Abstract talks Monday first session

Hybridisation, introgression and the potential threat of genetic assimilation in the Kidney saxifrage, *Saxifraga hirsuta*

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Hybridisation is considered one of the key driving forces in evolution. It is particularly common within the plant kingdom, and is generally considered a positive process which may result in the creation of new species. However, it has been noted that excessive unidirectional introgression of a more abundant species' alleles into the gene pool of a sympatric, rarer congener may lead to a loss of genetic integrity for the latter, and continued influx may ultimately lead to the genetic assimilation of the rarer species. *Saxifraga spathularis* and *S. hirsuta* are both members of the Lusitanian flora, whose disjunct distribution between Ireland and northern Spain has been of great intrigue to botanists. In Ireland *S. spathularis* is significantly more abundant than its rarer congener. Putative hybrids between these two species (*S. x polita*) have been identified in the Irish reaches of their ranges, where both species co-occur in Counties Cork and Kerry, but hybrids have also been found in Co. Galway, where only one of its parental species, namely *S. spathularis*, occurs. The main questions that will be addressed in this study are: What is the genetic composition of *S. x polita* hybrid populations? Is there evidence of cryptic introgression of *S. spathularis* alleles into *S. hirsuta*? If so, to what level is the introgression occurring and is it placing the gene pool the rare *S. hirsuta* under threat of genetic assimilation?

Genotypic and ecotypic variants of Ammonia beccarii (Linne) around the coastline of Great Britain

Saha Saad University of Nottingham

Genomics of invasion: Resequencing of introduced populations of monkeyflowers (*Mimulus guttatus*) reveals patterns of variation and selection across the genome

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The access to relatively low-cost sequencing techniques has opened a unique opportunity to investigate the consequences of species introductions on the structure of entire genomes. Here we use next-generation sequencing to compare the genome structure of native and introduced populations of the yellow monkeyflower (*Mimulus guttatus*, Phrymaceae), a herbaceous plant from Western North America that colonised the British Isles 200 years ago. Our specific aims are: (1) to determine the level of genome-wide diversity present in the United Kingdom. (2) to investigate the genetic relationships of introduced and native populations, and (3) to search for evidence of hard selective sweeps shaping genome structure in both native and introduced regions. We used complete genome re-sequencing to genotype individuals in 10 introduced populations of *M. guttatus* in Great Britain and Northern Ireland, and 12 native populations in North America. Genome sequences were aligned to a reference *M. guttatus* genome to produce genotypes at over 11 million variable sites. Overall, neutral genetic diversity was considerable in the United Kingdom (UK) (π syn =

0.031), but lower than diversity across North American populations, suggesting that a subset of the species-wide genetic diversity is represented in the introduced range. Genetic distance analyses at a random subset of 1.4 million SNPs indicate that all UK populations share a common origin, and are most closely related to native coastal, perennial populations of *M. guttatus*. Our analyses also revealed a significant localized reduction in nucleotide diversity, consistent with hard selective sweeps in some genomic regions. We speculate that UK populations have likely been derived from the same geographic region around the North Pacific, perhaps via multiple introductions from populations within this region, which has allowed the maintenance of relatively high levels of genetic diversity in the introduced range.

The harlequin ladybird invasion

Cathleen Thomas

School of Biology, Newcastle University

Dispersal is a key ecological trait, shaping spatial and temporal distributions of populations. Identifying barriers to dispersal is vital to understand range expansion, which is particularly important for invasive species. Invasive species are one of the greatest threats to biodiversity, yet factors underlying invasion success remain poorly understood, particularly factors such as population structuring and dispersal. Here, I investigated populations of the highly invasive ladybird *Harmonia axyridis* in its native range, to determine whether dispersal is limited by geographical barriers such as distance or physical features such as mountain ranges or bodies of water. Other studies have shown *H. axyridis* has a high rate of spread in the invasive range, but little is known about dispersal in the native range. A high dispersal capability could explain how this species dispersed to four novel continents, becoming the most invasive ladybird species on earth.

Impact of ploidy level and pollen donor on seed production in *Sorbus subcuneata*, an apomictic triploid

Tracey Hamston¹, James Cresswell¹, Natasha DeVere², Jamie Stevens¹ ¹Biosciences, University of Exeter;² National Botanic Garden of Wales & Aberystwyth University

The genus *Sorbus* is represented by more than 40 named species in the UK alone. This diversity has been brought about by repeated hybridisation events producing an array of taxa of varying ploidy levels. The majority are tetraploid (2n=4x=64) but a nearly a third of those with known ploidy are triploid. Despite potential meiotic difficulties during gamete formation, triploids have been identified as having an important role in the production of novel taxa by providing a pathway to tetraploid formation; the so-called triploid bridge. Many of the polyploid taxa are of conservation concern, some existing as only a handful of trees on single sites.

S. subcuneata is a triploid that exists as a population of circa 300 trees in N Devon. Reproduction rates are low, relative to sympatric tetraploid species, with few seedlings found in the wild. This study aims to investigate the effect of ploidy level and pollen donor on seed output of this triploid taxon. The interactions of sympatric *Sorbus* species have implications for evolutionary potential. Using microsatellite markers to identify pollen donors for any seed produced, we conducted hand pollination experiments using cultivated trees of wild origin as well as collecting data on seed produced in the wild population. The resulting dataset provided evidence for a close genetic relationship between the sympatric tetraploid and triploid and indicated a reliance on interspecific pollen flow for seed production. Our findings reiterate the need for a better understanding of

interspecific interactions to inform conservation policies that are currently targeted at individual species.

Second session

The meek shall inherit the earth: positive selection of deleterious alleles

Pim van Hooft

Wageningen University

Although generally rare, deleterious alleles can become common through reductions in selective constraints, genetic drift and linkage to a gene undergoing positive selection (hitchhiking). Here we present a potential new mechanism through which high population frequencies of deleterious alleles can be attained: positive selection of deleterious alleles induced by interactions with sex-ratio genes, which distort primary sex ratio, and suppressors of these genes. In African buffalo (Syncerus caffer) in Kruger National Park (South Africa) one in four males carries a Y-chromosomal sex-ratio suppressor whose activity appears to be associated with low body condition. Males with a sex-ratio suppressor, presumably activated by low body condition, seem to have a relative reproductive advantage compared to males without one, probably because the latter suffer from reduced fertility that generally accompanies sex-ratio distortion. We hypothesize that this body-condition associated reproductive advantage increases the fitness of deleterious alleles that negatively affect male body condition, causing genome-wide positive selection of these alleles. We uncovered the mechanism outlined above by finding correlations between microsatellite heterozygosity and body condition of individuals (heterozygosity-fitness correlations). Most microsatellites turned out to be linked to one of two gene types: one with elevated frequencies of deleterious alleles that have a negative effect on body condition, irrespective of sex, the other with elevated frequencies of sexually antagonistic alleles that are negative for male body condition but positive for female body condition. Positive selection and a direct association with a Y-chromosomal sex-ratio suppressor is indicated by, respectively, allele clines and relatively high numbers of homozygous deleterious alleles among sexratio suppressor carriers. The results from this study may have important implications for our understanding not only of the evolutionary and ecological dynamics of sex-ratio distorters and suppressors but also of the impact of deleterious and sexually-antagonistic alleles on population viability (genetic load).

Gynodioecy and molecular evolution in the flowering plant Plantago lanceolata

Nick Levsen

School of Biology, Newcastle University

Gynodioecy is a stable sex phenotype polymorphism that is recognized by the maintenance of both hermaphroditic and female (i.e., male sterile) individuals in a population. The polymorphism arises due to conflict between the nuclear and mitochondrial genomes and is maintained by density-dependent selection. Each genome accumulates mutations, which increase its own reproductive fitness at the relative expense of the other. This 'arms race' is expected to drive elevated substitution rates within the mitochondrial genome, a hypothesis which has been substantiated by early data in gynodioecious species in *Plantago* and *Silene*. We describe early results from an extensive test of the relationship between mitochondrial genome diversity and gynodioecy. Mitochondrial sequences (23 genes) from 19 *P. lanceolata* individuals and 1-5 outgroup individuals were analyzed to elucidate patterns of nucleotide variation within mt genomes and among individuals.

Revealing the genetic mating system of the reintroduced Asiatic wild ass using stochastic modeling of shifts in allele frequencies

Sharon Renan, Gili Greenbaum, Naama Shahar, Alan R. Templeton, Amos Bouskila^a Shirli Bar-David Department of Life Sciences, Ben-Gurion University of the Negev, Israel.

Small populations are prone to loss of genetic variation due to genetic drift and hence to a decrease in their evolutionary potential. Therefore studying the mating system of small populations and its potential effect on genetic drift and genetic diversity is of high importance for their viability assessment. The endangered Asiatic wild ass (Equus hemionus), as all Equids, show a behaviorally polygynous mating system. However, the level of polygyny was never measured genetically in wild Equids. The traditional method for studying genetic mating systems is paternity analysis, yet, since small populations are often rare and elusive, the genetic data required for it is frequently unavailable. Combining non-invasive genetic data with a stochastic model of allele frequencies, we developed an alternative approach to paternity analysis for studying the genetic mating system of the reintroduced Asiatic wild ass in the Negev desert, Israel. We compared the strength of genetic drift that occurred from reintroduction onset to that simulated under different proportions of mating males, extending a recently developed approach based on shifts of allele frequencies. We revealed a strong polygynous mating system whereas only 10-30% of all males participate in the mating process each generation. The strong polygynous mating system and its potential effect on the population's genetic diversity could have significant consequences for the long term persistence of the reintroduced population in the Negev. The stochastic model approach and the use of allele frequency-shifts can be further used to gain insights into processes which affect drift in systems where genetic data is limited.

Genome dynamics and population structure of *Spraguea lophii*, an intracellular eukaryotic parasite

Tom A. Williams¹, Sirintra Nakjang, Scott E. Campbell, Mark A. Freeman, Matthías Eydal, Robert P. Hirt, T. Martin Embley, Bryony A. P. Williams ¹Institute for Cell and Molecular Biosciences, Newcastle University

The Microsporidia are a diverse group of parasitic fungi that infect other eukaryotes, including insects, fish, and immunocompromised humans. Their genomes have undergone extreme reduction in both size and coding capacity, with the microsporidian *Encephalitozoon intestinalis* possessing the smallest known eukaryotic genome at 2.25 Mb. Nonetheless, there is at least ten-fold variation in genome size within the group and significant variation in genome structure, with the larger genomes containing longer intergenic spacers and more transposable elements, but not necessarily more protein-coding genes. Although the number of microsporidian genome sequences has been increasing in recent years, the evolutionary processes underlying this variation remain unclear. To gain insight into the evolutionary dynamics of these tiny eukaryotic genomes, we have sequenced geographically isolated strains of Spraguea lophii, a microsporidian parasite of monkfish (Lophius spp.) that is globally distributed in the world's oceans. Our analyses revealed strong population structure, perhaps imposed by the endemic monkfish host. They also revealed an unexpected level of variation in genome size and content, even over the relatively short evolutionary distances separating contemporary Spraguea populations. Spraguea isolates from New Brunswick, Canada, possessed significantly larger genomes than their relatives on the other side of the Atlantic (8Mb vs. 6Mb for English coastal isolates). Genome expansion in Canadian Spraguea is characterized not by

the proliferation of transposable elements, but by duplications of protein-coding genes, many of which have subsequently become pseudogenized. This flurry of genomic activity has affected not only families of putative effectors, such as leucine-rich repeat proteins, but also core components of the DNA replication and repair machinery. The presence or absence of these gene family expansions is polymorphic in contemporary *Spraguea* populations and correlates with differences in genome content and size, making these organisms an ideal system for investigating the molecular evolution of genome architecture in eukaryotes.

Tuesday

1st session

Selection on evolutionary and ecological timescales in closely related pine species

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The polygenic character of most quantitative traits in forest trees has frustrated progress in the search for molecular signatures of selection in studies of individual species. However, among recently diverged species it is possible that common genes are responsible for within and among-species divergence. Therefore, phylogenetically ordered analysis of genomic variation could provide new insights into the operation of selection at a molecular level. We studied patterns of nucleotide polymorphism and divergence in a set of 79 nuclear genes (1680 SNPs) and thirty populations (288 individuals) of the four closely-related pine species *Pinus mugo*, *P. sylvestris*, *P. uliginosa* and *P. uncinata* across their distribution range in Europe. Similar levels of polymorphism and an excess of low frequency variants were observed across species and in most individual populations. In each species, most of the variation (92-96%) was found within populations, with little evidence of population structure. However, clear divergence was observed among species, apart from *P. uliginosa* and *P. uncinata*, for which evidence of admixture was found. The majority of loci showing significant within-species differentiation also showed significant between-species divergence suggesting selection has operated at these loci on both evolutionary and ecological timescales.

Impact of recurrent gene duplication on adaptation of plant genomes

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Recurrent gene duplication and retention played an important role in angiosperm genome evolution. It has been hypothesized that these processes contribute significantly to plant adaptation but so far this hypothesis has not been tested at the genome scale. We studied available sequenced angiosperm genomes to assess the frequency of positive selection footprints in lineage specific expanded (LSE) gene families compared to single-copy genes using a dN/dS-based test in a phylogenetic framework. We found 5.38% of alignments in LSE genes with codons under positive selection. In contrast, we found no evidence for codons under positive selection in the single-copy reference set. An analysis at the branch level shows that purifying selection acted more strongly on single-copy genes than on LSE gene clusters. Moreover we detect significantly more branches indicating evolution under positive selection and/or relaxed constraint in LSE genes than in singlecopy genes. In this – to our knowledge –first genome-scale study we provide strong empirical support for the hypothesis that LSE genes fuel adaptation in angiosperms. Our conservative approach for detecting selection footprints as well as our results can be of interest for further studies on (plant) gene family evolution.

Invited speaker:

Gene flow, natural selection and historical contingency shape local adaptation across a latitudinal gradient in European aspen (*Populus tremula* L. Salicaceae)

Pär K. Ingvarsson

Umeå Plant Science Centre, Department of Ecology and Environmental Science, Umeå University, Sweden

In Scandinavia, admixture of post-glacial lineages of European aspen (*Populus tremul*a) has shaped the nature of clinal variation and local adaptation in a number of key phenology traits of great adaptive significance for temperate trees. Furthermore, population differentiation and adaptation is not only a result of historical processes, but is also predicted to shape future evolution, since population differences in genetic architecture will influence future responses to selection. Using common garden data on phenology and growth in *P. tremula* we highlight how population differentiation can result in differences in genetic architecture leading to origin- future responses to future selection. The data highlights a hitherto largely ignored link between past range shifts because of climatic oscillations, levels of standing variation currently available for selection and the potential for future adaptation in a terrestrial foundation species.

Second session

Polar bears exhibit genome-wide signatures of adaptation to life in the Arctic environment

Andreanna J. Welch, Oscar C. Bedoya-Reina, Lorenzo Carretero-Paulet, Webb Miller, Karyn D. Rode, and Charlotte Lindqvist Durham University

Polar bears (Ursus maritimus) face extremely cold temperatures and periods of fasting, which might result in more severe energetic challenges than those experienced by their sister species, the brown bear (U. arctos). We have examined the mitochondrial and nuclear genomes of polar and brown bears to investigate whether polar bears demonstrate lineage-specific signals of molecular adaptation in genes associated with cellular respiration/energy production. We observed increased evolutionary rates in the mito- chondrial cytochrome c oxidase I gene in polar but not brown bears. An amino acid substitution occurred near the interaction site with a nuclear-encoded subunit of the cytochrome c oxidase complex and was predicted to lead to a functional change, although the significance of this remains unclear. The nuclear genomes of brown and polar bears demonstrate different adaptations related to cellular respiration. Analyses of the genomes of brown bears exhibited substitutions that may alter the function of proteins that regulate glucose uptake, which could be beneficial when feeding on carbohydrate-dominated diets during hyperphagia, followed by fasting during hibernation. In polar bears, genes demonstrating signatures of functional divergence and those potentially under positive selection were enriched in functions related to production of nitric oxide (NO), which can regulate energy production in several different ways. This suggests that polar bears may be able to fine-tune intracellular levels of NO as an adaptive response to control trade-offs between energy production in the form of adenosine triphosphate versus generation of heat (thermogenesis).

Ecological consequences of evolutionary responses to climate change in a species-rich grassland

Raj Whitlock¹, Grime, J. P.²

¹Institute of Integrative Biology, University of Liverpool; ²Department of Animal and Plant Sciences, University of Sheffield

Buxton Climate Change Impacts Laboratory (BCCIL) maintains a long-running experiment in which a semi-natural grassland has been exposed to 20 years of simulated climate change. Ongoing climatic manipulations at the site are applied to 3 x 3 metre grassland plots containing intact species-rich grassland vegetation, and include summer drought, watering and winter warming treatments. Populations of several species coexisting within the grassland have responded to these altered climates with evolutionary shifts in phenotype. These changes in phenotype are heritable in the broad sense, and may contribute to the remarkable resistance of this grassland community to simulated environmental change. Here, we use a microcosm experiment to determine whether climatically-induced evolutionary responses that have occurred at BCCIL are able to modify neighbourhood-scale interspecific interactions.

Genetic variation in life history strategy and the responses of plant populations and communities to climate change

Sarah Trinder¹, Mike Fay², James Hartwell¹, Ilik Saccheri¹, Raj Whitlock¹ ¹University of Liverpool, ²Royal Botanic Gardens Kew

Adaptive genetic variation within populations offers the possibility for evolutionary responses to enable species' persistence through climate change. In grassland systems, climatic selection has been shown to result in variation in functional traits associated with different life-history strategies, indicating local adaptation through either competitive or drought avoidance strategies. However, we do not know whether climatic selection will result in adaptive phenotypes that are passed on to offspring, or how such adaptive responses in one species may enhance or inhibit the adaptive ability of other co-existing species.

We used long term experiments at the Buxton Climate Change Impacts Laboratory (BCCIL) to ask whether simulated climate change has resulted in heritable changes in life history strategy in the perennial grass *Festuca ovina*. At BCCIL, calcareous species-rich grassland has been subjected to experimental climate change in the form of annual two-month summer drought treatments for 20 years. We chose to focus on *F. ovina* because in this community it is the species that both occurs most frequently and has the greatest cover; its response to climate change has the potential to influence other co-existing species. Sexual offspring of *F. ovina* plants collected from BCCIL were grown in a common environment along with their parents, and a range of traits measured. We present the results of these phenotypic measurements, and discuss the extent to which phenotypes of offspring individuals vary predictably as a function of the maternal plants' climatic and local edaphic environment.

Potential genetic differentiation in a rare British plant (downy fruited sedge, Carex filiformis L.)

Jordan Bilsborrow, Mary Dean, Paul Ashton Edge Hill University

Population diversification is a product of natural selection, absence of gene flow and genetic drift. As such it is a precursor to gradual speciation. Thus rare species represented by isolated populations of various sizes are excellent vehicles to investigate these processes. *Carex filiformis* (Downy-fruited sedge) is such a rare species in the UK, comprising only a handful of populations of various size within the Thames valley. Morphometric approaches were used to determine the level of variation and extent of population differentiation at 10 locations. Population size at each site was also estimated. The results were compared both with a similar study undertaken over fifteen years ago and with a widespread congeneric species (*C. flacca*; Glaucous sedge). The widespread species forming a suitable comparison, given that gene flow and drift are both likely to be absent in populations of this plant.

Local adaptation in Festuca ovina: plant communities, allozymes and transgenes

*Honor C. Prentice*¹, Yuan Li¹, Mikael Lönn², Anders Tunlid¹, Lena Ghatnekar¹ ¹Department of Biology, Lund University;² School of Natural Sciences, Technology and Environmental Studies, Södertörn University, Sweden

The extensive "alvar" grasslands on the Baltic island of Öland (Sweden) are a perfect, naturally replicated, playground for ecological geneticists. The Great Alvar covers an area of 26 000 ha, and sites throughout the area are characterized by a repeating, fine-scale edaphic mosaic that supports different grassland plant communities. Earlier allozyme studies on the Great Alvar have revealed significant allozyme-microhabitat associations in a range of plant species. Studies of the outbreeding grass Festuca ovina show that the frequencies of cytosolic phosphoglucose isomerase (PGI) allozyme electromorphs (EMs) are related to fine-scale variation in soil pH and moisture, and to plant community composition. Experimental manipulation of the grassland microhabitats changes the frequencies of PGIC electromorphs. In S. Sweden (particularly on Öland), some populations of F. ovina contain individuals with two loci that code for PGIC. Recent genetic studies show that the second PqiC locus represents a fully functional, natural transgene which has been horizontally acquired from the distantly related genus *Poa*. We have developed primer pairs for the two *PgiC* loci (PgiC1 and the transgenic PgiC2(f)) and analysed relationships between the within-individual presence of allozyme EMs and PgiC2(f), and the relationships between EMs, PgiC2(f) and microhabitat variables. Our preliminary results suggest that local ecological adaptation may be contributing to the persistence of the transgene in local populations of *F. ovina*.

Wednesday

First session

Homing in on sea trout migrations: investigating the natal origins of sea trout entering the River Tamar, southwest England

R Andrew King¹, Paul Elsmere², Rob Hillman², Jamie R Stevens¹ ¹College of Life & Environmental Sciences, University of Exeter; ²Environment Agency, Cornwall; ³ Environment Agency, Cornwall

The perceived wisdom is that anadromous fish species such as sea trout and salmon, after spending time feeding at sea, return to their natal river to spawn, though straying is known to occur and is thought to play an important role in colonization and range expansion. However, the extent of straying is difficult to determine, particularly in rivers with established populations of trout and salmon.

At the University of Exeter, we are using genetic methods to study resident brown trout and migratory sea trout to inform on the management of trout stocks in southern Britain. The ultimate aim of this research is to improve our understanding of the marine phase of the sea trout life cycle, affording them the opportunity to be better protected by regional, national and European law. We have established a genetic baseline, comprising samples from >5000 brown trout from 71 southern British and northern European rivers, and screened for variation at 19 microsatellite markers. The utility of the genetic baseline for assigning marine and estuarine caught sea trout to river of origin will be demonstrated using a set of 700 sea trout obtained from an Environment Agency-run fish trap at the tidal limit of the River Tamar, as well as a set of fish caught in the rod-fishery within the Tamar catchment. Results indicate that a significant proportion of the sea trout entering the Tamar are strays, mainly from the two rivers that share an estuary with the Tamar, but that straying fish do not penetrate into the upper catchment.

Lack of genetic structure in ash (*Fraxinus excelsior*) populations under threat from an emergent fungal pathogen: implications for restorative planting

Jim Provan^{1,2,3}, Gemma E. Beatty^{1,2}, James A. Brown², Eamon M. Cassidy², Caroline M. V. Finlay², Lorraine McKendrick², W. Ian Montgomery^{1,2}, Neil Reid^{1,2}, David G. Tosh^{1,2} ¹ School of Biological Sciences ;² School of Biological Sciences; ³ Institute for Global Food Security, Queen's University Belfast

We carried out genetic analysis on populations of European ash (Fraxinus excelsior) throughout Ireland to determine the levels and patterns of genetic diversity in naturally seeded trees in ash woodlands and hedgerows, with the aim of informing conservation and replanting strategies in the face of potential loss of trees as a result of ash dieback. Samples from 33 sites across Northern Ireland and three sites in the Republic of Ireland were genotyped for eight nuclear and ten chloroplast microsatellites. Levels of diversity were high (mean $A_{\rm R}$ = 10.526; mean $H_{\rm O}$ = 0.709; mean $H_{\rm F}$ = 0.765), and were similar to those in Great Britain and continental Europe, whilst levels of population genetic differentiation based on nuclear microsatellites were extremely low (ϕ_{sT} = 0.0131). Levels of inbreeding (mean $F_{IS} = 0.067$) were significantly lower than those reported for populations from Great Britain, possibly as a result of allele-calling problems in earlier studies. Our results suggest that ash woodlands across Ireland could be treated as a single management unit, and thus material from anywhere in Ireland could be used as a source for replanting. Parentage analysis at the individual level carried out within two of the woodlands also indicated potential for seed dispersal over hundreds of metres, which also has implications for recolonization processes post-ash dieback infection, and aids our assessment of the capacity of ash to shift its range in response to global climate change.

Population structure and phylogeography of Tilia cordata and T. platyphyllos across Europe

Prattana Phuekvilai

Newcastle University

In this study we investigate patterns of population genetic structure and gain insight into postglacial recolonization in *Tilia* across Europe. Thirteen microsatellite markers were used to analyse 24 *T. cordata* and 15 *T. platyphyllos* populations. In addition, eight chloroplast regions were analysed with two individuals per country from each species. We identified low genetic diversity in the peripheral populations, which support the rapid expansion of tree species from southern Europe during postglacial periods. Some chloroplast haplotype were shared between the two species. The

haplotype network suggested that these shared haplotypes could be the result of incomplete lineage sorting rather than recent hybridization. Bayesian analysis revealed strong genetic structure in *T. platyphyllos* but weaker in *T. cordata*. This could be caused by the migration and colonization in the northern areas of *T. cordata* occurred before those of *T. platyphyllos*. Microsatellite analysis suggested different possible colonization routes between two *Tilia* species. However, *T. cordata* and *T. platyphyllos* seem to share the three main refugia in southern Europe (Iberia, Italy and Balkans). In addition, *T. cordata* seems to have additional putative refugia in Eastern Europe.

Genetic diversity of Atlantic salmon in the chalk streams of southern England

Charles Ikediashi and Jamie Stevens Biosciences, University of Exeter

Southern England contains 85% of the world's chalk streams, which -due to their underlying geologyprovide a rare and unique habitat for both the plants and animals found there. Atlantic salmon (Salmo salar L.) are well known for their natal homing ability and are intricately linked to the rivers from which they are spawned, despite spending the majority of their adult lives at sea. Atlantic salmon within England's chalks streams have previously been shown to be distinct from all other populations within Europe; however, previous studies included only a limited number of chalk stream populations. This study utilises 16 microsatellite loci and widespread sampling of all major UK chalk stream salmon populations, to characterize the genetic diversity of Atlantic salmon in this atypical habitat. Specifically, the study explores genetic variation in chalk stream salmon populations at three different levels: inter-regional, whereby the degree of genetic separation from neighbouring salmon populations in non-chalk catchments is explored; intra-regional, whereby the level of admixture between populations from each chalk streams is compared; and finally at the intra-catchment level, where population structure within an individual chalk stream is investigated. Using these and other genetic data, this study also explores the phylogeographic origins of chalk stream salmon, which may help to elucidate broader questions pertaining to post-glacial patterns of movement in European salmon.

Are populations of wild roach in rivers contaminated with estrogenic effluents self-sustaining?

Patrick B. Hamilton¹, Elizabeth Nicol², Eliane S. R. De-Bastos¹, Richard J. Williams³, John P. Sumpter ², Susan Jobling², Jamie R. Stevens¹, Charles R. Tyler¹ ¹University of Exeter, Biosciences; ²Institute for the Environment, Brunel University; ³Centre for Ecology and Hydrology, Oxfordshire

There is substantial evidence for widespread feminisation of male fish living in rivers contaminated with wastewater treatment works (WWTW) effluents. This has been attributed to exposure to natural and synthetic steroid estrogens which are biologically active at very low (ng/L) exposure concentrations, and include 17 alpha-ethinylestradiol (EE₂), a component of the female contraceptive pill. Studies suggest that long-term exposure of fish to estrogens could threaten the sustainability of fish populations. Some of the best evidence for effluent-induced feminisation comes from roach (*Rutilus rutilus*) living in English rivers, yet the full implications at a population-level are not well understood. We investigated the impact of exposure to estrogenic effluents on roach populations by examining the population structure and effective population sizes of roach in river stretches in Southern England. A total of 1769 roach from 32 sample sites were genotyped using a minimum of 14 DNA microsatellites. Analysis of population structure revealed distinct subpopulations inhabiting some river stretches demarked by physical barriers, such as weirs and

locks. We found no evidence for a relationship between predicted estrogenic exposure and effective population sizes calculated using the approximate Bayesian computation method. However, due to wide confidence intervals, a reduction of up to 65% in the most polluted river stretches could not be excluded. Surprisingly, analysis of the microsatellite data using an immigration with migration model indicated that roach populations in stretches of the River Lee, where effluents comprise approximately 30% of the flow, do not rely on immigration from less polluted stretches, suggesting they are largely self-sustaining. It is therefore possible that concentrations of estrogens in rivers heavily contaminated with WWTW effluents do not pose a substantial threat to roach populations, despite effects on individuals.

Second session

The importance of allelic diversity as a measure of genetic diversity: The case of founder events

Gili Greenbaum, Alan R. Templeton, Yair Zarmi, Shirli Bar-David Department of Solar Energy and Environmental Physics and Mitrani Department of Desert Ecology, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Israel

Allelic diversity is a measure of genetic diversity indicative of a population's long-term potential for adaptability and persistence. It is used less commonly than heterozygosity as a measure of genetic diversity. While both measures have ecological and evolutionary importance for populations, they differ in their implications as well as in their mathematical formulation. Heterozygosity and related measures are described by extended mathematical frameworks, most notably F-statistics, which allow for detailed analysis of different ecological scenarios. However, the mathematical framework for allelic diversity is not as developed, partially because it is more mathematically difficult to take into account the stochastic process of genetic drift for allelic diversity. Of particular importance, regarding genetic diversity, are scenarios of founder events. We developed a framework for studying allelic diversity using a stochastic model of a newly founded population experiencing genetic drift and gene flow. The model follows the dynamics of alleles lost during the founder event, and simulates the effect of gene flow on maintenance of allelic diversity. The probability of allele's presence in the population is identified as the relevant statistical property for a meaningful interpretation of allelic diversity. Additionally, the framework is extended to relate to all alleles in a polymorphic locus, by including the population's allele frequency spectrum. The model's analysis provides a simulation framework allowing assessment of allelic diversity maintenance in varied founder scenarios. Furthermore, the model illustrates that the 'One Migrant per Generation' rule, a commonly used conservation guideline derived from F-statistics, may be inadequate for preserving diversity at the allelic level. Hence, population genetic studies and conservation efforts aimed at preserving genetic diversity should consider both genetic diversity measures, since focusing merely on preserving heterozygosity might not preserve allelic diversity, which is crucial for species' persistence and evolution.

Weeds Inside

Sam Thomas

National Botanic Garden of Wales

The botanical gardens of Britain & Ireland are an important cultural resource and form a critical element of plant conservation strategy. Glasshouses are the architectural icons around which botanic gardens grow, they provide the normally botanically-apathetic public with encounters with fantastical species while furthering *ex-situ* conservation and taxonomic study. Alongside their

intended occupants exist a plethora of 'others': species that range from opportunistic weedy colonisers to those that, in UK terms, are obligately associated with glasshouses. Together these form a phytosociological community of glasshouse weeds that is distinct from any previously defined. Across Britain & Ireland its composition varies with some distant sites showing more similarity than those closer together. This variation in community ecology could indicate meta-populations reliant on humans for dispersal among & between the 'archipelagos' of glasshouse 'islands'. Using three key species groups we hope to answer the question: is the observed variation in glasshouse community ecology reflected in the population genetics of the constituent species?

Barcode UK: A complete national resource for people, plants and the planet

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We have DNA barcoded 90% of the native flowering plants and conifers of the United Kingdom using the core DNA barcode markers *rbcL* and *matK*. This represents the most complete DNA barcode coverage of any country in the world. For the 1479 species we have sampled over 6400 individuals and obtained 7583 DNA barcodes. Using both the *rbcL* and *matK* marker we can discriminate 81% of the UK native flora to species and 100% to genus.

We are working on a wide range of applications that make full use of our DNA barcode research platform. We are using our DNA barcodes to create the first, complete, species-level phylogeny of the UK flora and using this to investigate phylogenetic community ecology. We are using next generation DNA sequencing approaches to DNA barcode pollen mixtures, both from the bodies of pollinators and within honey. This allows us to answer diverse questions on pollinator ecology in innovative and novel ways.

DNA barcoding honey: pollinator focused plant surveying and drug discovery

Jenny Hawkins, Les Baillie, Natasha de Vere

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The pollen content of honey is a reflection of the plants which are visited by honeybees during its production. Understanding the floral composition of honey has a wide variety of applications. It can indicate what plant species are being used as food sources for honeybees in the habitat surrounding hives, providing a method for pollinator-focused plant surveying. It can be used to verify the stated floral sources of commercial honey and can be used to investigate the medicinal properties of honey.

We are using DNA barcoding as a tool to assess the floral composition of honey. DNA is extracted from the pollen within the honey sample and the core DNA barcode marker *rbcL* amplified. Next generation sequencing approaches (454 and Illumina) are used to sequence the amplicons. The entire native flowering plant flora of the UK has been DNA barcoded providing a reference database to compare the honey derived plant DNA samples to in order to identify them.

Here we present the results of the floral composition of 14 honey samples from throughout the UK. We illustrate an application of this technique in the assessment of the medicinal properties of honey. Three hundred honey samples have been screened to identify those which contain

potentially plant-derived antimicrobial compounds. DNA barcoding allows us to identify the plant species which may be contributing to the antimicrobial effect.

Posters

Landscape genetics of Tilia cordata

Carl Barker Edge Hill University

To understand the dynamics of species' distributions in response to changing climatic conditions, an understanding of the degree of isolation of a species is an important factor. *Tilia cordata* (Small-leaved Lime) is one such an isolated species, having historically been a major component of English forest canopies prior to human influence. It is now found in fragmented populations of variable size. Moreover climatic conditions directly impact its fertility and hence its ability to spread. This study aims to take molecular markers and assess the degree of connectivity of lime populations in areas where it is both densely packed and isolated.

Do current protected area designations consider the evolutionary potential, and therefore long term survival of Welsh Grasslands?

Elizabeth Chapman

National Botanic Garden of Wales

Plant communities exist within environmental gradients where slight changes can potentially lead to species loss and the resultant transition into another community type, potentially not of conservation value. Lowland grasslands are such an example, with certain types considered a conservation priority at country, national and European level.

However, existing conservation priorities, and site selection procedures, often focus on rare species and species richness, but does this reflect phylogenetic diversity; a proposed measure of evolutionary potential; and the ability to adapt to environmental or management change? The area of study which uses such techniques is 'Phylogenetic Community Ecology', with community analysis being based on evolutionary history and examines community phylogenetic composition to ask fundamental questions, including: how and when specific traits, families or groups of species arose and diverged.

A community phylogeny, constructed from Plant DNA Barcodes for the loci rbcL and matK, for all native grassland species included in the 'Lowland Grassland Survey of Wales' was created. The phylogeny provides a means to calculate phylogenetic diversity and phylogenetic species eveness, whilst datasets regarding trait data, abundance and rarity were transposed onto the phylogeny, to provide points for further analysis.

The study aims to:

- Examine the differing phylogenetic composition of a range of lowland grassland communities.
- Current conservation priority habitats have been chosen due to their species richness or presence of rare or threatened species-does this reflect their evolutionary potential?
- Understand whether there is a phylogenetic signal predisposing for species rarity.
- Investigate whether non conservation priority habitat types are of lower trait diversity, containing greater numbers of habitat generalists, potentially better suiting them to changes in the environment, such as resulting from climate change.

Understanding the reproductive ecology and genetics of *Succisa pratensis* to inform conservation management of marshy grassland for the endangered butterfly *Euphydryas aurinia*

Stefanie Carter^{1,2} Laura Jones^{1,2} Matt Hegarty² John Warren² Natasha de Vere^{1,2} 1 National Botanic Garden of Wales; 2 IBERS, Aberystwyth University

Succisa pratensis, devil's bit scabious, is a native perennial and the food plant of endangered butterfly *Euphydryas aurinia*, the Marsh Fritillary, populations of which have been declining for several decades. Conservation of *E. aurinia* is closely linked to the effective management and conservation of marshy grassland and *S. pratensis*.

The Mynydd Mawr SAC in Carmarthenshire holds an important metapopulation of *E. aurinia*, and the restoration of degraded marshy grassland in addition to the management of existing grassland has been identified as a key conservation aim. Vital to this aim is understanding the ecology and genetics of the current populations of *S. pratensis* within and around the SAC. In other areas of Europe it has been found that *S. pratensis* is an out-crossing species and that populations which are small and isolated contain less genetic diversity and can exhibit inbreeding depression leading to lowered survival.

28 sites within the metapopulation range of the butterfly were surveyed along with 4 further sites elsewhere in Wales. Leaf material and flower heads were collected and population estimates taken. Data was collected on seed production. The project aims to germinate the collected seed, monitoring germination rates and seedling survival, as well as testing general germination requirements on commercial seed. In addition, the project aims to develop SNP markers using RAD-seq in order to examine the genetics of existing *S. pratensis* populations. Together this information will provide insight into the ecology and genetics of *S. pratensis* in order to inform current and future management plans of marshy grassland, including the translocation or supplementation of *S. pratensis*.

Optimal strategies for finding a host plant in a complex world

Elizabeth Donkin and John Warren *IBERS, Aberystwyth University*

Increasing genetic diversity within monoculture crops has been found to alter the population dynamics of the associated insect herbivore species. Increasing genetic diversity is thought to disrupt specialist insect foraging behaviour by changing the spatial distribution of host plants. The extent to which this behaviour is affected may be determined by the host finding abilities and oviposition behaviour of the insects. Monitoring insect behaviour at a field scale is often not feasible. However, developing reliable models that can predict realistic insect behaviour and population dynamics on a variety of spatial scales provide a practical solution to this problem. A spatially explicit, individual based model has been developed to simulate the behaviour of generalist and specialist insect diversity and spatial distribution of plant species can be altered. As insect herbivores are known to alter their foraging and oviposition behaviour in response to changing plant diversity, the aim is to develop this model to investigate the coevolution of plant defences and insect foraging strategies over time. The project aims to scale up from an individual plant community to test the larger landscape scale effects of plant diversity on the behaviour and population dynamics of insect herbivores.

The genetic basis of self-incompatibility and heterostyly in Linum (Linaceae)

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Many angiosperm taxa have evolved a number of sophisticated mechanisms to prevent selffertilisation and promote outbreeding. Two of the most extensively studied are self-incompatibility (SI) (the recognition and rejection of self pollen) and heterostyly (the spatial separation of male and female sexual organs), with examples of both having evolved independently multiple times across the angiosperm lineage.

Most commonly known for cultivated flax (*Linum usitatissimum*), *Linum*, the largest genus in the Linaceae, is comprised of over 180 species with marked diversity in their reproductive biology: from SI to self-compatibility (SC) and various forms of heterostyly. The Linum system thus provides a perfect opportunity to study the dynamics of mating system evolution. While some studies have looked at genes involved in heterostylous polymorphisms, the genetic basis of SI has remained largely overlooked. We represent the first attempt to molecularly dissect the SI system in Linum and make inferences on its evolution among other species in the genus, largely focusing on southern Iberian species. We will also conduct a more in-depth study of the heterostyly syndrome, as the ancestral form to the genus remains unclear. Using a comparative transcriptomics approach we will search for S locus and heterostyly candidate genes. Using RAD-based techniques we will then assess how the mating systems have shaped the structures of different populations.

Ancient DNA preservation in mummified seals from Antarctica

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A great deal of information about species histories over time can be gained from studies of ancient DNA. It can reveal changes in genetic diversity, patterns of colonization and movement, and evolutionary relationships, as well as being a useful tool for determining baselines for conservation efforts. The amount of information that can be discovered from ancient DNA is dependent on the guality of its preservation. Mummified seal carcasses have been observed in the dry valleys of the Antarctic where the regional environment has been in a state of flux over at least the last 10,000 years. We scored the weathering of seal carcasses and extracted ancient DNA using silica-based spin-columns. Some samples were also radiocarbon dated. PCR amplification of the mitochondrial control region was used to verify the presence of DNA in samples, and relative concentration was compared to that of the nuclear DNA through amplification of a portion of the RAG1 gene using quantitative PCR. We found a weak positive correlation between the radiocarbon dates of the samples and the observed weathering stage. Overall, we were able to successfully amplify mitochondrial DNA from 63.6% of the samples, and success was independent of the collection site. This suggests that preservation is generally good within the dry valleys. There was no strong correlation between PCR success and weathering stage, which may indicate that microclimate around the carcass or sampling site on carcass leads to variation in success. The concentration of nuclear DNA in each sample was notably less than that of mitochondrial DNA. There was a positive correlation between the two, indicating that mitochondrial DNA concentration may predict nuclear DNA concentration to some degree. Successfully extracting and sequencing ancient DNA from these samples has the potential to tell us about demographic responses of seals to local environmental change.

Use of genetic monitoring of the endangered freshwater pearl mussel (*Margaritifera margaritifera*) to inform *ex-situ* conservation strategies

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Margaritifera margaritifera, the freshwater pearl mussel, is a long-lived bivalve which is the only globally endangered species as listed by the IUCN which is found in Ireland. Population declines have occurred throughout its Holarctic range over the 20th century. No natural populations in Northern Ireland have mussels under 20 years old, and these populations are regarded as being "non-functional" since there is little scope for recruitment. The Ballinderry River, a mesotrophic river flowing from the Sperrin Mountains into the western shore of Lough Neagh, is one of six rivers in Northern Ireland still containing pearl mussels, although surveys suggest as few as 1000 individuals still exist there. The Ballinderry Fish Hatchery (BFH) has been successfully cultivating mussels in the catchment as part of an *ex-situ* conservation programme since 1999 in collaboration with Queen's University Belfast (QUB). A previous genetic study (Wilson et al 2012) showed the Ballinderry *Margaritifera* population to be a unique Conservation Unit in Northern Ireland, thus meriting conservation in its own right. A new subpopulation found in the lower Ballinderry River in 2013 appears to be genetically distinct from the remaining mussels in the upper stretches, and whilst it does not harbour any unique alleles, differences in allele frequencies suggest that it may be prudent to consider it a separate Conservation Unit.

Samuel Logan

School of Biology Newcastle University

Hoverflies in Welsh Grasslands

Andrew Lucas

Department of Biosciences, Swansea University

Welsh grasslands support a diverse range of hoverfly species. Because hoverflies rely on nectar as an energy source, and pollen for egg formation, they are important pollinators.

My study looked at the hoverfly communities in two grasslands of conservation importance in west Wales (NVC communities M24 and MG5), and two communities that are the result of agricultural intensification (NVC MG6 and MG10) during 2011. Hoverflies were sampled regularly during the summer, using water traps, and all hoverflies identified to species.

Data analysis suggests that numbers were highest in the species-rich wet grassland community M24, and one exceptional species-rich dry grassland MG5 site. Hoverfly abundance was more influenced by available flower resources and management regime than by the grassland plant community, suggesting that creating wet grasslands of moderate botanical diversity could significantly increase the numbers of hoverflies in the wider countryside away from specially protected sites.

In future years, I hope to investigate pollen loads of hoverflies with DNA barcoding techniques, using the existing database of all plant species barcodes in Wales. I also aim to produce a database of DNA barcode sequences for all Welsh hoverfly species.

Population Genomics and Ecological Speciation in Poecilia mexicana

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The freshwater, live bearing fish Poecilia mexicana inhabits extreme environments rich in hydrogensulphide. Previous analyses have shown sulphide-inhabiting populations to be derived from nearby clear water populations, with low gene flow between the two despite no physical barrier to prevent fish migration (Plath et al. 2007, Tobler et al. 2011). Further evidence of adaptive trait divergence and reproductive isolation has shown that P. mexicana is an excellent model to study ongoing ecological speciation. We have performed a genome-wide scan and detected 20,528 SNP markers between adjacent sulphidic- and clear-water adapted populations located in the same river drainage (Rio Tacotalpa, Southern Mexico). Two-hundred and six (1%) SNPs were found to have extremely high F_{st} values (\geq 99% quantile of the F_{st} distribution) between the two populations. Elevated F_{st} is indicative of regions of the genome/genes under selection, making these highly differentiated SNPs prime candidates for further study. Analyses are ongoing and we intend to investigate the genomic distribution of SNP variation and identify the genes involved in the speciation process. Furthermore, P. mexicana have independently colonised sulphidic springs in other isolated river drainages and achieved similar adaptive trait divergence convergently (Tobler et al. 2011). Thus, we will be adding another sulphide/clear-water population pair from another isolated drainage (Rio Puyacatengo) to compare and contrast sulphur adaptation at the genomic level. We have been using the 'Pool-Seq' approach (Fabian et al. 2012): next-generation sequencing of genomic DNA pools, each pool containing a mixture of DNA from 100-200 individuals of the same population. Bioinformatic analyses have been performed using the 'Popoolation2' pipeline (Kofler et al. 2011).

Understanding macroalgal dispersal in a complex hydrodynamic environment: a combined population genetic and physical modelling approach

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Gene flow in macroalgal populations can be strongly influenced by spore or gamete dispersal. This, in turn, is influenced by a convolution of the effects of current flow and specific plant reproductive strategies. Although several studies have demonstrated genetic variability in macroalgal populations over a wide range of spatial scales, the associated current data have generally been poorly resolved spatially and temporally. In the present study, we used a combination of population genetic analyses and high resolution hydrodynamic modelling to investigate potential connectivity between populations of the kelp Laminaria digitata in the Strangford Narrows, a narrow channel characterised by strong currents linking the large semi-enclosed sea lough, Strangford Lough, to the Irish Sea. Levels of genetic structuring based on six microsatellite markers were very low, indicating high levels of gene flow and a pattern of isolation-by-distance, where populations are more likely to exchange migrants with geographically proximal populations, but with occasional long-distance dispersal. This was confirmed by the particle tracking model, which showed that whilst the majority of spores settle near the release site, there is potential for dispersal over several kilometres. This combined population genetic and modelling approach suggests that the complex hydrodynamic environment at the entrance to Strangford Lough can facilitate dispersal on a scale exceeding that proposed for *L. digitata* in particular, and the majority of macroalgae in general. The study demonstrates the potential of integrated physical-biological approaches for the prediction of ecological changes resulting from factors such as anthropogenically induced coastal zone changes.

Using genetic data to elucidate sea trout movements in southern British waters

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The Atlantic Aquatic Resource Conservation Project (AARC) is a European Union, Atlantic Area Transnational INTERREG IV-funded programme with partners in Britain, Ireland, France, Spain and Portugal. Projects include elucidation of marine movements of salmonids, evaluation of supportive breeding practices, aquaculture, river restoration, education and communication. More information can be found at http://www.aarcproject.org/.

At the University of Exeter, we are using genetic methods to study resident brown trout and migratory sea trout to inform on the management of trout stocks in southern Britain and to improve our understanding of the marine phase of the sea trout life cycle, particularly patterns of marine migration and mortality. To do this, we have undertaken microsatellite genotyping of resident trout populations to allow identification of the region (and in many cases the river) of origin of sea trout caught at sea. Initially, genetic data were gathered from resident brown trout populations from potential source rivers of sea-caught trout. Samples were collected by University of Exeter project staff and Environment Agency teams during annual surveys of salmonid stocks from principal sea trout rivers; coverage extended from the Severn in the Bristol Channel all the way around southern England to the Thames. Samples of trout from the marine environment were sampled from estuarine nets and by shore-based sea-anglers. Marine caught samples were then characterised with the same suite of 19 microsatellite loci as that used to construct the baseline. Subsequently, assignment analysis has been used to assign marine-caught trout to their river of origin, providing new insights into the marine movements of sea trout in southern British waters.

Scots pine: is there variation in pathogen resistance?

Annika Telford

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Scots pine (*Pinus sylvestris* L.) trees are a key component of the iconic Caledonian pinewoods. They are the only native pine species in the UK, and the newly designated 'National Tree of Scotland'. Native forest has declined to ~1% of its original area, and remaining fragments are managed to encourage regeneration and prevent further fragmentation and loss. Although previously thought to be highly resistant, *Dothistroma* needle blight (DNB; the causal agent is the ascomycetous fungal pathogen *Dothistroma septosporum*) has emerged in recent years as a serious threat to both commercially planted and native fragmented populations of Scots pine in Great Britain. Symptoms include distinct brick-red lesions on needles with erumpent black fruiting bodies, and infection can lead to needle loss, reduction in growth, and even death. Progeny and provenance trials have been established to determine whether there is any genetic variation for resistance to DNB in native Scots pine. These include an artificial inoculation trial, and one that has been planted in an area of high infection which will become naturally inoculated. The rate and extent of infection within the trees in these trials will be analysed to determine the variation in resistance to DNB in Scots pine populations across Scotland, the heritability of this variation, and whether resistance can be correlated to environmental or morphological differences between populations.

Responses to intraspecific outbreeding within animal and plant species: a systematic metaanalysis

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When individuals from separate populations mate, the resulting hybrid offspring can experience fitness benefits (heterosis) or costs (outbreeding depression) relative to their parents. Understanding the distribution and extent of these genetic benefits and costs is essential for guiding conservation plans that seek to mix wildlife populations. We used systematic review and meta-analysis to synthesize outbreeding responses in natural populations of plant and animal species. Our dataset included 528 effect sizes, describing intrinsic outbreeding responses from 98 studies (involving 79 species). We found that outbreeding responses varied significantly with hybrid generation, and between life history and other traits. In addition, we found that outbreeding depression and heterosis could be predicted by combining information on population demography, environmental and cytogenetic contexts. Studies for which we predicted a risk of outbreeding depression showed a cost to fitness in the F₂ generation, relative to mid-parent performance. In cases predicted to exhibit heterosis, we observed a corresponding fitness benefit relative to the mid-parent. We consider whether and how these results, and our approach to predicting outbreeding responses, might be useful in conservation practice.