**“Species Trees”**

What is the “species tree?”
- The true tree (when there is one)
- The population tree
- The dominant history
- ???

Populations are composed of contemporaneous individuals with a high chance of sharing common descendants.

A population lineage is a time-extended population “worm”
- Defines the limits of gene flow

Population lineages can split to generate population trees
- The trees define the limits of coalescence/lineage sorting

Gene trees can disagree within the population tree due to ILS
If there is a strict population tree, it can be estimated using multilocus sequence data

- Given a set of nodal ages (in units of $N_{e}$ generations) one can determine the likelihood of a particular gene tree topology (and branch lengths)
- With enough genes, you can find the population tree (and nodal ages) that maximize the likelihood of the gene trees

STEM (Kubatko et al. 2009)

But what if the population “tree” is not a tree? What should we estimate?

The full population history?

- Would need priors on hybridization and related phenomena
- Computationally challenging (but progress being made)
- Assumes that individual gene tree estimates are valid
- A reticulogram is not very useful for classification

BEST

- A Bayesian MCMC method
- Assumes no recombination within loci, free recombination between loci, and no gene flow following speciation
- Does not mix well
**An alternative: the primary concordance tree**

- A tree composed of clades that are true for a plurality of the genome
- A first order summary of the distribution of gene genealogies

![Concordance tree diagram](image)

**Implications for “species”**

- If species are taxa, they may be defined as clade on the primary concordance tree
- Are they taxa?
- If so, what rank of taxa?

**The dual burden of species**

- Species are units of taxonomy
  - Part of the hierarchy of named groups
- Species are units of evolution
  - Entities that participate in evolution

**Three responses**

- Species are taxa. Period.
- Species are evolutionary units. Period
- Species are both.

**Species are taxa**

- All organisms are assigned to species
- Subspecific taxa may be raised to species rank and subgenera may be “demoted” to species
- Species are described and keyed much like taxa at other ranks
- Named species play a role in communication

**Three responses**

- Species are taxa. Period.
- Species are evolutionary units. Period
- Species are both.
Evolutionary units and taxa need not coincide

Three responses

- Species are taxa. Period.
- Species are evolutionary units. Period
- Species are both.

Monophylyphil

- Taxa are historical entities, hence clades
- To form a strict nested hierarchy, we should only recognize clades that are true for more of the genome than they are false

A bold claim:

We will never find an evolutionary criterion that will assign all individuals to species and maintain perfect hierarchical nesting with taxa at other ranks

Species are taxa/clades

- When we name a species we are hypothesizing the existence of a clade (on the true concordance tree)
If species are taxa/clades they must be ranked clades

- Ranking criterion?

Is there an objective and universal ranking criterion?

...in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow.

Which is to say, “No!”

The “art” of monography

- Use assorted subjective ranking principles to select set of clades that approximate evolutionary units
- Judicious compromises to reconcile conflicting criteria

The phylogenetic concept of “speciation”

- The emergence and persistence of distinct clades
- Differential gene lineage extinction (isolation; selection; drift)
- Ecological divergence/specialization and Reproductive isolation