“What are we even talking about when we say “species tree’?”

Anne D. Yoder
Department of Biology
Duke University
August 6, 2019
Themes from yesterday … (thank you Peter, Laura, and Claudia!)

In no particular order …

• The coalescent is a powerful tool for understanding historical demography (e.g., ancestral Ne and divergence times)
• Branch lengths can have an enormous impact on recovering the species tree from gene trees
• Rapid radiations with short internal branches can really F* U up!
• Ancestral population size (the size of “the box”) can have a huge impact on coalescent rates
• Assumed mutation rate can have HUGE impact on estimation of Ne (recall Peter’s whales)
• Increasingly clear that concatenation is inferior to MSC for estimating species tree
• Theoretically, coalescent times should be as old or older than speciation events
Themes from yesterday … (thank you Peter, Laura, and Claudia!)

BOTTOM LINE:

IT'S BLOODY COMPLICATED!!!
Gene flow only makes matters worse!

Lateral Gene Transfer
Gene flow only makes matters worse!

Jiggins, Mallet, and colleagues (over the years)

Ongoing gene flow during speciation
So ... do we give up???
One million species face extinction

Landmark United Nations report finds that human activities threaten ecosystems around the world.

BY JEFF TOLLEFSON

Up to one million plant and animal species face extinction, many within decades, because of human activities, says the most comprehensive report yet on the state of global ecosystems.

The rate of species extinction is already tens to hundreds of times higher than the average across the past ten million years. Without decisive action to conserve habitats, the extinction rate will only increase, says a United Nations-backed panel called the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

About 75% of land and 66% of ocean areas have been “significantly altered” by people, driven in large part by agriculture, according to a summary of the work, released on 6 May (see go.nature.com/2v4zbn9). The loss of species and habitats poses a much greater threat to life on Earth as climate change unfolds, the IPBES report says.

The analysis distils findings from nearly 15,000 studies and government reports, integrating information from the natural and social sciences. Indigenous peoples and traditional agricultural communities are the first major international appraisal of biodiversity since 2010. Representatives of 132 governments met last week in Paris to finalize and approve it.

“We have never had a single unified statement from the world’s governments that unambiguously makes clear the crisis we are facing for life on Earth,” says Thomas Brooks, chief scientist at the World Wildlife Fund for Nature, who helped to edit the report. “That is really the shocking part of what we have here.”

Without “transformative changes” to the world’s economic, social and political systems to address this crisis, the IPBES panel projects that major biodiversity losses will continue to 2050 and beyond.

The analysis, which will be released in full later this year, also inextricably links biodiversity to climate change. An estimated 5% of all species would be threatened with extinction by 2°C of warming above pre-industrial levels—a threshold that the world could breach in the next few decades, unless greenhouse-gas emissions are drastically reduced.

The biodiversity crisis should be at the top of the global agenda alongside climate, and Anne Largardère, IPBES executive secretary, at a 6 May press conference in Paris: “We can no longer say that we did not know” she said.

Brooks says that the IPBES report will help to set the agenda when governments negotiate conservation goals for the next decade at the UN Convention on Biodiversity next year.

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Nature (May, 2019)
We want to know things like:

Conservation concern:
• How many species are out there and where do we find them?
• Are their populations growing, declining, holding steady?
• How does present-day demography relate to ancestral demography? (this is another way of saying the same thing)

Basic science:
• When did species diverge from one another?
• Why and how did they diverge?
• What is maintaining species boundaries?
• Are they exchanging genes?
• And if so, is this a neutral ("speciation with gene flow") or selection-driven ("adaptive introgression") process?
Madagascar = 0.0001 (0.01%) of Earth’s surface
Almost 20% of primate species diversity is found on an island roughly the size of California.
IUCN has declared lemurs to be the most threatened mammals on earth
MAKE WAY FOR THE MOUSE LEMUR

If a US biochemist has his way, the world’s tiniest primate could become a top research animal for genetics.

BY LESLIE ROBERTS

O nga is struggling tonight — her hands keep slipping off a miniature grip bar used to measure her strength. “Come on, you can do better,” coos Zeph Pendleton, who is gently supporting the mouse lemur as she tries to get a firm hold. Finally, the animal gets her fingers around the bar and gives it a tug. It records a force of 1 kilogram, impressive for a creature weighing only 41 grams. “Good,” says Pendleton, a research assistant who is working here in the rainforest at Centre ValBio, a research station at Ranomafana National Park in Madagascar.
Why mouse lemurs???
Snoozing through the storm: torpor use during a natural disaster

Received: 24 February 2015
Accepted: 14 May 2015

Julia Nowack, A. Daniella Rojas, Gerhard Körtner & Fritz Geiser
Fig. 2.2: An ancestral lemur makes its way across to Madagascar.
~ 24 species described at present
“The anomaly zone” where gene trees are more likely to be recovered than the species tree.
Finding Evolutionary Processes Hidden in Cryptic Species

Torsten H. Struck,1,* Jeffrey L. Feder,2 Mika Bendiksby,1,3 Siri Birkeland,1 José Cerca,1
Vladimir I. Gusanov,1 Sonja Kistenich,1 Karl-Henrik Larsson,1 Lee Hsiang Liow,1,4
Michael D. Nowak,1 Brita Stedje,1 Lutz Bachmann,1 and Dimitar Dimitrov1,5

Trends in Ecology & Evolution

CellPress

REVIEWS

2018
Can *you* tell them apart???
18

The ideal species concept – and why we can’t get it

D. L. Hull

Contacting address: Department of Philosophy, Northwestern University, Evanston, IL 60208, USA
Figure 1. Hypothetical axes of morphological and genetic diversity within a species group. Area circumscribed by black ellipse represents systems where species delimitation is usually simple. The two areas circumscribed in brown represent conditions under which species delineation is often problematic, but conceptually interesting.

Barley et al. (2014) Evolution
The majority of named species appear to be *microendemics*, though others have much broader geographic distributions ...
ENVIRONMENTAL HETEROGENEITY!
Has climate change been a driver of speciation?

Climate Fluctuation during the Pleistocene

~ 2.6 mya through ~ 12 kya

Lineage diversification within hominins
Sound
Smell
Male advertisement calls for three species

Braune et al., 2008
Mouse lemur sampling (TCI grant)

5 field sites
29 mouse lemurs
7 dwarf lemurs
4 flights
4200Km by road

Slide courtesy of Marina Blanco
(or, “It takes a village to study mouse lemurs”)
$N = 283$ individuals from $> 20$ species
The nose knows …
Woods Hole, 2008

But how can I tell if they are receiving different olfactory signals???

I've been working on this really cool system called the vomeronasal receptor Class I genes (V1R)

Joe Bielawski
Molecular Evolutionary Characterization of a V1R Subfamily Unique to Strepsirrhine Primates

Anne D. Yoder¹,*, Lauren M. Chan¹,†, Mario dos Reis²,†, Peter A. Larsen¹,†, C. Ryan Campbell¹, Rodin Rasoloarison³,⁴, Meredith Barrett⁵, Christian Roos⁴, Peter Kappeler⁶, Joseph Bielawski⁷, and Ziheng Yang²

¹Department of Biology, Duke University
²Department of Genetics, Evolution and Environment, University College London, London, United Kingdom
³Département de Biologie Animale, Université d’Antananarivo, Antananarivo, Madagascar
⁴Gene Bank of Primates and Primate Genetics Laboratory, German Primate Center (DPZ), Göttingen, Germany
⁵UCSF Center for Health & Community
Our hypothesis: nocturnal primates (like mouse lemurs) will show higher diversity of V1Rs than will diurnal primates, and these gene copies will be under strong positive selection.

Our results: based on targeted PCR, cloning, and Sanger sequencing we discovered a gene family, apparently unique to the strepsirrhines, that was under strong positive selection but did NOT show any particularly compelling patterns regarding nocturnality and diurnality.
Elaborate expansion of syntenic V1R hotspots correlates with high species diversity in nocturnal mouse and dwarf lemurs

Kelsie E. Hunnicutt, George P. Tiley, Rachel C. Williams, Peter A. Larsen, Marina B. Blanco, Rodin M. Rasoolarison, C. Ryan Campbell, Kevin Zhu, David W. Weisrock, Hiroaki Matsunami, Anne D. Yoder

doi: https://doi.org/10.1101/637348

This article is a preprint and has not been peer-reviewed [what does this mean?].
Speciation by sensory drive can occur if divergent adaptation of sensory systems causes rapid evolution of mating traits and the resulting development of assortative mating.
Whole genome analysis indicates that mouse and dwarf lemurs have the most diverse portfolio of V1Rs, with highest proportion of intact copies, in all of primates.
Figure 5 Intraspecific *Microcebus murinus* V1R repertoire size diversity
We can know precisely which stimuli effect the evolution of which genes (*in mice*):

For example, this V1R subfamily is receptive only to the stimuli from female mouse bedding.

On the other hand, this subfamily responds to female mouse bedding, snake bedding, and ferret bedding.
In conclusion (re: are they using different sensory signals, perhaps driving and/or maintaining species boundaries?):

YES!!!
GENE TREES IN SPECIES TREES

WAYNE P. MADDISON

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, USA

Gene trees often don't match the species tree

A "species tree" can contain many "gene trees"

Behavior of gene trees relates to MANY factors, including ancestral population sizes

Figure 1. A gene tree contained within a species tree leading to three extant species: A, B, and C. Bold branches of gene tree show relationships among the sampled copies of the gene (●). Sampled copies from sister species B and C are sister copies.

Figure 2. Discord between gene and species trees. At left is the species tree of four species, A, B, C, and D, and at right is the tree of a gene sampled one copy per species. Species B and C are sister species, but their gene copies are not sister copies.
Even small sample sizes (in terms of individuals) can yield powerful results.
Though sampling strategy must be carefully considered! (remember the frogs in a single pond)
The Multispecies Coalescent is a powerful toolkit for estimating:

- The **species tree** (i.e., phylogeny)
- **Effective Population Size** ($N_e$) through time
- **Divergence ages**
- **Patterns of gene flow** (both rate and direction)
Our mission:

To harness the power of **empirical genomic approaches**, combined with the **multispecies coalescent**, for species discovery and characterization

\[ f(\theta|x) = \frac{f(\theta)f(x|\theta)}{f(x)} \]
Recall from yesterday:

Ideally, we want multiple loci that are independently segregating in the genome
The entire field of population genetics will benefit from increased exchange between coalescents and phylogeography ... [and] the future availability of multilocus genetic data will serve as a bridge between these two approaches.”

“Intralocus recombination is quite problematic for inferred gene-tree approaches since the genealogy is no longer a bifurcating tree (Hein, 1993).”

Wakeley, 2003
RADseq: Tens of thousands of unlinked SNPs from across the genome!
ddRADseq Data Workflow

Input (Samples)

NextGen Sequencing

Library Prep

Output (Results)

Data Types

Cluster Data/Call SNPs

Slide courtesy of C. Ryan Campbell
Filtering thresholds:
- **Invariant loci are retained**: minimum locus size: 100; maximum % of missing data: 10.
- Total number of loci (that passed filtering): 15,267.
- Nr of invariant loci: 1,822.

**Mean locus length**: 231 bp.
**Mean nr of variable sites**: 4.7.
**Mean nr of parsimony-informative sites**: 3.29.
**Mean % of missing data (Ns)**: 5.53.
Remember Peter’s whales …
Pedigree-based measurement of the de novo mutation rate in the gray mouse lemur reveals a high mutation rate, few mutations in CpG sites, and a weak sex bias

C. Ryan Campbell, George P. Tiley, Jelmer W. Poelstra, Kelsie E. Hunnicutt, Peter A. Larsen, Mario dos Reis, Anne D. Yoder

doi: https://doi.org/10.1101/724880

This article is a preprint and has not been peer-reviewed [what does this mean?].
Campbell et al. (in prep.)

DLC Mouse Lemur Mutation Rate Study Sampling Strategy
Measuring de novo mutation rate:

- Count number of mutations
- Divide by size of the genome
- \# mutations/size of genome = rate

Easy, right?
Problems (just a few):

- Depth of coverage (some mutations will be called with more confidence than others)
- Genome assembly really, really matters (need long contigs to avoid, as much as possible, missing or misassembled regions due to highly repetitive regions)
- The number of “mutations” caused by sequencing error will VASTLY exceed biological mutations (replication errors)
- Ironically then, the false negative rate can be just as error prone (if not more so) than the false positive rate due to extreme filtering stringency
Estimating generation times:

Key parameters
• Age at onset of first offspring to last reproductive event
• Number of offspring produced from first to last reproduction
• Probability of surviving to age of last reproduction
1.64 x 10^-8

(one of the highest rates yet measured for a mammal)
Four case studies (all in prep):

1. Genomic homogeneity in the face of ecological divergence

2. Intraspecific divergence driven by natural climate change (incipient?)

3. Lineage diversification in close geographic proximity (ongoing?)

4. Reproductive isolation in sympatry (complete?)
Break, anyone???
Case #1: “False alarm!” Investigating the genomic signal underlying (apparent) incipient speciation

Genomic homogeneity in the face of morphological and ecological diversification: detecting hidden functional loci via genome scans in the grey-brown mouse lemur: *Microcebus griseorufus*

Jelmer Poelstra, Emilienne Rasoazanabary, Gina-Marie Agostini, Alison Richard, Laurie Godfrey, and Anne D. Yoder

[in prep]
Parapatric Speciation

(at or to one side of; beside; side by side)
Beza Mahafaly Special Reserve (~ 6 km²)
“Dissertation in a Box”: 256 samples

- Gallery = 92
- Ihazoara = 70
- Spiny = 94
Gallery forest
Spiny forest
Ihazoara forest
Three Distinct Color Morphs
Earliest stages of speciation?

Morphological distinction

mtDNA (near) identity
Beza samples (RADseq)

- Andrendahy
- Antabore
- Beza_gallery
- Beza_ihazoara
- Beza_spiny
- Mahavelo
- Tongaenoro
- Tsimanampetsotsa
- Vohondava
- Vombositse

region
- Beza
- SE
- SW
As with mtDNA analysis, complete lack of genetic structure within Beza Mahafaly
Conclusions (Case #1):

• Despite strong (for mouse lemurs!) indication of morphological and ecological divergence, this occurs on a background of seeming genomic homogeneity

• Fine-scale analysis of whole genome scans will be needed to fully explore this apparent anomaly

Poelstra et al. (in prep)
Case #2: Intraspecific divergence driven by natural climate change? (Goodman’s mouse lemur, *M. lehilahytsara*)

An expanded geographic perspective of Goodman’s mouse lemur reveals the effects of Pleistocene forest fragmentation in Madagascar's Central Highland Savannah with early symptoms of lineage diversification

**George P. Tiley**, Marina B. Blanco, Rodin M. Rasoloarison, José M. Ralison, Paul A. Hohenlohe, and Anne D. Yoder

[In progress ...]
Peripatric Speciation

Figure 1: Peripatric speciation

Figure 2: Centrifugal speciation

(all around; near --- think “periphery”)
Geogenetic patterns in mouse lemurs (genus *Microcebus*) reveal the ghosts of Madagascar’s forests past

Anne D. Yoder*a,b, C. Ryan Campbell*, Marina B. Blanco*, Mario dos Reis*, Jörg U. Ganzhorn*a, Steven M. Goodman*a,b, Kelsie E. Hunnicutta, Peter A. Larsena, Peter M. Kappelera, Rodin M. Rasoloarison*a, b, José M. Ralison*a, David L. Swofford*a, and David W. Weisrocks

*aDepartment of Biology, Duke University, Durham, NC 27708; bDuke Lemur Center, Duke University, Durham, NC 27705; School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, United Kingdom; cTierkologie und Naturschutz, Universität Hamburg, 20146 Hamburg, Germany; dField Museum of Natural History, Chicago, IL 60605; eAssociation Vohetra, BP 3012, Antananarivo 101, Madagascar; fBehavioral Ecology and Sociobiology Unit, German Primate Centre, 37077 Göttingen, Germany; gDépartement de Biologie Animale, Université d’Antananarivo, BP 906, Antananarivo 101, Madagascar; and hDepartment of Biology, University of Kentucky, Lexington, KY 40506
There appears to be higher genetic diversity within this tiny patch of relicual forest than can be seen at any other locality (thus far sampled).
Previous locality information appeared to indicate a rainforest edge specialist.
Have now extended its range by ~150 km to the west
Have revised our view from edge specialist to plateau specialist
Mrufus myoxinus (~55K ybp)

M. marohita
M. mittermeieri
M. lehilahytsara
M. nyoxinus
M. rufus
M. berthae

~500K ybp
~55K ybp
Microcebus rufus
"Geogenetic patterns" indicate that there were forest "bridges" across Madagascar that must have entirely disappeared by ~ 50K ybp
Tiley et al. (in prep)
Both analyses show a marked decline in $N_e$ coincident with the LGM.

Tiley et al. (in prep)
Though somewhat surprisingly, panmixia is the most probable model of genetic relationships among populations.

<table>
<thead>
<tr>
<th>Model</th>
<th>Marginal Likelihood</th>
<th>Bayes Factor*</th>
<th>Posterior Probability</th>
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<td>0A – East to west</td>
<td>-408766.23</td>
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<td>0</td>
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<tr>
<td>0B – West to east</td>
<td>-408169.12</td>
<td>1194.22</td>
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<td>1 – Stepping stone</td>
<td>-404252.47</td>
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<td>2 – Panmixia</td>
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<td>3 – Divergence and isolation</td>
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<td>4 – Divergence and migration</td>
<td>-407777.86</td>
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</table>

*Bayes factors computed with natural logarithms of marginal likelihoods with respect to model 0A as $2 \times (\ln L - \ln L_{0A})$
  **The values are presented as $10^{-3}$**
peripatric speciation?

Mittermeier's mouse lemur

Goodman's mouse lemur
Geogenetic patterns in mouse lemurs (genus *Microcebus*) reveal the ghosts of Madagascar’s forests past

Wide credible intervals around the age estimates = uncertainty
Comparison of divergence times between MSC and concatenated uncorrelated molecular clocks.

Tiley et al., in prep.
Comparison of divergence times between MSC and concatenated uncorrelated molecular clocks.

Tiley et al., in prep.
Phylogenetic rate higher than SMR

SMR higher than phylogenetic rate
Conclusions (Case #2):

- Forest fragmentation occurred rapidly and affected both the eastern rainforests and Central Highlands during a period of decreased precipitation near the last glacial maximum (LGM).

- Population substructure is evident but with a high degree of connectivity still detectable between the eastern rainforests and the Central Highland Savannah.

- Origin of the Central Highland Savannah predates human arrival, but also shows that continued habitat loss from deforestation will likely endanger Goodman’s mouse lemur.

- We’re very worried/intrigued by the apparent conflict between different methods for estimating divergence times.

Tiley et al. (in prep)
Case #3: Lineage diversification in close geographic proximity (ecological speciation?)

Complex processes of cryptic speciation in mouse lemurs from a micro-endemism hotspot in Madagascar

Dominik Schüßler¹#, Jordi Salmona²#, Marina B. Blanco³,⁴#, Jelmer Poelstra⁴#, George P. Tiley⁴#, Jean B. Andriambeloson⁵, Guillaume Besnard², Olivier Bouchez⁶, C. Ryan Campbell⁴†, Paul D. Etter⁷, Amaia Iribar Pelozuelo², Paul A. Hohenlohe⁸, Kelsie E. Hunnicutt⁴®, Eric A. Johnson⁷, Peter A. Larsen⁴&, Jasmin Mantilla-Contreras¹, Sophie Manzi², Alexandra Miller⁹, Blanchard Randrianambinina¹⁰,¹¹, David W. Rasolofoson¹⁰, Amanda R. Stahlke⁸, David Weisrock¹², Rachel C. Williams³,⁴, Lounès Chikhi¹,²,⁹, Edward E Louis Jr.¹³, Anne D. Yoder⁴*, Ute Radespiel¹⁴*
In sympatric speciation, reproductive isolation evolves within a population without the aid of geographic barriers.
Putatively five species of mouse lemur in this one corner of Madagascar.
Morphological distinctions are cryptic and/or overlapping

Schüßler et al. (in prep)
At least three cases of independent evolution in sympatry
One case of mitonuclear discordance and another of paraphyletic “species”
Genealogical Discordance Index (gdi) delimits one but not both sister-species pairs.
GPhoCS without migration yields very different divergence time for species pair #2 versus with migration (~100 ka ago versus 400 ka ago)
(Presently) undescribed species shown to be in precipitous decline with both RADseq (GPhoCS) and whole genome data (MSMC) --- making it even more vulnerable to human impacts.
Conclusions (Case #3):

• Evolutionary divergence is ongoing for five metapopulations lineages in a geographically constrained region of Madagascar of acute conservation concern

• There are at least two instances of sympatric overlap of diverging lineages

• It is presently unclear what is driving diversification

• There appears to be a correlation between Ne and and ability to delimit species: cause or effect?

• Presently undescribed species has been in steep decline for tens of thousands of years (reflecting natural climate change?)

Schüßler et al. (in prep)
Case #4: Reproductive isolation in allopatry with secondary contact?

RADseq reveals lack of evidence for recent gene flow across previously characterized mouse lemur hybrid zone

Jelmer Poelstra, Jan Lüdemann, Karina Montero, Jacques Rakotondrany, Tobias Lenz, Andreas Hapke, Paul Hohenlohe, Jordi Salmen, Lounès Chikhi, Edward E Louis Jr., Ute Radespiel, Simone Sommer, Jörg Ganzhorn, Anne D. Yoder

[In progress ...]
Allopatric Speciation

A population becomes separated by a geographic barrier; reproductive isolation develops, resulting in two separate species.
Figure from Setash et al., 2017
Figure from Setash et al., 2017
Combination of microsatellite data, subtle morphological distinctions, and parasite loads have suggested that there is an active hybrid zone in the southeast.
- 80 individuals from two contact zone sites
- 20 individuals from nearby micro-allopatric sites
- 38 individuals from distant allopatric sites
- 3 outgroup individuals (*M. rufus*)
Site 1: syntopic overlap  
Site 2: “micro-allopatry”

Poelstra et al. (in prep)
ADMIIXTURE shows no evidence of admixed individuals

Poelstra et al. (in prep)
PCA shows no evidence of admixed individuals

Poelstra et al. (in prep)
When K = 3

Poelstra et al. (in prep)
Very low levels of gene flow since initial divergence

Zero at present
Conclusions (Case #4):

- RADseq data data have revealed that previous hypotheses of hybridization between syntopic species occurrence is erroneous.

- The two species show very strong ecological preferences which is likely to reinforce reproductive isolation.

- It is unclear if F1 hybrids exist, and if they do, what is their fate?

- Future directions call for detailed field studies of individual interactions among and between *M. murinus* and *M. griseorufus*. 

Poelstra et al. (in prep)
Adaptive introgression in dwarf lemurs

Conservation genomic analysis reveals ancient introgression and declining levels of genetic diversity in Madagascar’s hibernating dwarf lemurs

Rachel C. Williams, Marina B. Blanco, Jelmer W. Poelstra, Kelsie E. Hunnicutt, Aaron A. Comeault, Anne D. Yoder

doi: https://doi.org/10.1101/620724

This article is a preprint and has not been peer-reviewed [what does this mean?].
Conservation genomic analysis of Madagascar's hibernating dwarf lemurs reveals unexpected patterns of ancient introgression

Rachel C. Williams, Marina B. Blanco, Jelmer W. Poelstra, Kelsie E. Hunnicutt, Aaron A. Comeault & Anne D. Yoder
Pairwise Sequentially Markovian Coalescent (PSMC)

A lot going on between 200 kya – 20 kya ago!
The “ABBA-BABA” test (i.e., Patterson’s D statistic)

• If incomplete lineage sorting (ILS) is causing most of the gene-tree/species-tree discordance, then ABBA and BABA sites will be roughly equal (ABBA/BABA = 1.0)
• If gene flow is acting to create discordance this relationship will break down

Figure from Goulet et al., 2017
Red Species

Blue Species
Hybrids (shown in purple) are less fit than parent species, the hybrid zone is said to be “reinforced”
Even so, **back-crossing** can occur (when a hybrid mates with an individual from one of the parent species)
When that individual again crosses with a pure parent individual portions of the Blue species genome (blue circle) are transmitted even though the offspring is not a classic hybrid.
That individual can then mate with a pure parent individual, again transmitting portions of the Blue Species genome, but less will be represented in that offspring.
That individual can then mate with a pure parent individual, again transmitting portions of the Blue Species genome, but less will be represented in that offspring.
The process can continue, with less and less of the Blue Species genome transmitted, but those portions that persist probably do so because they are advantageous.
The process can continue, with less and less of the Blue Species genome transmitted, but those portions that persist probably do so because they are advantageous.
A process called “Adaptive Introgression”
You can think about this occurring over space
Or time ....

Present

Past
And in fact, it is usually both

Past

Present

West

East
“Adaptive introgression” can create classic cases of gene tree/species tree mismatches
NEANDERTHAL-INFLUENCED TRAITS

- Depression
- Addiction to tobacco
- Hypercoagulation
- Actinic keratosis
- Malnutrition
- Urinary tract disorders
Looking at introgressed genes between dwarf lemur species

Neuropeptide Y (NPY) receptors: stimulation of food intake and modulation of circadian rhythm

Williams et al. (in press)
Looking at introgressed genes between dwarf lemur species

ABCA10: Probable transporter which may play a role in macrophage lipid homeostasis

Williams et al. (in press)
Table S4. Gene ontology results for introgressed regions of the genome for tests between *Cheirogaleus medius/C. major*, and *C. medius/C. sibreei*. All results are significantly over enriched for both tests respectively (*p* < 0.00006, *p* < 0.00009).

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Wrapping it up …

• There are many (exact count still unknown) species of mouse lemur

• It will take continuing and intensive field study, and international collaboration, to get to the bottom of it

• Speciation is a **process** so it should not be surprising that some lineages will be less diverged than others

• The point of it all is **both** to learn about the processes that drive speciation in these small mammals, **and** to identify those populations/species that are under immediate threat from human impacts
Taking genomics to the field ....

Next-generation in situ conservation and educational outreach in Madagascar using a mobile genetics lab

Marina B. Blanco, Lydia K. Greene, Rachel C. Williams, Lanto Andrianandrasana, Anne D. Yoder, Peter A. Larsen

doi: https://doi.org/10.1101/650614

This article is a preprint and has not been peer-reviewed [what does this mean?].
Biodiversity = (θ)