embryophyte was more complex than has been envisaged based on topologies recognising liverworts as the sister lineage to all other embryophytes. This evolutionary picture requires many phenotypic character losses and transformations in the liverwort lineage, diminishes inconsistency between phylogeny and the fossil record, and prompts a re-evaluation of the phylogenetic affinity of early land plant fossils, the majority of which are considered stem tracheophytes.

Phylogenomics, polytomies and the K-Pg boundary: legume evolution in deep time

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The order of magnitude larger DNA sequence datasets used in phylogenomics offer excellent scope to build enhanced phylogenies with robust resolution. However, even with data from 1000s of genes, some parts of the Tree of Life remain as polytomies resilient to resolution. The Neoaves clade of birds and the placental mammals provide good examples. Here I explore and contrast two such polytomies in the early evolution of legumes. Despite the spectacular diversity, ecological prominence and enormous economic importance of legumes, the origin and early evolution of the family remain poorly understood. I present results of phylogenomic studies addressing these questions based on complete chloroplast exomes and thousands of nuclear gene alignments. Our results suggest rapid initial divergence of the six main lineages of legumes (i.e. the six subfamilies) around the Cretaceous-Paleogene (KPB) boundary from a paleopolyploid ancestor. Our study revises previous placements of whole genome duplications (WGDs) in early legume evolution, and demonstrates at least one round of pan-legume WGD. We show that rapid diversification, WGD and the KPB are linked, causing a complex phylogenomic tangle at the base of the legumes characterized by conflicting evolutionary histories of individual genes caused by incomplete lineage sorting and differential loss of paralogs. The implications of this new view of early legume

evolution for the timing of diversification of the six subfamilies and reconstructing trajectories of trait evolution across the first few divergences within the family are discussed. I also characterize a second polytomy subtending a large pantropical clade of 2000+ species within the mimosoid clade of legumes. In this second example, lack of signal in 1300 homologs derived from hybrid capture, rather than conflict among gene trees, is causing this polytomy, suggesting rapid diversification of this clade. Contrasting underlying causes of polytomies can be effectively revealed using a range of phylogenomic methods.

Completing the Plant Tree of Life

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Evolutionary trees are powerful tools for prediction, species discovery, monitoring and conservation. Through comparative analysis of DNA sequence data, the backbone of the plant tree of life is relatively well understood, and many subcomponents have been studied in great detail. However, DNA data are still lacking for numerous plant and fungal genera and the vast majority of species, preventing their accurate placement within an evolutionary framework, in turn hindering downstream science. To better understand how the world's plants and fungi have evolved, we have initiated the Plant and Fungal Trees of Life (PAFTOL) project at the Royal Botanic Gardens, Kew. PAFTOL aims to generate extensive new data for every genus of plant and fungi using high-throughput DNA sequencing technologies. In this talk, we report on progress in the plant component of PAFTOL. We have established a targeted sequence capture approach and have designed a single probe kit that can isolate up to 353 nuclear genes across all angiosperm families. Data obtained with this kit effectively resolve both deep and species-level relationships and is currently being evaluated as a "next generation" barcode. A refined bioinformatic pipeline is also in preparation. We have now generated data for more than 25% of the 14,000 angiosperm genera, and focused studies on families such as orchids, palms, sedges, daisies and legumes are also underway. PAFTOL aspires to be highly open and collaborative, sharing data and tools at the earliest opportunity, and integrating with the broader global genomic agenda. Researchers who share an interest in our project are warmly invited to get in touch.

Targeted sequence capture allows recovery of hundreds of nuclear genes from herbarium specimens across the plant tree of life

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Herbaria are an invaluable collection of millions of plant specimens that span most of the world's known plant species. Unlocking genomic data from herbarium specimens, including type specimens and rare or extinct taxa, has traditionally proven difficult. DNA from herbarium specimens is typically highly degraded which makes it notoriously difficult to retrieve reliable DNA sequence data from such material using PCR-based methods. The development of next-generation sequencing approaches revolutionised the potential of herbarium specimens in genomic research as such processes can be applied to low quantities of severely fragmented DNA to generate genomic-scale DNA sequence data. One such next-generation sequencing technique, called target enrichment or targeted sequence capture, uses short molecular (RNA) probes (baits), to isolate and enrich genomic regions of interest for sequencing. In this study, we sequenced herbarium specimens of varying age and taxonomic affinity, representing the diversity of flowering plants, using a set of targeted sequence capture baits that has recently been developed to recover up to 353 low-copy nuclear genes across angiosperms. We report the percentage recovery of the

target loci in relation to a range of explanatory factors. We found that high-quality, high-coverage nuclear sequence data for hundreds of target genes can successfully be obtained from herbarium material up to 200 years old, from across a broad range of angiosperm orders and families. Namely, ~50 target genes were successfully recovered from a herbarium specimen of a critically endangered species of Boxwood, *Mellissia begonifolia*, collected between 1805 and 1810. The targeted sequence capture approach therefore has huge potential to help retrieve what was thought to be unobtainable genomic data from old herbarium specimens which will hugely contribute to phylogenomic research and help further our understanding of plant evolution and diversity.

Micro-endemism in Madagascar's Highland Flora: have rare species always been rare?

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Bangor University

Madagascar is home to a large number of endemic species, many of which occupy extremely restricted ranges and are threatened by extinction (micro-endemics). The flora of Madagascar is thought to have undergone dramatic changes since humans arrived on the island. Habitat loss, long generation times and the extinction of seed dispersers are all thought to have played a role in population declines. However, despite the large number of rare species found on the island we know relatively little about their demographic history - did they experience population decline in the recent past or were they simply always rare? Here, we examine trends in past population size across a variety of common and rare Madagascan species, spanning seven plant families. We investigated locally important species, which are used as traditional medicines or as sources of local timber, and members of the highly diverse and vulnerable Palm family. Using double digest restriction site associated DNA sequencing we generate genomic data for 10 species and reconstruct the demographic histories for each. Our results provide compelling evidence that human influences on the Madagascan environment are likely to have driven the establishment of the highly restricted endemism observed today.

Angiosperm speciation heats up near the poles

Javier Igea
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The Latitudinal Diversity Gradient (LDG), whereby species richness increases towards the Equator, has long fascinated biologists but its causes remain largely unknown. A major class of explanations proposes that elevated rates of speciation generate the higher diversity in the tropics primarily creating the LDG, and has received empirical support from a wide range of taxa. This increase in speciation is generally attributed to higher environmental energy in the tropics, which in turn can hasten evolution and foster more complex biotic interactions. However, recent studies have found no latitudinal differences or higher rates of speciation in temperate areas, particularly when focusing on recent rates of speciation. In angiosperms, whether variation in speciation rates contributes to the LDG remains relatively unexplored at a species-level. Higher rates of speciation in the tropics have been found with family-level data and in certain clades; and no latitudinal differences were found in a species-level study that assumed that all rate differences in the angiosperm tree of life were due to distribution alone. Using data from over 28,000 angiosperm species and allowing for time heterogeneity in speciation rate estimates, we found that the LDG does not arise from variation in speciation rates because lineages speciated faster outside the tropics. These results show that speciation rates may instead reflect global variation in species richness. Greater ecological opportunity in the temperate zones, stemming from less saturated communities and greater environmental change, may ultimately explain these patterns

Closing Talk

Invading the desert: allotetraploid *Nicotiana* sect. *Suaveolentes* (Solanaceae) radiates in the Australian arid zone in the last million years

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Long-distance dispersal was responsible for allotetraploid *Nicotiana* reaching Australia from South America about six million years ago (mya) based on molecular clock analyses. This group of species, recognized taxonomically as *N.* section *Suaveolentes*, originated from diploids now found only in South America and comprises species found in Africa (one species, *N. africana*), several on Pacific islands and c. 50 in Australia (more than half of which have been newly identified in this project), principally found in the deserts of central Australia. Using standard phylogenetic markers, we established that *N. africana* is sister to the rest, followed by *N. fatuhivensis* (French Polynesia), but in terms of understanding phylogenetic relationships in the core group of Australian species and how they reached the central deserts, we soon reached an impasse. The level of variation was too low to obtain well-supported results, so we used restriction site-associated DNA sequencing (RADseq). We further made use of a reference genome of *N. bethamiana* to extract over 100K high-quality variant positions from accessions representing all but one of the described species to determine relationships and how genetically distinct the new species are from those previously known. Finally, we used unlinked biallelic data (SNPs) with a full coalescent method to sample phylogenetic trees from the posterior distribution of species trees and parameters. Our species tree produced a set of relationships nearly identical to those observed in the standard ML tree based on concatenated SNPs. Finally, we rescaled the species tree, applying a generation time of one year and a general genome-wide mutation rate. This produced an estimate of one million years for their radiation in the Australian desert, which agrees in general with our previous molecular clock estimates and is noteworthy due to its recentness, severity of habitats colonized and number of species involved.

POSTER ABSTRACTS

Polysaccharide composition of folded cell walls in drought-stressed succulent *Aloe* species

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Plants have evolved a multitude of adaptations to survive extreme conditions. Succulent plants have the capacity to tolerate periodically dry environments, due to their ability to retain water in a specialized tissue, termed hydrenchyma. Cell wall polysaccharides are important components of water storage in hydrenchyma cells. However, the role of the cell wall and its polysaccharide composition in relation to drought resistance of succulent plants is unknown. We investigate the drought response of leaf-succulent *Aloe* (Asphodelaceae) species using a combination of histological microscopy, quantification of water content, and Comprehensive Microarray Polymer Profiling. We observed a previously unreported mode of polysaccharide and cell wall structural dynamics triggered by water shortage. Microscopical analysis of the hydrenchyma cell walls revealed highly regular folding patterns indicative of predetermined cell wall mechanics in the remobilization of stored water, and the possible role of homogalacturonan in this process. The *in situ* distribution of mannans in distinct intracellular compartments during drought, for storage, and apparent up-regulation of pectins, imparting flexibility to the cell wall, facilitate elaborate cell wall folding during drought stress. We conclude that cell wall polysaccharide composition plays an important role in water storage and drought response in *Aloe*.

The ecology of hybrid speciation in Eyebrights

Max Brown

University of Edinburgh

Hybrid speciation has been recorded in a number of taxonomically distinct plant groups. Reproductive isolation of the hybrid lineage is paramount. In the generalist hemiparasitic genus of Eyebrights (*Euphrasia*), a potential way in which reproductive isolation could be achieved is through host specialisation. Therefore, we ask: are *Euphrasia* hybrid species reproductively isolated by host preference? We used common garden experiments where we grow *Euphrasia* with host species individually under standardised conditions to explore (1) whether variance in reproductive output of *Euphrasia* explained by host species and (2) whether hybrid species *Euphrasia vigursii* perform better with host species from its own environment. Hybridisation is an underestimated force in the creation of species and we hope this work will shed light on fundamental evolutionary processes.

Cryptic taxa discovery in the Mediterranean Tamus group of *Dioscorea* using a target-capture method

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Dioscorea is the largest genus in Dioscoreaceae with approximately 650 species, however the systematic relationships between and within sections of *Dioscorea* are still not fully resolved. Yams are distributed mainly in pantropical regions, although a few species have adapted to temperate regions. For example, the so-called Tamus and Borderea groups are sister clades that contain species inhabiting the Mediterranean and Macaronesian regions. Borderea contains two well-defined and narrow endemic species, while Tamus currently comprises three species: *D. communis*, distributed throughout the Mediterranean basin; *D. edulis*, a Macaronesian endemic; and *D. orientalis*, restricted to the Eastern Mediterranean. However, there are no robust phylogeographic and systematic studies for the Tamus group although several infraspecific taxa have been described within *D. communis* mainly based on morphological variations in leaf shape. Our main objective is to study the extent of congruence between morphological and genetic variability in the Tamus group. To address this, we selected a set of samples that covers the full taxonomic diversity and distribution ranges for the three species of Tamus. A *Dioscorea*-specific target capture method was used to sequence hundreds of nuclear and plastid genes and infer phylogenetic trees and haplotype networks. The congruence of the phylogeographic patterns with morphology was assessed using quantitative and qualitative macro- and micromorphological traits. The results have reveal cryptic taxa in the Mediterranean group of Tamus, while the inferred phylogeographic patterns and the characterization of the morphological variation have improved our ability to distinguish the different taxa.

The role of niche dynamics and ploidy flexibility in the diversification of the Malagasy endemic yams (*Dioscorea*, Dioscoreaceae)

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Dioscorea L. is an economically important genus due to its starchy tubers or secondary metabolites. It comprises approximately 650 species mainly distributed in seasonal tropical regions of both the Old and New World. Yams have been a focus of interest due to their ecological and morphological variability; however, the drivers involved in their diversification remain poorly studied. For example, little is known about the role of polyploidy in the evolution of *Dioscorea*, for which chromosome counts are available for only 15% of the species. According to this data, 80% of species are polyploid with ploidy levels reaching up to 14x. Previous phylogenetic studies have highlighted the existence of a well-supported Malagasy clade that likely originated ca. 28.3 Ma and which experienced a Late Miocene rapid diversification. It currently includes 42 taxa endemic to Madagascar and the Comoro archipelago and one species that also occurs in continental Africa. Currently, 29 species have IUCN assessments of conservation status, of which 13 are stated to be threatened. Most Malagasy yam species possess edible tubers and some are key seasonal food sources in parts of Madagascar. They exhibit a high level of morphological and ecological diversity and contrasting distribution ranges: some are widespread on the island, while others are narrowly distributed. Regardless of the distribution extent, most of the species are restricted to a single bioclimatic region. To better understand what drivers led to the diversification of the Malagasy yam species, we investigated the role of climatic niche and ploidy variations. First, we built a phylogenomic

tree using hundreds of nuclear and plastid genes for all the known taxa. A target capture-based method allowed us to estimate which taxa were polyploid. Then we characterized their climatic niches using species occurrence data. Finally, we reconstructed ploidy and niche ancestral states across the phylogeny. We discuss the implications of these findings for the conservation of Malagasy yams.

Whole genome duplication and the origin of Equisetaceae

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Coincident with WGD events in angiosperm clades, the WGD event in *Equisetum* is believed to coincide with the Cretaceous-Paleogene (K-Pg) boundary and, in the absence of high species diversity, it has been invoked as facilitating the long-term survival of the genus. However, the characterisation of the *Equisetum* WGD event did not account for historical diversity. We analyse all available transcriptomes and confirm support for a history of WGD in *Equisetum* but show that it is shared among the majority of extant *Equisetum* species. We use improved dating methods to estimate the age of gene duplications in geological time and identify two bursts of duplication, putatively two ancient WGD events. The oldest WGD event likely occurred between the Carboniferous and Devonian, with a younger duplication occurring close to the Triassic-Permian boundary rather than, as previously argued, in association with the K-Pg boundary. We analyse trends of morphological evolution to test hypotheses relating WGD to innovation and find the historical diversity of *Equisetum* provides little evidence for further macroevolutionary consequences following WGD events. The WGD event cannot have conferred 'extinction resistance' to the *Equisetum* lineage through the K-Pg boundary and, indeed, we find evidence of extinction of polyploid *Equisetum* lineages. Our findings highlight the need to explore the role of WGD in angiosperm and non-angiosperm lineages alike.

Comparative genomics of drought-related genes and genetic diversity of *Guazuma* (Malvaceae)

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Guazuma is a representative of the tribe Theobromeae within the family Malvaceae. There are three accepted species: *G. crinita* (rain forest of Perú and Bolivia), *G. ulmifolia* (neotropical dry forest) and *G. longipedicellata* (dry forest, restricted to El Salvador). However, some taxonomic inconsistencies persist and currently, there are no phylogenetic studies that explore the patterns of diversity and structure of the group that include all species from across their distribution range. As an important component of dry forest, *G. ulmifolia* can also be used to investigate local genetic adaptation to dry climates. The aim of this project is to understand species relationships, biogeography and patterns of diversity of *Guazuma*, and to investigate the genomics and evolution of drought-related genes across the Theobromeae tribe, that includes rain forest restricted genera and, in particular, the economically important source of chocolate, *Theobroma cacao*. To accomplish this, a set of Hybrid Capture baits will be used to produce two overlapping sets of data: a) Phylogenetically useful genes to infer species relationships, explore genetic divergence and test species hypothesis along with morphological data, and b) Drought-related genes for comparative genomics.

Variation in self-incompatibility and selfing syndromes in sympatric *Hedyotis* species (Rubiaceae)

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The majority of *Hedyotis* species (Rubiaceae) are morphologically distylous, with distinct pin (exserted stigma and inserted stamens) and thrum (exserted stamens and inserted stigma) morphs, and are suitable models for investigating the functional roles of distyly. Significant levels of discordance among gene trees based on chloroplast and nuclear DNA markers suggest the possibility of interspecific hybridisation. Selection to prevent interspecific mating can cause an increase in self-pollination in sympatric populations. In this study, we investigate the breeding systems of three phylogenetically closely related species: *H. acutangula*, which is widespread in Hong Kong, and two narrow endemics (*H. vachellii* and *H. bodinieri*). All three species are locally sympatric, have overlapping flowering seasons, and reproductive active stages, and share pollinators, thereby enhancing opportunities for interspecific pollen transfer. Controlled pollination experiments were performed on the three taxa in the field, including spontaneous and artificial self-pollination, geitonogamy, inter- and intra-morph xenogamy, and the controls (natural conditions and emasculated). Our results suggest a lack of strict self-incompatibility. The capacity of the thrum morph (Ss) to undergo autogamy in *H. acutangula* ensures dimorphic founder populations. The functional break-down of distyly and relaxed style dimorphism in *H. vachellii* favours autogamy. Anther dehiscence prior to anthesis, pre-anthetic receptive stigmas and high rates of selfing provides rich opportunities for “pre anthesis” cleistogamy in *H. bodinieri*. Our study demonstrates that distyly and self-incompatibility are not tightly associated in these three *Hedyotis* species.

Using genome skimming for polymorphic SSRs discovery and comparative analysis of repeatomes and plastomes in a mixed-ploidy population of *Senecio daronicum* (Asteraceae)

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Senecio daronicum is a relatively common species in the European Alps for which tetraploids (4x) and octoploids (8x) have been reported. Our field survey results evidenced a wider distribution of the 8x cytotype, while the 4x rarely forms established populations. Among all the areas prospected in the westernmost French Alps, we have only found a population in the Alps of Haute Provence with both 8x and 4x co-existing. Furthermore, we have detected the presence of 6x individuals in this population, which could be either the result of hybridization, resulting from the little overlap in phenology between cytotypes, or through uni-parental production of unreduced gametes. The main goal of this project is to provide insights into the population dynamics of this species, aiming to better understand the evolutionary relationships between the different cytotypes in this population and its genetic diversity. We used genome skimming data (i) to discover and to design primers for polymorphic SSRs among the three cytotypes and (ii) to compare the repeatome and the plastome of one individual of each cytotype. Our results will be analysed to provide further insights into the likely genesis of the 6x cytotype by comparing the composition of the repetitive fraction, the plastid genomes and the microsatellite patterns.

Monitoring and managing genetic diversity in Sitka spruce *Picea sitchensis* (Bong.)

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The Sitka spruce breeding programme in Great Britain (GB) started in 1963 by selecting around 1800 plus trees from the forest tree stands in GB that were believed to originate from Haida Gwaii populations in Canada. The products of this programme are estimated to have formed the basis of 97 % of all Sitka trees planted in Scotland in the 2016/2017 season. From a seemingly infinite large population with high genetic diversity the process of domestication results in a hierarchical stepwise change to an improved population, characterised by smaller effective population size (N_e) and lower genetic diversity. However, maintaining the desired level of genetic diversity is crucial in retaining the resilience and the resistance of forest tree crops to disturbance: pests, pathogens and climatic extremes. It also lowers the financial risks to forest landowners and managers under ever-changing environmental conditions. The genetic diversity of the improved GB Sitka spruce stands remains unknown, and therefore the main aim of this PhD study is to quantify baseline levels and identify the stages at which changes in genetic diversity occur during the GB's Sitka spruce improvement programme by examining several populations in Scotland and Pacific Northwest. To assess the course of loss of genetic variability in Sitka spruce during improvement, the following sampling points have been identified: 1.) natural populations; 2.) selected provenances from the unimproved provenance trial; 3.) seed orchards containing selected genotypes 4.) tree nurseries in Scotland propagating improved families; 5) the Dryfe Valley Forest Complex (DVFC) containing stands at different stages of improvement. Across the sampling sites, more than 1000 individuals will be assessed using microsatellite molecular markers (SSR). The presented poster overviews the concepts, methodology and current progress in this ongoing PhD project. Funding is provided by the Conifer Breeding Co-operative, the Forestry Commission and the Scottish Forestry Trust.

Research on the epigenetic regulation of seed dormancy using *Capsella bursa-pastoris* as a model species

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Seed dormancy has evolved in plants to ensure that seed germination and plant establishment are spread in time. This project aims to increase knowledge of epigenetic processes involved in the entrance and maintenance of seed dormancy in response to various environmental factors, using *Capsella bursa-pastoris* (L.) Medik. as a reference. **Background:** Epigenetics is the study of heritable changes in gene expression that occur without changes in DNA nucleotides sequence. DNA methylation, covalent histone modifications and some aspects of small-interfering RNA pathways are the most common ones. Seed dormancy is the temporary failure of a seed to germinate under conditions that in non-dormant seeds are favourable for germination. The regulation of seed dormancy is poorly understood and different studies using annual species have shown large implications of epigenetic modifications in its control. We have selected *Capsella bursa-pastoris* as a model due to it being an annual, wild species with worldwide distribution. **Results:** Germination tests were carried out using 9 different accessions of *Capsella bursa-pastoris* in which seeds were imbibed in solutions of two compounds: trichostatin A (TSA) and valproic acid. TSA and valproic acid inhibit HDAC activity, thereby inducing hyperacetylation. Based on the results from tests using dormancy conditions we were able to identify a deep dormant and a non-deep dormant accession. In addition, protocols for genomic DNA and RNA extractions from whole seeds of *Capsella bursa-pastoris* in different states of dormancy were optimized. DNA was extracted from primary dormant and secondary dormant seeds from the deep and the non-deep accessions previously selected.

Quantification of global DNA methylation showed differences in relation to the type of dormancy and dormancy state. Finally, RNA was extracted and sequenced from seeds from the deep and non-deep dormant accessions imbibed in valproic acid and water during the induction of secondary dormancy and differentially expressed genes are being analyzed to identify patterns associated with dormancy depth and hyperacetylation.

Improving the pollination of the strawberry, *Fragaria x ananassa*

Hamish Symington

University of Cambridge

Strawberry (*Fragaria x ananassa*), a commercially important fruit crop with worldwide sales in excess of \$3.5bn per year, contributes significant levels of micronutrients to the human diet. The flowers are hermaphrodite and self-compatible but do not readily self-pollinate without physical transfer of pollen to stigma. The long-term goals of this study are to contribute to an understanding of how strawberry flowers attract pollinators, and to provide advice on future breeding strategies to maximise pollinator attraction and yield while providing support to pollinator populations. Fruits which are more even in shape command a higher market price than irregular ones; this evenness is linked to the quality of pollination, as each strawberry requires several hundred separate pollination events. I have conducted pilot studies which show that there is significant variation in a number of pollinator-relevant traits of strawberry flowers, and have also developed a tool to expedite field measurement of floral size. Future work will involve further trait measurement in larger sample sizes and more varieties of strawberry, and investigating bee responses to the extremes of floral variation, to identify traits which are potentially important. I will also be investigating the molecular basis of the lack of pigmentation in strawberry flowers, attempting to introduce genes which restore this pigmentation, and testing bee responses to pigmented flowers.

Evolutionary history of *Descurainia* in the Canary Islands: understanding the role of hybridisation

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Along with geographic isolation and ecological shifts, a growing body of genomic evidence have suggested that hybridisation has played an important role in the evolution and diversification of oceanic island flora. However, hybridisation is challenging to detect due to confounding evolutionary processes, such as incomplete lineage sorting (ILS). Therefore, there is a needs to incorporate methods that differentiate between ILS and gene flow in phylogenetic studies. Here, we used genotyping-by-sequencing (GBS) data collected from all seven *Descurainia* species within the Canary Islands and two continental outgroups to investigate the contribution of hybridisation of the diversification of the group. The species are distributed along an altitudinal gradient (between 100 – 2200 m), occupying different vegetative zones (e.g. lowland scrub, laurel forest, pine forests and high altitude scrub) separated by short geographical distances. We used multiple analytical approaches to understand patterns of diversification and the role that hybridisation has played in the speciation process. Phylogenetic relationships were inferred using maximum likelihood, and gene flow between taxa was examined using three approaches: STRUCTURE, ABBA-BABA (D-statistics), and species networks generated from gene trees using *Phylonet*. All analyses revealed two major clades with an East-West colonisation route occurring in both and only one ecological shift for high-altitude taxa. *Phylonet* analysis suggested different evolutionary hypotheses depending on the number of reticulations specified and identified patterns that were consistent with STRUCTURE and ABBA-BABA tests. The results indicate a possible ancient hybrid event between taxa situation in high altitude pine forests, and with taxa found in high altitude scrub land and those in lowland scrub. Out study highlights the necessity to use phylogenetic network approaches that can simultaneously accommodate

ILS and gene flow when studying groups that are prone to hybridisation; patterns that might otherwise be hidden in species trees.

Chromosome evolution and heterochromatin variation in Australian *Nicotiana* sect. *Suavolentes* (Solanaceae)

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Nicotiana (Solanaceae) is a New World, mostly tropical, genus except for sect. *Suaveolentes*, found in Australia (36 species), Oceania (three species) and Africa (one species). In 1954, Goodspeed suggested that allotetraploid *N. sect. Suaveolentes* had multiple origins from South American diploids, which would easily explain the diversity of chromosome numbers in the section (a nearly complete dysploid series $n = 15-24$). However, recent evidence indicates a single origin. We present a RADseq phylogenetic analysis of nearly all species and use this to provide a framework for a detailed chromosome characterization of the section based on differential staining with the fluorochromes chromomycin A₃ (CMA) and 4',6-diamidino-2-phenylindole (DAPI), which preferentially stain heterochromatic regions CG and AT rich, respectively. Chromosome numbers were recorded for 18 species of *Nicotiana* sect. *Suavolentes*, including $n = 15$ in *N. suaveolens* and *N. yandinga* to $n = 24$ in *N. heterantha*. All species possessed only one type of GC-rich heterochromatin, with predominantly CMA⁺ terminal bands at almost all telomeres, some of them forming satellites in prometaphases, probably corresponding to NORs. CMA⁺ pericentromeric bands were also visualized in some species. These strongly stained CMA-blocks are also visualized in interphase nuclei randomly distributed throughout the nucleus. The phylogenetic positioning of these species shows a clear reduction in chromosome numbers along the clade diversification, probably through independent events of chromosome condensation. These data corroborate the hypothesis, initially proposed by Darlington in 1937, that the reduction in chromosome numbers is related to the fixation of favorable allelic combinations, a short-term strategy that favours short-lived herbs (especially annuals), often associated with self-pollination, exactly the situation we observe in *N. sect. Suaveolentes*.

The struggle for space:

stamens packing strategies in male flowers of *Croton* and related genera

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Euphorbiaceae is an enormous family with great diversity of floral forms. While female flower architecture is remarkably stable throughout the family, male flowers from different groups are extremely divergent. A striking case is tribe Crotonae, a group of six genera with a high diversity in male flowers. However, previous studies on flower morphology and development have focused on only a few species of *Astraea* and *Croton*. To understand ontological and evolutionary processes underlying the diversity in this tribe, flower buds from at least one species from each genus were examined under the light microscope and by scanning electron microscopy. Stamen shapes in bud are highly diverse among Crotonae ranging from typical erect forms (*Acidocroton*, *Brasiliocroton*, *Croton* section *Moacroton*), to sessile (*Sagotia*), twisted filaments (*Sandwithia*), and inflexed filaments (*Astraea* and *Croton*). Moreover, stamen arrangement in bud is also found to be variable. In *Astraea* and *Croton*, the outermost stamens are generally opposite the petals contrary to other genera that have the outermost stamens alternate with petals. Evidence from ontogeny suggests that the outermost antepetalous stamens of *Croton* generally arise centrifugally. However, in *Croton* species with less than 10 stamens, the outermost whorl of antepetalous stamens is

the first to develop. In *Croton* section *Moacroton* which has a low stamen number, the outer stamen whorl alternates with petals suggesting a reduction of the antepetalous stamen whorl. Furthermore, break-down of the whorled arrangement is observed in *C. celtidifolius* with numerous stamens (>50) that develop rapidly. The diversity of stamen forms within Crotonaeae may be an independent innovative strategy of each genus to pack a maximum number of stamens (generally >10) in a limited space. Different stamen arrangements in each genus may arise through developmental modification from an ancestor with two stamen whorls that develop simultaneously.

Genomics of introgression in ecologically divergent Amazonian tree species

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Introgression can generate or homogenize biodiversity, and it is as yet unclear what effect it has on speciation. This is particularly true in Amazonian rainforests, which harbour some of the highest levels of species diversity on Earth. One group of trees characteristic of Amazonia is the genus *Brownea* (Leguminosae), which is made up of ~27 species, many of which hybridize. Using two sympatric *Brownea* lineages which differ in their floral morphology, pollination syndrome and habitat preferences (*B. jaramilloi* and *B. grandiceps*), we investigated the patterns of introgression and selection associated with inter-specific gene flow in order to ascertain whether the divergence between species is maintained in the face of introgression. One hundred and seventy-one accessions of the two *Brownea* lineages were collected from Yasuní National Park, Ecuador and were genotyped using the ddRADSeq approach. Genomic cline analysis was used to estimate the 'direction' (α) and 'propensity' (β) of introgression for 19,130 RADseq loci within the lineages. These analyses suggested that introgression only occurs across a subset of the genome and is asymmetric, with the much more numerous *B. grandiceps* donating a greater number of alleles to *B. jaramilloi* than *vice versa*. *Bgc* also inferred that there were no loci with an extreme propensity for introgression when compared to the genome-wide average, as would be expected if differential selection was maintaining divergence. Despite this, we identified many hundreds of candidate loci under selection, as well as several hundred loci associated with different aspects of topography, soil chemistry and leaf morphology. This suggests that selection driven by environmental factors structures the observed genetic diversity, and possibly allows the much less numerous *B. jaramilloi* to resist genetic swamping through selection against hybrids. These results may help to reveal how closely related species can coexist in sympatry, despite undergoing introgression.

Hybridisation and speciation in the genus *Alpinia* Roxb. (Zingiberaceae)

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Understanding the causes and maintenance of high tropical diversity is one of the major goals of evolutionary biology. My aim is to explain the origins of plant diversity in the tropics focusing on the genus *Alpinia*, a species-rich group in the ginger family (Zingiberaceae). This will be done by investigating crossing barriers and potential for hybridisation by means of experimental crosses, and using NGS methods to resolve intraspecific and interspecific relationships, giving a better insight into the maintenance of species cohesion in *Alpinia*. The preliminary results indicate that these species are capable of hybridising, but the strength of reproductive barriers increases with increasing genetic distance. Fieldwork carried out in India in the Western Ghats and North-East indicate that species in both regions are from the same clades but a comprehensive population genetic analysis is required to elucidate the species boundaries. Using experimental and genetic approaches, this study is aimed at understanding speciation histories to elucidate the basis of tropical diversity.

Phylogeny of Plantaginaceae focused on Neotropical genera

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Researches on the phylogeny of Plantaginaceae has shown that much more changes will be needed in order to make all the components of this group coherent with the concepts of phylogenetic systematics. In this study, we analyzed chloroplast and nuclear DNA sequences, as well morphology data, including many Neotropical genera not contemplated in previous works, and genera from others parts of the world. The results show that many traditionally recognized genera are not monophyletic, such as *Bacopa*, *Angelonia* and a polyphyletic *Stemodia*. At the family level, our results indicate that the tribes Gratiolieae and Angelonieae - both very well represented in Neotropics - have a strong support. Preliminary studies indicate the likely need to recognize these tribes as distinct families (Gratiolaceae and Angeloniaceae, both previously published), contradicting previously published works. The genera recently described *Anamaria* and *Ameroglossum* have an uncertain position. These data reinforce the need to include a large sample of genera in phylogenetic studies in order to have strong and stable results, especially in Lamiales, a group that has a poor understanding of the evolution of characters.

Phylogenetic revision of the family Neuradaceae *Kostelvsky*

A morphological and molecular treatment

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Neuradaceae *Kostelvsky* is a small family of annual to perennial herbs located in semi-arid to arid regions of southern Africa, north Africa, through the Arabian Peninsula to India. It currently contains three genera; *Neurada* B.Juss., *Grielum* L. and *Neuradopsis* Bremek. & Oberm. and 10 species. The family has been given scant attention since its circumscription in 1835 and until recently was considered to be part of Rosales. Molecular work has moved Neuradaceae into Malvales, but its position within this order remains poorly resolved, with studies suggesting it may be sister to the rest of the order. Furthermore, the relationships between the three genera remain unclear, with their disjunct distribution adding ambiguity. The family displays many interesting morphologies including its unique pollen structure, hypothesised to reduce transpiration in arid habitats, characteristic fruit, an indehiscent woody capsule, dispersed either by wind or as a trample bur, and flower iridescence. In this study we use molecular and morphological techniques to produce a phylogenetic analysis of Neuradaceae, improve its resolution within Malvales and develop a field key. Horticultural protocols will be developed for the family which has rarely, if ever, been grown, testing whether the seeds exhibit physical dormancy, and working out a simple and quick method for seed-raising plants.

Is mutational meltdown a threat to the mega-diverse genus *Begonia*?

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Until recently the use of herbarium specimens has been mostly restricted to morphological studies and limited sequencing analysis, mainly due to the high degradation of the genetic material in old plant samples. Recent technical improvements as massively parallel sequencing analysis and target capture amplification are enabling the study of ancient specimens with higher throughput and sequencing resolution for phylogenetic analysis, biogeography, or functional studies. This project focuses on investigating the genetic variations between populations of *Begonia* and their evolution through time using herbarium specimens collected at different time points. The large *Begonia* genus includes many examples of species having small, endemic, and scattered populations. The isolation and low pollen flow between them can promote a high degree of homozygosity and make them vulnerable to a specific type of genetic drift called mutational meltdown, driving eventually the entire population to extinction.

To check the genetic health of isolated *Begonia* populations, we have collected herbarium specimens of *B. socotrana* and *B. samhaensis* from different populations and geographical area collected between 1880 and 1999 in the Socotra archipelago. A multi-locus genomic set of markers has been selected to provide phylogenetic data at population-level, and informations about the gene flow between population, and their level of homozygosity. It will be correlated to the genetic health of these populations, and its evolution over time.

More of the same or something new: comparing plant diversification in novel and expanding habitats

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Understanding the mechanisms of lineage diversification is a fundamental question of evolutionary biology. Changes in topography, particularly mountain uplift, are thought to increase diversification in a region through range fragmentation and the generation of novel niches. Speciation can also be promoted by expansion of existing habitat. The relative roles of novel habitat and expanding preexisting habitat in promoting diversification have not been fully explored, however. Is novel habitat a more powerful driver of species radiation than increased availability of preexisting habitat? The objective of this study is to estimate the dispersal, contraction, and cladogenesis of a New Zealand angiosperm radiation, the genus *Veronica* (Plantaginaceae), in response to new and expanding habitat in the form of marine retreat in the last 24 million years and uplift of the Southern Alps in the last 3-8 million years, respectively. I will improve the resolution and the taxonomic coverage of the existing New Zealand *Veronica* phylogenetic tree by sequencing low copy nuclear markers. I will then model historical biogeographical reconstructions on the improved phylogeny and current distributional patterns to understand how the *Veronica* clade responded to changes in habitat area and availability over geological time. With the species assigned to elevational bands including alpine, subalpine, and lowland regions, paleogeological maps will provide estimations of terrestrial extent of the lowland since the peak inundation of New Zealand, and uplift rates calculated from rock cooling ages in the Southern Alps will allow estimation of the emergence time of elevational bands. With the best-fitting model scenario of dispersal and cladogenesis, we will compare rates of cladogenesis within lowlands over the period of marine retreat and within subalpine and alpine regions tracking mountain uplift. Comparing cladogenesis rates in these contexts can shed light on the global mechanisms of biodiversity generation.

The unexpected evolutionary history of *Heteropogon* and *Themeda* (Andropogoneae): stories from nuclear genes

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The pantropical and ecologically dominant savannah grass genera *Heteropogon* and *Themeda* are closely related and share similar morphology, yet a solid phylogenetic framework is lacking. In this study, nuclear data retrieved from genome skims were analysed using concatenation and coalescence approaches. The phylogenetic trees showed that the *Heteropogon*–*Themeda* group is polyphyletic and contains two major clades. In one, *T. arundinacea* and *T. villosa* are more closely related to *H. contortus* and *H. triticeus*. In the other clade, *H. melanocarpus* and *H. ritchiei* are close to several *Themeda* species. These results suggest that convergent evolution underlies the similarity of *Heteropogon* and *Themeda*, especially in inflorescence structure, challenging assumed synapomorphies in this group. However, nuclear genes may also reflect a complex past evolutionary history including, for example, horizontal gene transfer, incomplete lineage sorting, or hybridization. A comparison with plastome data is in progress to resolve this. At the population level, the widespread *Themeda triandra* illustrated geographic patterns confirming a previous study, whereas such patterns were ambiguous in the equally widespread *Heteropogon contortus*. More variable DNA regions, such as introns, and plastome data will be applied to resolve the phylogeography of *H. contortus*.

Nuclear loci mining from transcriptomes for improved identification of aloes and derived products in trade

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International trade in aloes and derived products is at its peak due to high interest in their horticultural value and alleged medicinal properties. Trade is regulated for these endangered plants but identification using morphology and traditional DNA barcodes is not sufficiently accurate. Furthermore, the genus has recently undergone a number of taxonomic revisions and infrageneric relationships remain largely unresolved. To solve these problems, we designed a hybrid capture study to target more than 300 low-to-single copy nuclear loci for phylogenomic inference and to aid in species-level identification. We sequenced transcriptomes of three *Aloe* L. species, including *A. vera* and *A. arborescens*, two of the most commonly traded aloes. Using Marker Miner 1.2 and the rice genome as a reference we mined hundreds of low-to-single copy nuclear loci from these transcriptomes and selected the best ones based on exon length and sequence divergence. We included the transcriptome of *Aloidendron barberae* as an outgroup to make the hybrid baits set more robust. A set of functional genes involved in succulence-related traits have been identified and included in the baits set to study the evolution of succulence in this group. The hybrid baits set will be applied to a range of more than 200 species sampled across the genus, to resolve infrageneric relationships and to identify a subset of loci suitable for species-level identification. Our results should give stakeholders a stronghold for confident identification of aloes and their derived products in trade, providing honest traders an improved image and protecting biodiversity of aloes across the African continent. Our study furthermore highlights the importance of working in an evolutionary context when designing practical conservation tools.

Genetic Dissection of a Carnivorous Plant

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John Innes Centre

Leaves display amazing diversity and complexity in size and shape. The majority of leaves have the main axis of growth predominantly in two-dimensions. One of the most complex leaf structures found in the plant kingdom are the three-dimensional cup-shaped (epiascidiolate) leaves of certain plants. Epiascidiolate leaves have evolved four times independently: in the families Nepenthaceae, Sarraceniaceae, Cephalotaceae, and Lentibulariaceae (Lloyd, 1942, Ellison and Gotelli, 2008). In all these cases, the epiascidiolate form is associated with carnivory – animals or their faeces are trapped within the cup-shaped vessel. A key question is: are the genetic and mechanistic rules underlying leaf development conserved between two-dimensional and three-dimensional leaves? To elucidate how an epiascidiolate leaf forms I study the carnivorous traps of *Utricularia gibba*. These are highly modified and adapted organs which perform elaborate suction-trapping of aquatic prey. *U. gibba* has one of the smallest genomes known in the plant kingdom (~100Mb), which makes it amenable to the analysis of the forward genetic screen I am currently working on where some mutant lines have an altered final trap morphology. We know that cellular growth dynamics involving spatial variations in rates and orientations of growth are required differentially for correct trap formation, how have these dynamics changes in mutated traps? By using molecular and bioinformatic approaches, I have isolated a gene from one mutant line, the first time that this has been accomplished in a carnivorous plant. I am exploring how this mutation has affected development in spatiotemporal terms by aiming to uncover the phenocritical point in the mutant compared to wild type traps and in turn what the impact of these perturbations are in the formation of complex shapes. References ELLISON, A. M. & GOTELLI, N. J. 2008. Energetics and the evolution of carnivorous plants--Darwin's 'most wonderful plants in the world'. *Journal of Experimental Botany*, 60, 19-42. LLOYD, F. 1942. The carnivorous plants.

DOG1 functional variation is associated with flowering and germination syndromes that determine life-history variation in *Arabidopsis thaliana*

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The seasonal timing of germination greatly determines the environment that an annual plant experiences. Germination along with flowering and senescence, combine to generate diverse life-history strategies. A seed can germinate once dormancy is released, through after-ripening or short exposure to chilling, and prolonged chilling can induce dormancy, and these mechanisms control the timing of germination. Our study characterizes natural variation in germination responses to cold and its association with other life history traits, its genetic basis, and its association with climate to understand the evolution of life-history variation in the annual plant *Arabidopsis thaliana*. We used nearly 500 fully-sequenced accessions from a wide climate range. Plants were grown under natural conditions, including full vernalization, and seeds were harvested at maturity. We tested germination on fresh seeds and dark stratified seeds exposed to a series of chilling treatments of varying lengths. We found a continuum of germination strategies varying in two axes: low-to-high germination and responsive-to-cold that combine to generate different germination niches. Both germination axes and life-history syndromes are associated with DOG1 functional variants. Individuals carrying a non-synonymous variant in the self-binding domain of DOG1 were later-flowering and showed cold induced secondary dormancy, while early-flowering individuals carried an alternate allele and had high germination to chilling. Environmental conditions influence correlated selection on multiple loci underlying these syndromes to give rise to spring annuals, winter

annuals, and rapid cyclers. Climate cycling during the Pleistocene likely promoted the diversification of DOG1 haplotypes. Thus, the germination niche of *Arabidopsis thaliana* resulted from the interaction between expansions and contractions into glacial refugia, followed by local adaptation to temperature gradients which structure DOG1 allele turnover on the landscape today.

The evolution and development of petal spots in a south African daisy species

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The South African daisy species *Gorteria diffusa* exhibits extreme intraspecific variation in floral phenotype and is composed of over 14 floral morphotypes. The variable positioning and complexity of petal spots between morphotypes is a key element in determining pollinator behavioural responses. This research aims to investigate the genes underlying petal spot development in *G. diffusa* by providing a more comprehensive understanding of *GdMYB8*, a gene thought to be involved in petal spot anthocyanin regulation. Three paralogous genes have been isolated: *GdMYB8a*, *GdMYB8b*, and *GdMYB8c*. Expression analyses indicate that all of these genes are upregulated within spotted petal tissue compared with non-spotted tissue, and transgenic approaches suggest that each paralog functions in anthocyanin production. To contextualise *GdMYB8* genes within the spot regulatory pathway potential downstream targets encoding anthocyanin pathway enzymes, *DFR* and *ANS*, are being investigated. *DFR* and *ANS* are highly expressed in spotted petal tissue and we are currently isolating the promoter regions of these genes as a first step in identifying whether *GdMYB8* is an upstream regulator. *GdMYB8* gene function and expression patterns will be compared between a subset of morphotypes to provide insight into the role of these genes in intraspecific variation. Ultimately, this will enhance understanding of molecular evolution and diversification within *G. diffusa*.

C4 photosynthesis evolved via a burst of changes followed by sustained adaptation in the Andropogoneae grasses

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The Andropogoneae grasses includes some of the world's most important crop plants, such as maize, sugarcane and sorghum, and numerous dominant species of tropical grasslands. Its ~ 1,200 species all use C4 photosynthesis, which sustains their fast growth and high productivity in tropical conditions. Inferring the changes linked to this key physiological adaptation in Andropogoneae has been hampered by a lack of closely-related C3 lineages for comparative analysis. Using nuclear genome-wide data to screen the diversity stored in herbarium collections, we identified rare C3 species that are sister to Andropogoneae. Phylogenomics revisit the timing of C4 origin in this group, and analysis of leaf anatomy and protein sequence evolution show that the initial transition to a C4 metabolism involved a burst of changes that was followed by sustained adaptation along the diversification of the group. Our study shows that a key transition can lead to a plethora of phenotypes following sustained adaptation of the ancestral state.

Correlated evolution of seed and fruit traits in *Artabotrys* (Annonaceae) and the potential role of frugivore-mediated selection

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The existence of dispersal syndromes remains contentious: only a subset of studies have found evidence for sets of fruit traits that are associated with distinct frugivore guilds. The relationship between seed traits and dispersal agent is furthermore often neglected. *Artabotrys* (Annonaceae), a palaeotropical genus of lianas with substantial variation in fruit and seed morphology, is an excellent study group for evaluating correlated evolution of seed traits in association with climatic variables and dispersal-related traits. Seed and fruit functional traits were evaluated for 43 *Artabotrys* species, with locality data gathered from herbarium records and GBIF. The values of WorldClim bioclimatic variables were in turn extracted for each locality. Bayesian phylogenetic reconstruction and divergence time estimation were based on ca. 15.7 kb of chloroplast and nuclear DNA sequence data. The functional trait data were fitted to various Brownian motion and Ornstein-Uhlenbeck models, in order to assess whether testa thickness and seed volume evolved towards distinct optima in lineages with different combinations of dispersal-related traits and/or lineages with different precipitation regimes. The modelling results unequivocally rejected non-adaptive explanations for both seed traits and suggest a potential role of frugivore-mediated selection. Lineages with slippery testa and thin pericarp (SP) have evolved towards smaller seeds and a thinner testa, whereas lineages with other combinations of pericarp thickness and testa texture have evolved towards larger seeds and a thicker testa. The lower seed physical defence in SP lineages may be because a slippery testa facilitates spitting and/or swallowing of intact seeds by primates while birds (which swallow fruits whole) generally prefer fruits with thin pericarp. The two distinct trait optima may therefore correspond to two seed dispersal regimes in *Artabotrys*: (1) birds and primates with seed-swallowing and seed-spitting behaviours that disperse SP lineages; and (2) primates with more destructive oral processing habits that disperse other lineages.

Slow Y-degeneration and early rise of dosage compensation on *Silene* sex chromosomes

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Y degeneration, where genes on the Y chromosome become non-functional over time, may be much slower in plants due to strong purifying selection against deleterious mutations in the haploid gametophyte. Testing for differences in Y degeneration between the kingdoms has been hindered by the absence of accurate age estimates for plant sex chromosomes. We used genome resequencing in parents and progeny to estimate the spontaneous mutation rate and the age of the sex chromosomes in white campion (*Silene latifolia*), which yielded a rate of 7.31^{E-09} (95%CI: 5.20^{E-09} - 8.00^{E-09}) mutations per site per generation. Given this mutation rate, the old and young strata of *S. latifolia* sex chromosomes are 11.00 and 6.32 million years old. The analysis of Y-degeneration revealed that at least 47% of *S. latifolia* Y-linked genes are already dysfunctional and the rate of Y degeneration in *S. latifolia* is nearly two-fold slower than in animals. Y-degeneration creates imbalance of gene product between the sexes, which is compensated by dosage compensation (DC) system. Previous studies reported the presence of a partial DC in *S. latifolia*, but it is not known whether that DC has to evolve gene-by-gene or some form of chromosome-wide dosage compensation is already present in this species. To shed light on this question we used artificially created Y-deletion mutants to manipulate gene dose and analyse gene expression in *S. latifolia*. We demonstrate that deletions of Y-linked genes result in immediate up-regulation of X-linked gametologs,

indicating the presence of chromosome-wide dosage compensation system that arose surprisingly early in sex chromosome evolution in *S. latifolia*.

Anthropogenic changes drive repeated evolution of metal tolerant ecotypes in *Silene uniflora*

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Adaptation in response to novel environmental opportunities is a key driver of plant trait and species diversity. Whilst rapid anthropogenic changes provide a variety of novel habitats for plants to exploit, the genetic features associated with rapid adaptation are unclear. Human mining activities in the past 250 years have produced novel environments contaminated with high levels of heavy metals, which have been colonised by a number of species including the usually coastal *Silene uniflora*. Ecotypes of *S. uniflora* growing on mine sites display high levels of metal tolerance compared to their coastal counterparts, but the genetic basis and number of origins of this trait remain uncertain. Using common garden experiments and ddRAD sequencing, we investigate the extent of zinc and copper tolerance across geographically disparate pairs of coastal and mine populations, and identify at least three independent origins of heavy-metal tolerance in the UK and Ireland. F_{st} outlier analysis identifies a number of shared genomic regions associated with the evolution of metal tolerance across these independent origins, identifying a number of plausible candidate genes previously implicated in metal tolerance. These results show human-induced environmental changes have the potential to cause rapid and repeated adaptations in plant species.

The evolution of fog-harvesting adaptations in the genus *Eriospermum*

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Eriospermum (Asparagaceae) is a plant genus native to sub-Saharan Africa with more than two third of the estimated 125 species occurring uniquely in semi-arid deserts in Southern Africa. *Eriospermum* demonstrate a remarkable range of unusual leaf morphologies, including reduction of the leaf lamina and the production of remarkable compound leaf enations on the adaxial surface of the leaf. These enations have been suggested to be associated with the harvesting of non-precipitating moisture in the form of fog, mist, and dew although this hypothesis has yet to be rigorously tested. In this study, we applied a BGISEQ-500 next generation sequencing approach to generate a species level phylogeny using complete plastid genomes and nearly complete nuclear ribosomal DNA. Approximately 50 species were chosen to represent the main genus of *Eriospermum* with the aim of investigating the relationships within the genus and understanding the evolution of the putative fog-harvesting leaf morphologies. Contrary to earlier classification, our analyses indicate that all species exhibiting fog-harvesting enations fall within a single monophyletic lineage - *Eriospermum* subg. *Eriospermum*. However, the occurrence of enations appears to be homoplasious within subg. *Eriospermum* indicating either recurrent origins of enations, or their repeated loss. Analysis of leaf morphology reveals a phylogenetic trend towards reduction in leaf surface area, but an increase in the length of surface edges, consistent with the physics of moisture interception in fog-harvesting structures. Finally, the appearance of enations seems to be associated with faster species diversification rates within subg. *Eriospermum* in the context of semi-arid fog deserts. Our phylogenetic analyses provide a solid evolutionary framework for physiological and morphological experiments on enations in *Eriospermum*, to further elucidate the mechanisms by which non-precipitating moisture is captured and assimilated.