

Phylomania 2012

University of Tasmania, School of Mathematics and Physics, 8-9 Nov 2012

Program

Thursday, 8 November

- 8.15am-9:00am Coffee and tea
- 9:00am-9:10am Welcome
- 9:10am-9:50am **Jeremy Sumner**, University of Tasmania
Markov and phylogenetic invariants: let's get together, man
- 9:50am-10:10am **David Bryant**, University of Otago, New Zealand
Phylogenetics with Nets and a Lasso
- 10:10am-10:30am **Melissa Humphries**, University of Tasmania
To gamma or not to gamma – Testing the fit of RAS models
- 10:30am-11:00am Morning Tea
- 11:00am-11:40am **Andrew Francis**, University of Western Sydney, Australia
Circular permutations, affine symmetric groups, and inversion distances in bacterial genomes
- 11:40am-12:20pm **James Degnan**, University of Canterbury, New Zealand
Some properties of rooted and unrooted anomalous gene trees
- 12:20pm-1:40pm Lunch
- 1:40pm-2:20pm **Mike Fellows**, Charles Darwin University, Australia
FPT Algorithms in Phylogenetics and Epistemological Frustration
- 2:20pm-3:00pm **Arndt von Haeseler**, Center for Integrative Bioinformatics, Vienna, Austria
Exploring the Sampling Universe of RNA-Seq
- 3:00pm-3:30pm Afternoon Tea
- 3:30pm-3:50pm **Jessica Leigh**, University of Otago, New Zealand
Tight Span Walker: Using the tight span to infer haplotype networks
- 3:50pm-4:30pm **Steffen Klaere**, University of Auckland, New Zealand
Do your data fit your phylogenetic tree?
- 4:30pm- **Barbara Holland (Panel Discussion)**, University of Tasmania
Residual Diagnostics for Phylogenetics
- 7:30pm- **Phylomania 2012 Pub Dinner: The Brunswick Hotel, 67 Liverpool St**

Friday, 9 November

- 8:30am-9:10am Coffee and tea
- 9:10am-9:30am **Sarah Fayed**, University of Tasmania
The significance of dating: the evolutionary history of Roupaleae (Proteaceae)
- 9:30am-9:50am **Simon Ho**, University of Sydney, Australia
Choosing the number of relaxed-clock models in molecular phylogenetic analysis
- 9:50am-10:10am **Sebastián Duchene**, University of Sydney, Australia
Understanding evolutionary rate variation in viruses
- 10:10am-10:30am **Martyna Molak**, University of Sydney, Australia
A study of time-dependent evolutionary rates and a guide to molecular-clock calibration in higher vertebrates
- 10:30am-11:00am Morning Tea
- 11:00am-11:40am **Chris Burridge**, University of Tasmania
Divergence of island biotas when they were not always islands
- 11:40am-12:20pm **Mike Charleston**, University of Sydney, Australia
A Practical Integer Linear Program Formulation for the Cophylogeny Reconstruction Problem
- 12:20pm-1:40pm Lunch
- 1:40pm-2:20pm **Lars Jermiin**, CSIRO Ecosystem Sciences, Canberra, Australia
Evidence of model misspecification in a recent phylogenomic study of yeast
- 2:20pm-2:40pm **Greg Jordan**, University of Tasmania
Can we sometimes use palaeoendemics to avoid bias in ancestral states derived from directional selection?
- 2:40pm-3:00pm **David Duchene**, Australian National University, Australia
Rates of molecular evolution and diversification in plants: chloroplast mutation rates correlate with species richness in the Proteaceae
- 3:00pm-3:30pm Afternoon Tea
- 3:30pm-4:10pm **Dorothy Steane**, University of Tasmania
Delights and dilemmas of DArT
- 4:10pm-4:30pm **James Worth**, University of Tasmania
*Northern richness and southern poverty: Contrasting genetic footprints of glacial refugia in the relictual tree *Sciadopitys verticillata* (Coniferales: *Sciadopityaceae*)*
- 4:30pm-4:50pm **Klaas Hartmann**, University of Tasmania
Constructing a complete global bird phylogeny
- 4:50pm-6pm Drinks and cheese

Saturday, 10 November

- 12pm- **Phylomania 2012 bushwalk** (details TBA)

Abstracts

David Bryant

University of Otago, New Zealand

Phylogenetics with Nets and a Lasso

Joint work with Alethea Rea

The (positive) lasso is a widely used method in statistics which selects variables and improves least squares estimates. The key idea is to find the best non-negative least squares estimate

$$\min_{\beta \geq 0} \|\mathbf{X}\beta - \mathbf{y}\|_2$$

while slapping on the constraint $\|\beta\|_1 \leq \lambda$. Increasing λ gives (usually) solutions with more non-zero variables. Efron et al (2004) present an algorithm which efficiently explores lasso solutions for all λ , but it doesn't always work. We describe an algorithm which does, and look at applications to phylogenetic network methods like NeighborNet.

Chris Burridge

University of Tasmania

Divergence of island biotas when they were not always islands

Joint work with Danielle Nankervis, Lindi Olivier, Jessica Wadley, Bill Brown, and Jeremy Austin

Continental shelf islands are islands that possessed terrestrial connections to other landmasses via exposed continental shelf during low sea stands. These islands often contain lineages that are related but distinct from those on the adjacent mainland, and their divergence is usually assumed to reflect isolation initiated by the post LGM marine transgression. However, a range of alternate divergence scenarios exists. Divergence may have been initiated by an earlier marine transgression and was retained through subsequent glacial periods of terrestrial connection, or may have been dissociated from sea level changes, involving marine dispersal. Here we test these alternate scenarios for a species that exhibits morphologically distinguishable lineages between Tasmania and the Australian mainland, but also has marine dispersal potential – the wedge-tailed eagle *Aquila audax*. Genetic variation was surveyed at 20 microsatellite loci and in mitochondrial DNA, from 148 Tasmanian and 48 mainland individuals. The populations differed significantly in allele frequencies, and gene flow subsequent to the initiation of their divergence was rejected. While this is consistent with marine transgression initiating lineage divergence, estimates of age of this divergence substantially post-dated the most recent marine transgression, rejecting this mechanism. Instead, the data are consistent with a small number of mainland individuals colonising Tasmania by marine dispersal, and subsequent isolation. This study highlights that divergence of continental shelf island biotas from those of the adjacent mainland do not necessarily follow the paradigm of initiation by marine transgression, and have bearing on the conservation status applied to putatively 'long-isolated' lineages on such islands.

Mike Charleston

University of Sydney, Australia

A Practical Integer Linear Program Formulation for the Cophylogeny Reconstruction Problem

The problem of uncovering ancestral relationships between ecologically linked species is of fundamental interest in evolutionary biology. Given a pair of evolutionary trees, which in the treatment here are rooted and binary, and the observed links between their tips such as “this pathogen strain infects that host species,” an explanation is sought of how the two trees have grown in evolutionary time. Such

explanations are generally couched in terms of a most parsimonious solution to the optimisation problem of mapping one tree, the dependent P, into the other, the independent H, such that the coevolutionary events the mapping implies have a minimal total cost. This optimisation problem is NP-complete and fast exact methods have been lacking. Also lacking has been a complete and correct delineation of the requirements of such maps, such that the problem can be solved with pre-existing computing tools such as integer linear programs. We fill both these gaps with the method presented herein.

James Degnan

University of Canterbury, New Zealand

Some properties of rooted and unrooted anomalous gene trees

A result from a few years ago is that when gene trees evolve within species trees under the multispecies coalescent, the most likely gene tree topology can differ from the topology of the species tree. This phenomenon, called “anomalous gene trees”, can occur for any rooted species tree topology with 5 or more species given certain patterns of branch lengths in the species tree. Here I discuss the analogous result for unrooted gene trees: for any rooted species tree topology with 7 or more taxa, there exist branch lengths such that the most likely unrooted gene tree has a different unrooted topology from that of the species tree. I’ll discuss patterns of branch lengths that lead to rooted and unrooted anomalous gene trees and look at some questions about relationships between species tree shapes and shapes of anomalous gene trees.

David Duchene

Australian National University, Australia

Rates of molecular evolution and diversification in plants: chloroplast mutation rates correlate with species richness in the Proteaceae

Joint work with Lindell Bromham

Many factors have been identified as correlates of diversification rate, such as size, polyploidy, and dispersal mechanism. Analysis of many molecular phylogenies has also revealed a common link between substitution rate and species richness. This suggests an important link between rates of molecular evolution and the process of diversification. However, this link is not universal and its cause is a matter of debate. We used a dataset with 6200 (4400 coding) base pairs of chloroplast genes from the highly diverse angiosperm family Proteaceae to test for a correlation between diversification and the rate of substitutions. We focus on chloroplast genes because they have been proposed play a crucial role in the formation of reproductive isolation between plant species. Using phylogenetically-independent sister pairs, we show that species rich lineages of Proteaceae have significantly higher substitution rates, for both synonymous and non-synonymous substitutions. This is consistent with a role for mutation rate of chloroplasts driving the speed of reproductive isolation. However, we find no significant differences in the ratio of non-synonymous to synonymous substitutions between lineages differing in net diversification rate, which means that there is no detectable signal of population size changes or selection in causing this relationship.

Sebastián Duchene

University of Sydney, Australia

Understanding evolutionary rate variation in viruses

Joint work with Simon Ho

Viruses evolve at rates that are orders of magnitude higher than those of eukaryotes and prokaryotes. This accelerated pace of evolution is hypothesised to be a result of their life-cycle as infectious agents

and obligate parasites, and their dependence on their host's cellular machinery for replication. However, estimates of rates of viral evolution vary widely among lineages and sampling scales. In turn, this has led to discordant estimates of the timing of viral evolutionary origins and long-term associations with their hosts.

By analysing published rate estimates and conducting phylogenetic analysis of viral molecular sequences we have pinpointed possible causes of rate variation across timescales. Purifying selection, underestimates of saturation, and substitution model inadequacy were found to have a strong influence on rate estimates. These results suggest that current phylogenetic models fail to account for these factors, leading to biased estimates of evolutionary rates and timescales in some viral datasets.

Sarah Fayed

University of Tasmania

The significance of dating: the evolutionary history of Roupaleae (Proteaceae)

Joint work with Greg Jordan, Peter Weston, Peter McQuillan, Simon Saulie, and Fu Chengxin

Tribe *Roupaleae* (~ 176 spp., 12 genera, Proteaceae) is distributed across Australia, New Guinea, Asia, New Caledonia, New Zealand and South and Central America. The most recent age estimate for *Roupaleae* is ~ 63Ma, and during this time the landmasses in its contemporary distribution have undergone significant tectonic movement, marine submergence and aerial orogenesis. Current molecular phylogenetic inferences for *Roupaleae* show the relationships between genera are not well supported, and this is not improved in morphological studies. Previously this group has been unsuitable for testing biogeographic hypotheses. We rectify this by strengthening the inferences of temporal, phylogenetic, and geological constraints on the tribe, and then test whether clade structure is uncorrelated with biogeographic disjunctions. We do this by i) revising the phylogenetic estimates with new taxa and six DNA fragments some of which are new to Proteaceae studies; ii) constraining this estimate with four fossil calibration points; iii) reviewing the current tectonic evolution theory of the region; iv) using this information to age disjunctions and categorize them as either vicariant or dispersal events; iv) and finally testing whether tree topology and dating is uncorrelated vicariant and dispersal events.

Mike Fellows

Charles Darwin University, Australia

FPT Algorithms in Phylogenetics and Epistemological Frustration

My talk will: (1) briefly survey the main idea of parameterized complexity, and some recent results in the area of algorithms and complexity analysis for combinatorial problems modeling issues in Phylogenetics; (2) attempt to open a discussion and/or raise or sharpen awareness about the interface problems between Phylogenetics and Algorithmics that are (perhaps) qualitatively different from the way Computer Science relates (quite productively) to other areas of Biology.

Andrew Francis

University of Western Sydney, Australia

Circular permutations, affine symmetric groups, and inversion distances in bacterial genomes

Joint work with Attila Egri-Nagy, Volker Gebhardt and Mark Tanaka

Bacterial genomes consist of a single circular chromosome, and an inversion event on a bacterial genome is a rearrangement of the DNA that reverses the sequence (and orientation) of a segment. An estimate of the number of genomic inversion events between two genomes is often used as a proxy for the evolutionary distance between the two. This distance is in turn used to construct a phylogeny describing the

relationships among a set of genomes.

In this talk I will describe how the problem of estimating the number of inversion events can be translated into a family of group-theoretic models, and how in a simple case we can use affine symmetric groups to quickly find the inversion distance between two genomes.

Klaas Hartman

University of Tasmania

Constructing a complete global bird phylogeny

Phylogenetic trees frequently omit some extant species due to a lack of sequence data. These ‘missing’ species are often non-randomly distributed in the tree, for example due to the remote habitats of some clades. This non-random distribution can bias the insights gained from the phylogeny. We developed a methodology for combining multiple sources of data to enable inclusion of all known species (for the study group) in a distribution of trees. This methodology was applied to produce a global phylogeny of birds, revealing novel spatial and temporal patterns in distribution. These trees have also been used to produce a prioritisation of birds for biodiversity conservation.

Simon Ho

University of Sydney, Australia

Choosing the number of relaxed-clock models in molecular phylogenetic analysis

Joint work with Sebastián Duchene and Martyna Molak

Estimating evolutionary timescales is a common aim of molecular phylogenetic analysis. This can be done using methods based on the molecular clock, which postulates a constancy of substitution rates among lineages. Most data sets, however, exhibit significant levels of rate variation among lineages. This can be caused by differences in population size, mutation rate, or the strength of natural selection. Relaxed molecular clocks allow the phylogenetic estimation of evolutionary timescales even when substitution rates vary among branches.

In analyses of large and informative data sets, it is often appropriate to use multiple relaxed-clock models to accommodate differing patterns of rate variation among genes. In most cases, however, there is no clear rationale for preferring one clock scheme over another. If the evolutionary process is modelled with an inadequate number of relaxed clocks, the resulting estimates of rates and timescales might be misled. On the other hand, increasing the number of relaxed-clock models carries the risk of model over-parameterization. We are developing an objective method for selecting the number of relaxed clocks for analyses of multigene data sets.

Barbara Holland

University Tasmania, Australia

Residual Diagnostics for Phylogenetics

In R if you were doing a linear regression analysis you’d go

```
> fit <- lm(y ~ x)
> plot(fit)
```

Where the first command fits a linear model and the second command gives you an array of useful residual diagnostics that address questions such as

- Is there any pattern in the residuals?

- Are there any data points that are highly influential?
- What proportion of the variation in the data is captured by the model?

This won't be a talk but instead a group discussion addressing the question: In phylogenetics what should this do ... ?

```
> fit ← phylom(alignment, tree, model)
> plot(fit)
```

Melissa Humphries

University of Tasmania

To gamma or not to gamma – Testing the fit of RAS models

Since the introduction of explicitly model based methods of phylogenetic inference (e.g. maximum likelihood and Bayesian approaches) the complexity and biological realism of models of sequence evolution has increased. An important advance in this regard was the introduction of models that allowed rate variation across sites (RAS), i.e. they modelled the fact that some sites in a gene may be more or less likely to accept substitutions than others. The most common way of accomplishing this is to use a discrete approximation to a gamma distribution. This has the computational advantage of allowing (usually 4 or 8) different rate categories with the addition of a single extra parameter into the model.

However, overly simplistic models of RAS can cause problems for phylogenetic inference and for estimating dates of divergences. In particular, a recent study has shown that if there are a small number of sites that mutate very frequently compared to other sites (so called hot spots) this can lead to time-dependence of rate estimates (Soubrier et al 2012).

In this study we used amino-acid data from a study by Grahnen et al (2011) who simulated data using a biophysical model of protein folding and binding. We extracted the number of mutations at each site and fit this data to a variety of models. In particular:

- Constant RAS implies the frequency distribution of counts of mutations should follow a Poisson distribution
- Gamma distributed RAS imply that the counts should follow a negative binomial distribution
- Gamma distributed RAS with invariants sites imply that counts should follow a zero inflated negative binomial distribution.

We will discuss the merits of these models and whether or not any of them provide an acceptable fit to data generated under biologically realistic conditions.

Lars Jermiin

CSIRO Ecosystem Sciences, Canberra, Australia

Evidence of model misspecification in a recent phylogenomic study of yeast

The architecture and evolution of yeast genomes has been the focus of much research in recent years, in part because different species of yeast display a range of differences in their phenotypic traits (e.g., level of ploidy, synteny, mating systems, pathogenicity, and environmental and host preferences). In this seminar, I focus on the evolutionary history of 18 species of yeast. I do so from the point of view of some of the commonly used phylogenetic assumptions (e.g., evolution under globally stationary, reversible, and homogeneous [SRH] conditions). Initially, I present three statistical tests that may be used to determine whether aligned sequence data are consistent with evolution under globally SRH conditions. I then focus on the genomic data used to infer the phylogeny of 18 species of yeast belonging to the *Saccharomyces* and *Candida* clades (Nature 459, 657-662). A parametric bootstrap analysis of these data disclosed a disturbing result – the fit between the data and the optimal tree and substitution model was significantly

better for the real data than for data generated by simulation on the optimal tree and substitution model. The underlying cause of this perplexing result was assessed using a number of analytical methods, including the parametric bootstrap, matched-pairs tests of symmetry, and phylogenetic analysis of data generated by simulation. I show that the data are inconsistent with the assumption of evolution under globally SRH conditions. However, neither violation of this assumption nor violation of the assumption of sites evolving independently can explain the perplexing result. Evidence supporting another explanation is presented. Jointly, these findings: (i) call into question our understanding of the evolution of yeast, and (ii) highlight that there is an urgent need for phylogenetic methods that can model covarion evolutionary processes under non-SRH conditions.

Greg Jordan

University of Tasmania

Can we sometimes use palaeoendemics to avoid bias in ancestral states derived from directional selection?

Ancestral state analyses provide some of our most important tools for understanding evolution. However, these analyses assume non-directional evolution, but many important aspects of environment have changed systematically through time (e.g. climate, size of animals, CO₂ concentrations in the air). Furthermore, there is fossil evidence that these changes have imposed strong directional selection. Directional selection can lead to convergent evolution of the favoured form of a trait and systematic extinction of groups carrying the unfavoured forms. These processes can lead to misleading ancestral state reconstructions, in which the favoured form appears older and less convergent than it really is. I will argue that differences in relative abundance of clades can be evidence that the less abundant clade has been subject to greater selection than the more abundant clade. This means that concurrence of a trait in groups with low abundance (best measured in geographic extent) can be evidence for systematic past selection against this trait, and can therefore be used to infer where directional selection has biased ancestral state analyses. I would like to enter into a discussion on how to implement this approach.

Steffen Klaere

University of Auckland, New Zealand

Do your data fit your phylogenetic tree?

Phylogenetic methods are used to infer ancestral relationships based on genetic and morphological data. What started as more sophisticated clustering has now become a more and more complex machinery of estimating ancestral processes and divergence times. One major branch of inference is maximum likelihood methods. Here, one selects the parameters from a given model class for which the data are more likely to occur than for any other set of parameters of the same model class. Most analysis of real data is executed using such methods.

However, one step of statistical inference that has little exposure to application is the goodness of fit test between inferred model and data. There seem to be various reasons for this behaviour, users are either content with using a bootstrap approach to obtain support for the inferred topology, are afraid that a goodness of fit test would find little or no support for their phylogeny thus demeaning their carefully assembled data, or they simply lack the statistical background to acknowledge this step.

Recently, methods to detect sections of the data which do not support the inferred model have been proposed, and strategies to explain these differences have been devised. In this talk I will present and discuss some of these methods, their shortcomings and possible ways of improving them.

Jessica Leigh

University of Otago, New Zealand

Tight Span Walker: Using the tight span to infer haplotype networks

Joint work with David Bryant

Haplotype networks are used for visualising gene genealogies at the population level and for inferring demographic and phylogeographic scenarios. These are graphs in which sequences sampled from a population are represented by vertices connected to one another and to vertices representing unsampled sequences by edges that often represent a single mutation event. Ancestral sequences are often present in haplotype datasets, and sequences are very closely related, differing by one or a few substitutions. For these reasons, phylogenetic inference methods are unsuitable for reconstruction of haplotype genealogies. However, some methods developed specifically for haplotype network inference use algorithms involving arbitrary choices and penalties. We have developed a method for inferring haplotype networks that uses the tight span. I will describe our method and provide a brief tour of GUI-based software in which it has been implemented.

Martyna Molak

University of Sydney, Australia

A study of time-dependent evolutionary rates and a guide to molecular-clock calibration in higher vertebrates

Joint work with Simon Ho

The molecular clock allows us to infer the timing of evolutionary events using analyses of DNA sequences. Molecular clocks need to be calibrated using independent information about time, which usually comes from the fossil record, biogeographic events, ancient DNA, or pedigree studies.

Rates of molecular evolution vary with the timescale upon which they are inferred. For example, very high rates have been measured in pedigree studies, and these approximate the spontaneous mutation rate of DNA. In contrast, estimates of rates calibrated using the fossil record are up to several orders of magnitude lower. The fact that different evolutionary rates are observed on different timescales has important consequences for studies of molecular clocks and evolutionary timescales.

Various factors, including natural selection and genetic drift, can influence the disparity between short- and long-term evolutionary rates. We will present the preliminary results of a large-scale study investigating the time-dependent patterns of molecular evolutionary rates. We examine rates obtained for different molecular markers, for various taxa distributed throughout reptiles, birds, and mammals. We will demonstrate the importance of using appropriate calibration points when estimating evolutionary timescales using phylogenetic methods.

Dorothy Steane

University of Tasmania

Delights and dilemmas of DArT

The development of a set of around 8000 Diversity Arrays Technology (DArT) markers for *Eucalyptus* heralded an exciting technical advance for population genetic and phylogenetic research in this ecologically and economically important genus. Pilot studies demonstrated the potential of DArT to differentiate species, resolve biogeographic disjunctions within species, detect signals of environmental adaptation and reconstruct phylogenies. The genome complexity reduction method of DArT is now being combined with Next-Generation Sequencing in a methodology (DArTseq) that can be applied to any organism without the requirement of array development. In *Eucalyptus*, DArTseq provides tens of thousands of markers that can be linked to the *Eucalyptus grandis* genome sequence. While this is all very exciting, biologists feel like they are drowning in data! Where to from here?

Jeremy Sumner

University of Tasmania

Markov and phylogenetic invariants: let's get together, man

Joint work with Elizabeth Allman, Peter Jarvis and John Rhodes.

I will outline some (very) recent work that provides a unified algebraic framework for understanding invariants of all sorts phylogenetic. In particular, I will explain why “phylogenetic invariants” is a misnomer and present a new method that systematically derives all phylogenetic invariants [*sic*] using group character computations alone.

Arndt von Haeseler

Center for Integrative Bioinformatics, Vienna, Austria

Exploring the Sampling Universe of RNA-Seq

Joint work with Stefanie Tauber

How deep is deep enough? While RNA sequencing states a well-established technology the required sequencing depth for detecting all expressed genes is not known. If we leave the entire biological overhead and meta-information behind we are dealing with a classical sampling process. Such sampling processes are well known from population genetics and thoroughly investigated. Here we use the Pitman Sampling Formula to model the sampling process of RNA sequencing. By doing so we characterize the sampling by means of two parameters which grasp the conglomerate of different sequencing technologies, protocols and their associated biases. Additionally we evaluate the theoretical expectation of uniform coverage. Most importantly, given a pilot sequencing experiment we provide an estimate of the size of the underlying sampling universe and an estimate of the number of newly detected genes when sequencing an additional sample of arbitrary size.

James Worth

University of Tasmania

*Northern richness and southern poverty: Contrasting genetic footprints of glacial refugia in the relictual tree *Sciadopitys verticillata* (Coniferales: *Sciadopityaceae*).*

Sciadopitys verticillata is amongst the most relictual of all plants, being the last living member of an ancient conifer lineage, the *Sciadopityaceae*, and is distributed in small and disjunct populations in high rainfall regions of Japan. While mega-fossils indicate the persistence of the species within Japan through the Pleistocene glacial-interglacial cycles, how the species withstood the colder and drier climates of the glacials is poorly known. This study utilises phylogeography and paleodistribution modelling to test whether the species survived within pollen-based coastal temperate forest glacial refugia or within previously unidentified refugia close to its current range. Sixteen chloroplast haplotypes were found that displayed significant geographic structuring. Unexpectedly, northern populations most distant from coastal refugia had the highest chloroplast diversity and were differentiated from the south, a legacy of glacial populations possibly in inland river valleys close to its current northern range. In contrast, populations near putative coastal refugia in southern Japan, harboured lower chloroplast diversity and were dominated by a single haplotype. A highly variable and homoplasious mononucleotide repeat region in the trnT-trnL fragment reinforced the contrasting patterns of diversity observed between northern and southern populations. The divergent histories of northern and southern populations revealed in this study will inform the management of this globally significant conifer.

List of participants

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