

Genomic data highlight the complexity of species delimitation within the *Sorex cinereus* complex.

Andrew G Hope

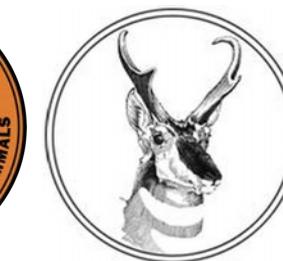
Ben J. Wiens

John R. Demboski

Joseph A. Cook

Acknowledgements

- Highly collaborative research spanning decades and many institutions
 - **Agencies** – USGS, NPS, USFWS
 - **States** – AK, NM, CO, UT, WY, MT, ID, WA, OR, CA, ND, SD, KS, WI, MN
 - **Provinces** – YT, NWT, BC, AB, MB, ON
 - **Museums** – MSB, DMNS, KSB, MVZ, UAM, UWBM, NMNH
 - **Others** – S.O. MacDonald, R. Rausch, V. Rausch, J. Findley, T. Jung, J. Whitman, B. Wrigley, J. Lackey, A. Shafer
 - **Field Crews** – Beringian Coevolution Project, Hope Lab, many others...



The *Sorex cinereus* “complex”

noun: **complex**

/,käm'pleks, kəm'pleks, 'käm,pleks/

1. a group or system of different things that are linked in a close or complicated way; a network.

adjective: **complex**

2. not easy to analyze or understand; complicated or intricate.



Taxonomy and systematics through time

Variation in:

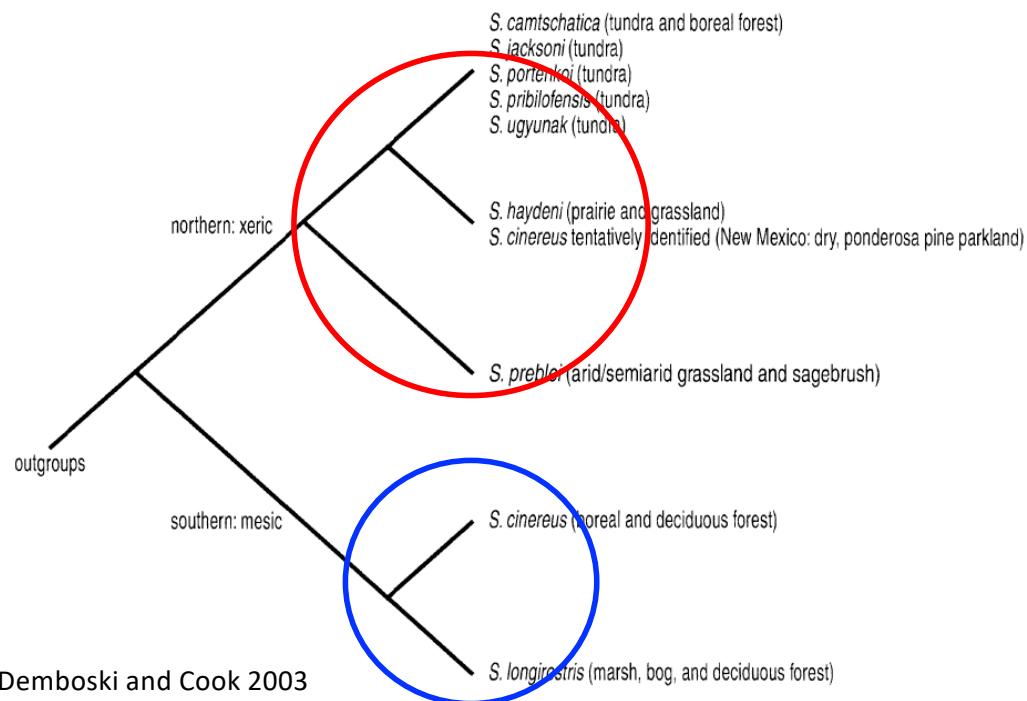
- Morphology
- Karyotypes
- Allozymes
- DNA sequences

Demboski and Cook 2003

Type of data	Study	Taxonomic conclusion
MC, ME	Jackson (1928)	<i>Sorex cinereus</i> group proposed
MC, ME, ED	Hoffmann and Peterson (1967)	Beringian species allied with <i>S. cinereus</i>
K	Meylan (1967)	Specific distinction of <i>S. cinereus</i>
ME, MP	Yudin (1969)	Specific distinction of <i>S. cinereus</i> , <i>S. beringianus</i> (= <i>S. leucogaster</i>), and <i>S. hydrodromus</i> (= <i>S. pribilofensis</i>)
ME, MC, ED	Okhotina (1977)	Palearctic subspecies of <i>S. cinereus</i> (<i>S. c. camtschatica</i> , <i>S. c. leucogaster</i> , and <i>S. c. portenkoi</i>)
ME, MC	van Zyll de Jong (1980)	Specific distinction of <i>S. haydeni</i>
MC, ME, MP, K	van Zyll de Jong (1976, 1980, 1982, 1991), Volobouev and van Zyll de Jong (1994)	Beringian species and <i>S. haydeni</i> distinct from <i>S. cinereus</i>
K	Ivanitskaya and Kozlovsky (1985)	Specific status of <i>S. camtschatica</i> , <i>S. leucogaster</i> , and <i>S. ugyunak</i>
A	George (1988)	Monophyly of <i>S. cinereus</i> , <i>S. fontinalis</i> , <i>S. haydeni</i> , and <i>S. preblei</i> , including <i>S. longirostris</i>
MC	van Zyll de Jong and Kirkland (1989)	Specific distinction of <i>S. cinereus</i> and <i>S. haydeni</i>
A	Stewart et al. (1993)	Paraphyly (<i>S. cinereus</i> and <i>S. haydeni</i>)
D	Stewart and Baker (1994b, 1997), Brunet et al. (2002)	Paraphyly or mtDNA introgression (or both) of <i>S. haydeni</i> and <i>S. cinereus</i>
K, MP	Rausch and Rausch (1995)	<i>Sorex jacksoni</i> subsumed to <i>S. c. jacksoni</i>
ED	Dokuchaev (1997)	Multiple colonization of Asia by members of the <i>S. cinereus</i> group
D	Fumagalli et al. (1999)	Sister relationship of <i>S. cinereus</i> and <i>S. haydeni</i>

Current knowledge

- 13 described species in two primary mtDNA clades (Demboski and Cook 2003; Hope et al. 2012):



- “Southern Clade”

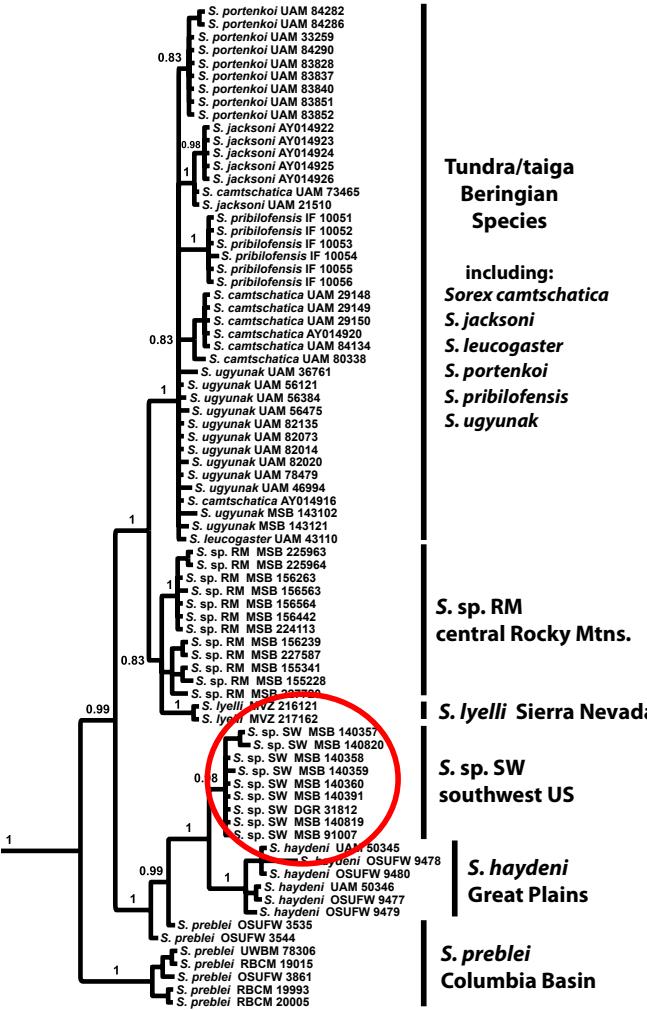
- *Sorex cinereus* – masked shrew
- *Sorex longirostris* – southeastern shrew

- “Beringian Clade”

- High Latitude
 - *Sorex ugyunak* – barren-ground shrew
 - *Sorex jacksoni* – St. Lawrence Is. shrew
 - *Sorex pribilofensis* – Pribilof shrew
 - *Sorex portenkoi* – Portenko’s shrew
 - *Sorex camtschatica* – Kamchatka shrew
 - *Sorex leucogaster* – Paramushir shrew
- Low Latitude
 - *Sorex haydeni* – Prairie shrew
 - *Sorex preblei* – Preble’s shrew
 - *Sorex lyelli* – Mount Lyell shrew
 - *Sorex milleri* – Carmen Mtn. shrew
 - *Sorex emarginatus* – Zacatecas shrew

Current knowledge

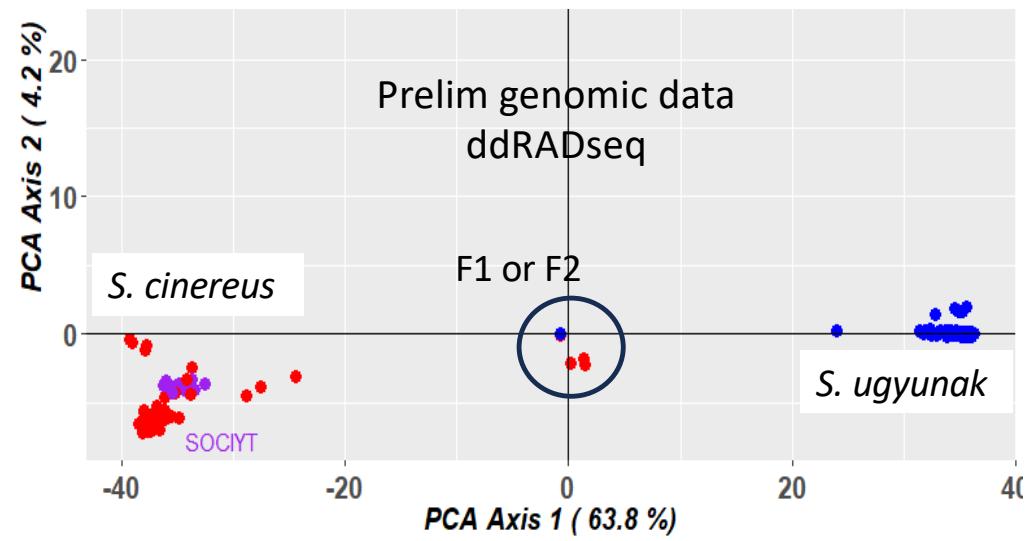
- A taxon in the Jemez and San Juan Mtns. of the Southwest appears to be distinct, but...
 - mtDNA similar to *S. haydeni*
 - nuDNA similar to *S. preblei*
 - → hybridization??



Hope et al. 2012

Current knowledge

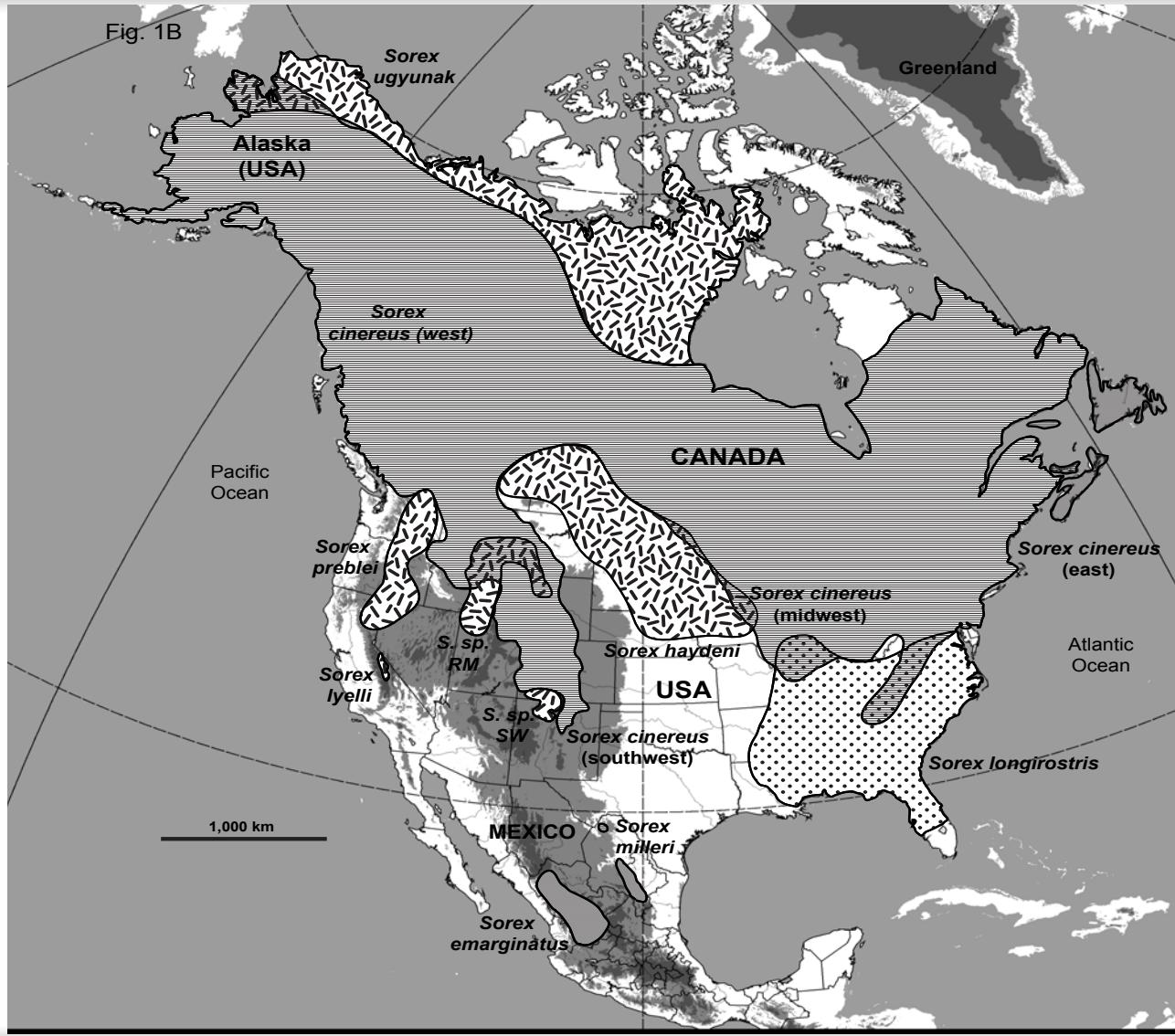
- Also evidence for hybridization in northern AK between *S. cinereus* and *S. ugyunak*, but...
 - Very few and all early generation
 - → reinforcement zone
- Also evidence for hybridization in Great Plains between *S. cinereus* and *S. haydeni*, but...
 - Based on morphology and mtDNA only
 - Not great evidence to date (Brunet et al. 2002)

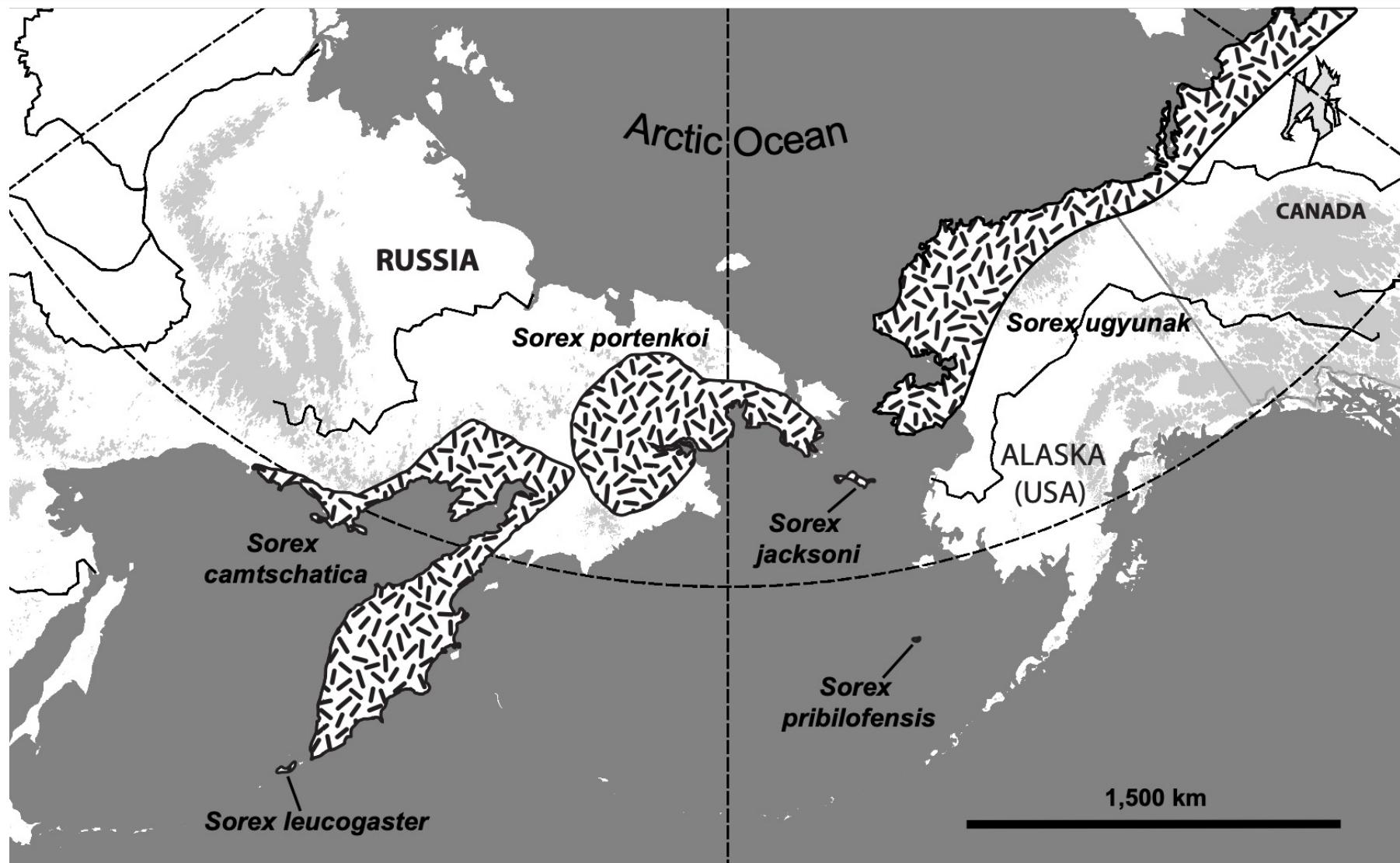


What is the complexity?

- Some species have enormous ranges with really high intra-specific diversity (e.g., *S. cinereus*)
- Some species have very limited ranges (e.g., *S. lyelli*)
- Some species have “patchy” distributions (e.g., *S. preblei*)
- Some species are insular with very low diversity (e.g., *S. pribilofensis*)
- Lots of described species have a very recent evolutionary history (e.g., Beringian species fragmented following LGM)
- Other species are older (e.g., *S. longirostris*)
- Lots of (shaky) evidence for hybridization

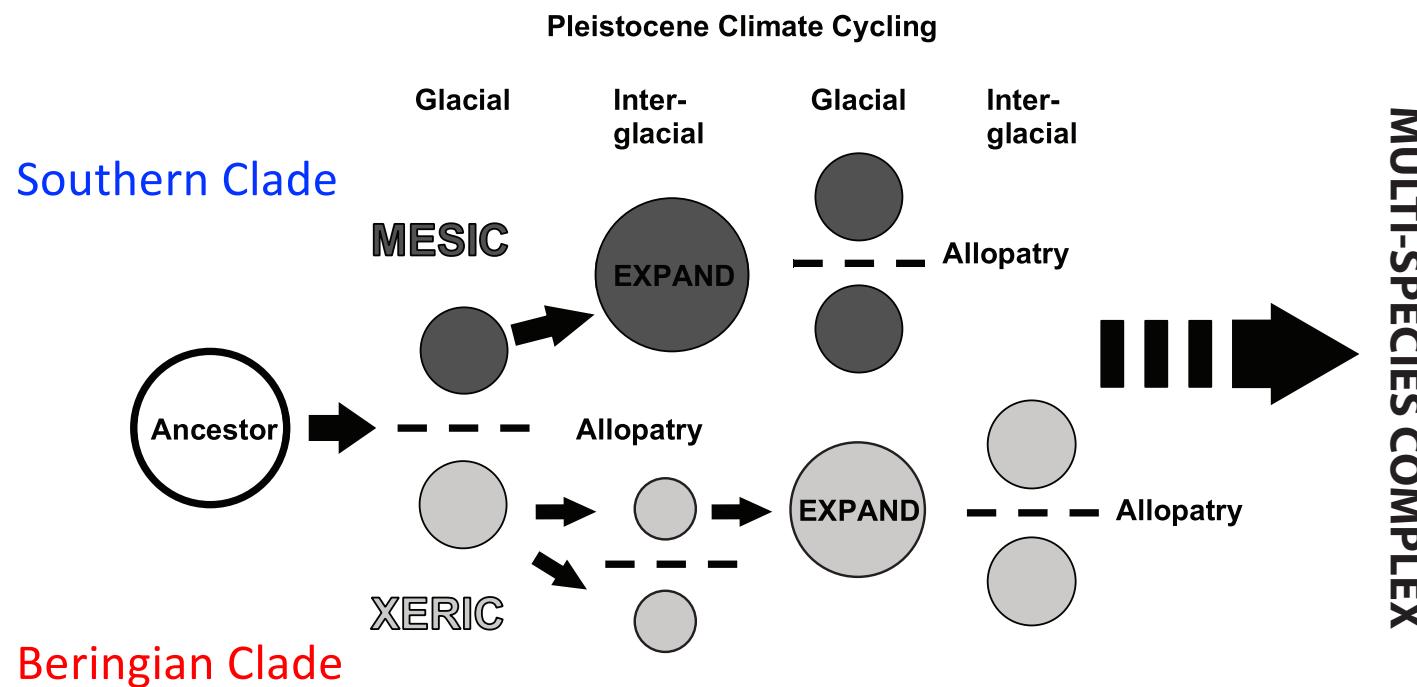
Species ranges





What is the complexity?

- Vastly different ecology among species
 - Xeric vs. mesic habitats
 - Correspondingly complex responses to environmental change



What are the problems?

- After all these years we still don't have a good handle on taxonomy or systematics within this complex.
- Nominal species have been described based on inconsistent criteria
- More complexity with more data → continued ambiguity

Why does this matter beyond simply knowing?

- Effective management and conservation rely on diagnosable taxa and knowledge of evolutionary (and ecological) dynamics
 - Assessment of hybrid status
 - Genomic flatlining
 - Independent evolutionary trajectories
 - Distinct population segments
- Understanding the evolutionary process of speciation
 - Allopatry vs. sympatry vs. parapatry
 - Speciation with gene flow
 - Adaptive divergence
 - Drift
- Resulting co-evolutionary dynamics of host speciation
 - Parasites/pathogens
 - Disease → wildlife health → human health

Goals

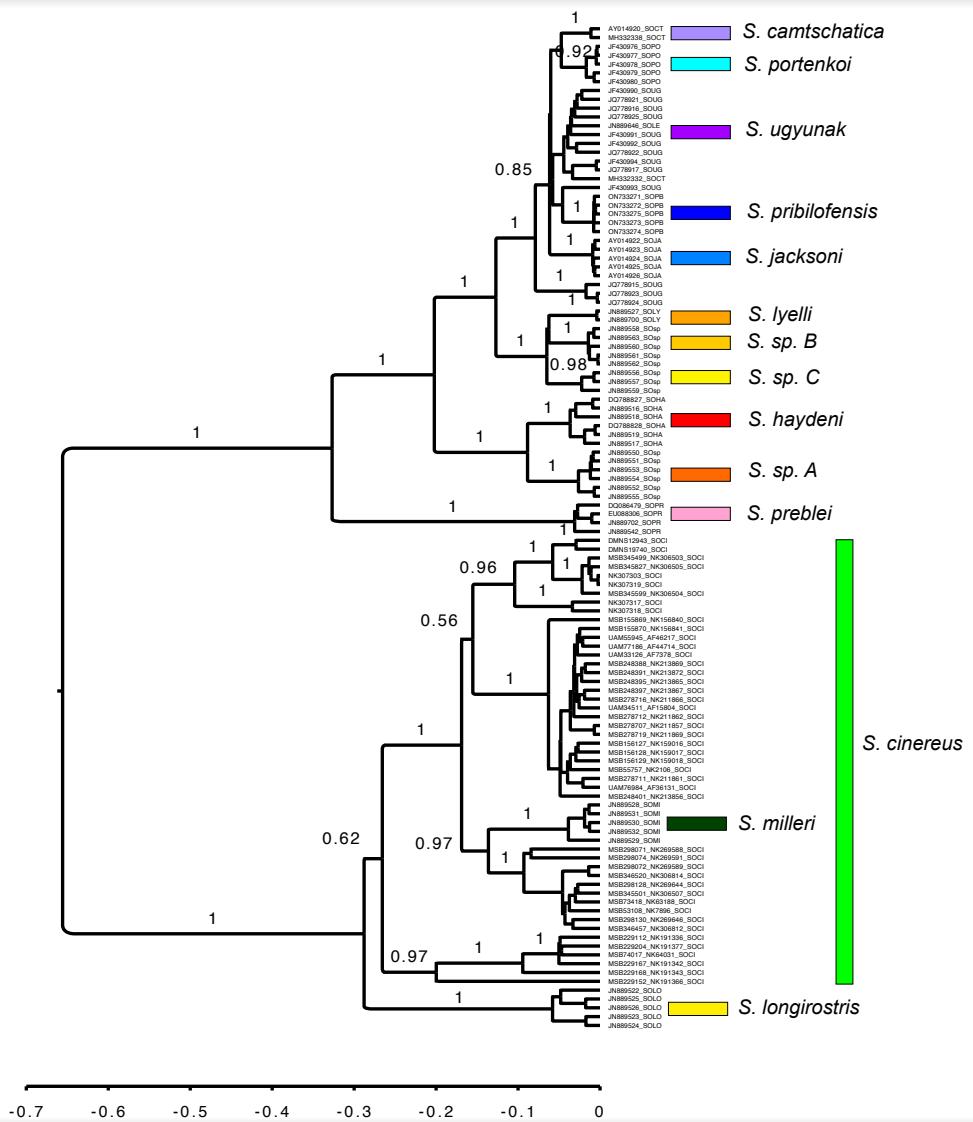
- Assess species limits with data from genomic subsampling
 - Qualify current taxonomy
 - mtDNA designations vs. ddRADseq
- Investigate hybridization
 - Mitonuclear discordance
 - Intermediate genomic signatures
- Investigate evolutionary history and genomic legacies
 - Phylogeography
 - Conservation
- Overcome issues of complexity
 - Develop framework for implementing with other species complexes

Methods

- ~700 samples genotyped for mtDNA cytochrome b
 - All nominal taxa except *S. emarginatus*
- ~400 sequenced using ddRADseq
 - 8 described species and other taxa
 - 5,000-12,000 SNPs depending on group and analysis
- Analyses (ongoing)
 - Phylogeny reconstructions
 - Clustering analyses
 - Genomic diversity

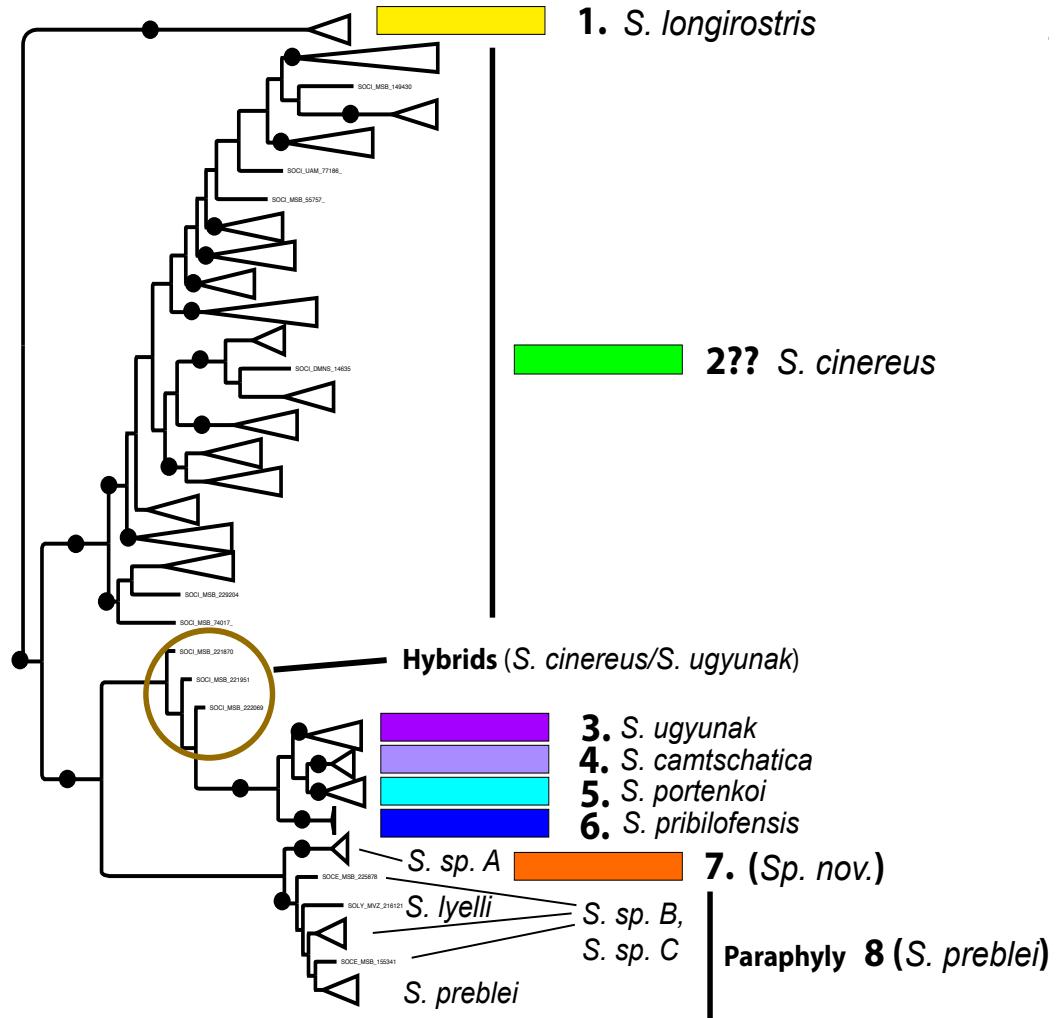
mtDNA tree

- 2 clades
- No consistent reciprocal monophyly between recognized species
- Lots of paraphyly and polyphyly
- Lots of undescribed diversity
- Huge amounts of diversity within *S. cinereus* compared with other species



SNP tree

- 4 primary monophyletic clades
 - *S. longirostris*
 - *S. cinereus*
 - High-latitude Beringian
 - Low-latitude Beringian
- Well-supported monophyly among northern species
- Poorly differentiated southern species
- A few hybrids

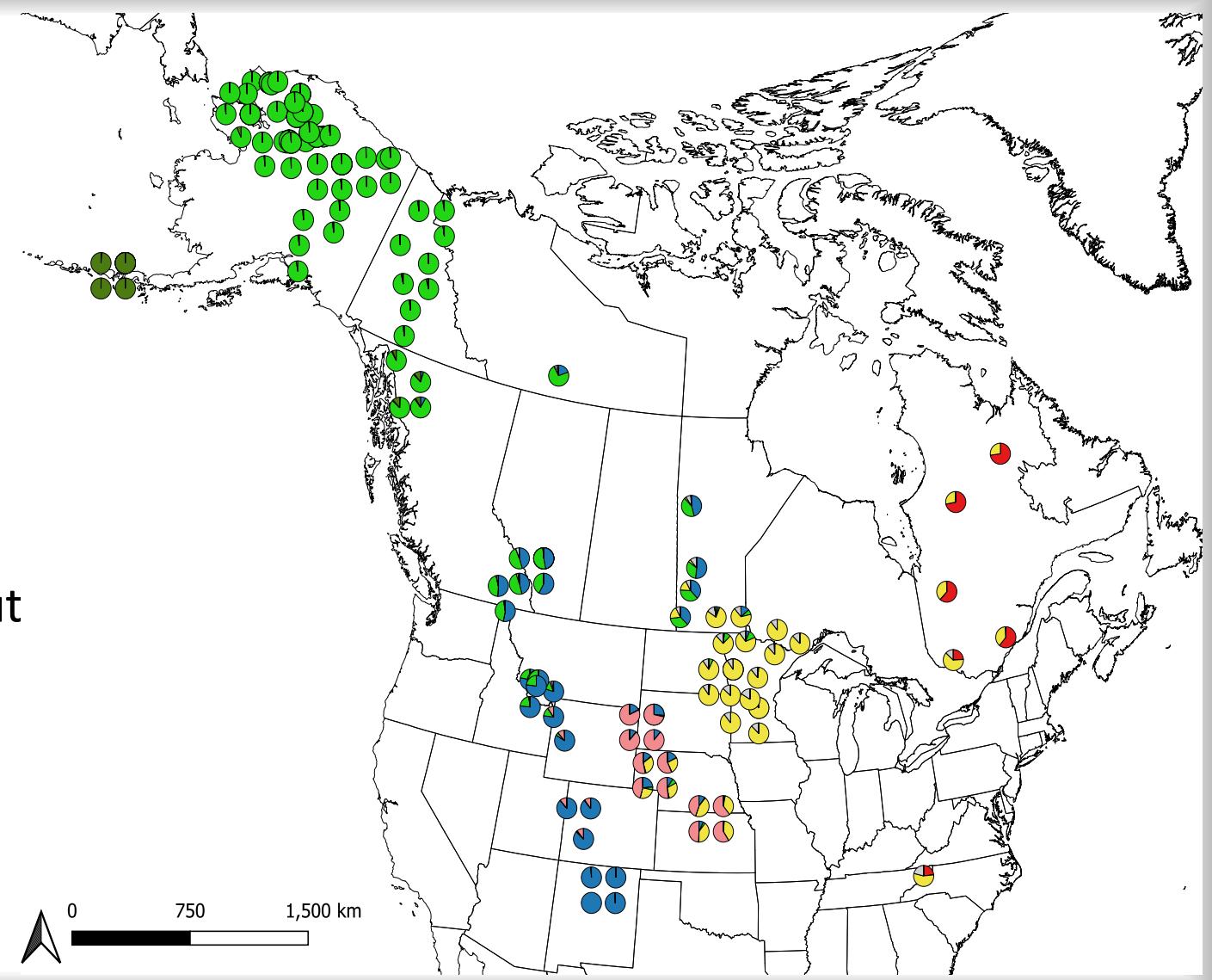


Hybridization between species

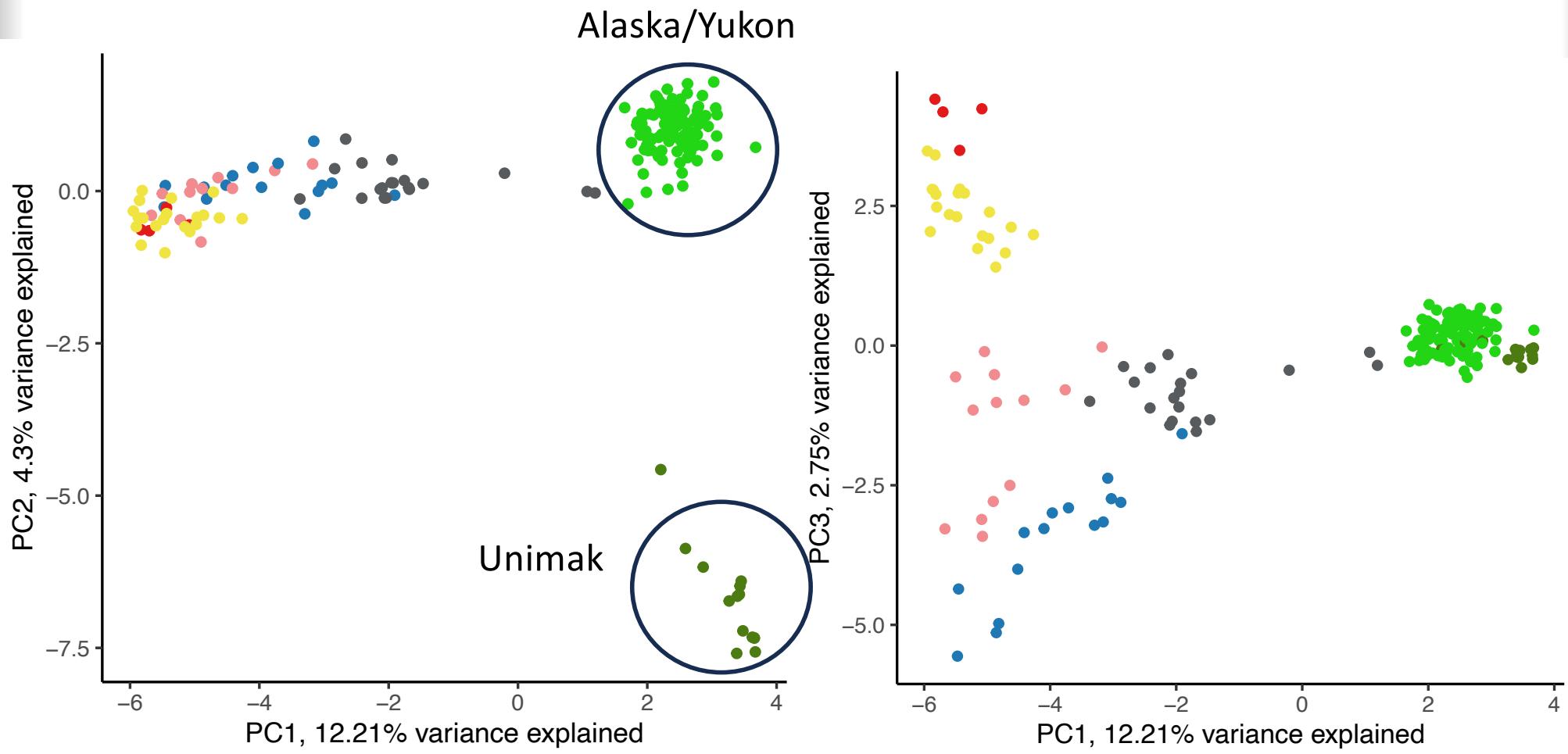
- Northern Alaska (*S. cinereus* and *S. ugyunak*)
 - Very few hybrids
 - All early generation (F2)
 - No evidence of mito-nuclear discordance
- Great Plains (*S. cinereus* and *S. haydeni*)
 - All samples thought to be *S. haydeni* were actually *S. cinereus*
 - No evidence of mito-nuclear discordance
- Jemez Mtns taxon
 - Seemingly unique based on all evidence to date

Phylogeography of *S. cinereus*

- Very few distinct populations
 - Alaska/Yukon
 - Unimak Island, AK
 - New Mexico
- Regional lineages but lots of gene flow
- Strong isolation by distance



Phylogeography of *S. cinereus* – Beringian refugium?



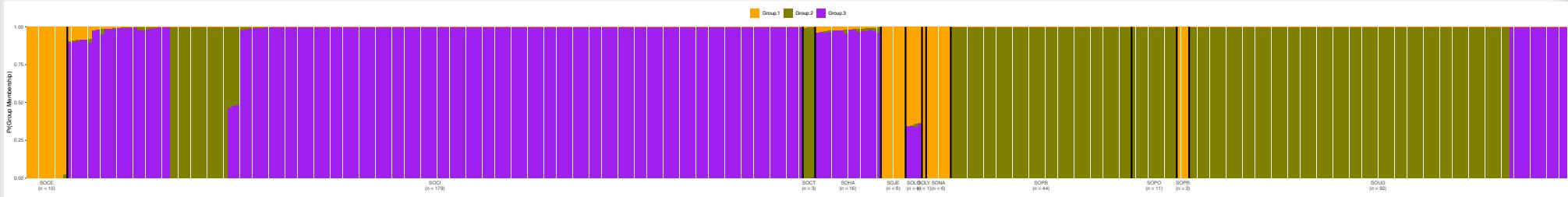
How do we delimit species within complexes?

- Sample comprehensively through space and time
- Use a combination of ecological and evolutionary knowledge
- Use mtDNA only as supporting evidence for genomic legacies
- Assess dynamics of gene flow
- Identify major genomic groups/clades
- Look for reciprocal monophyly in conjunction with statistically discrete clusters
- Diagnose species

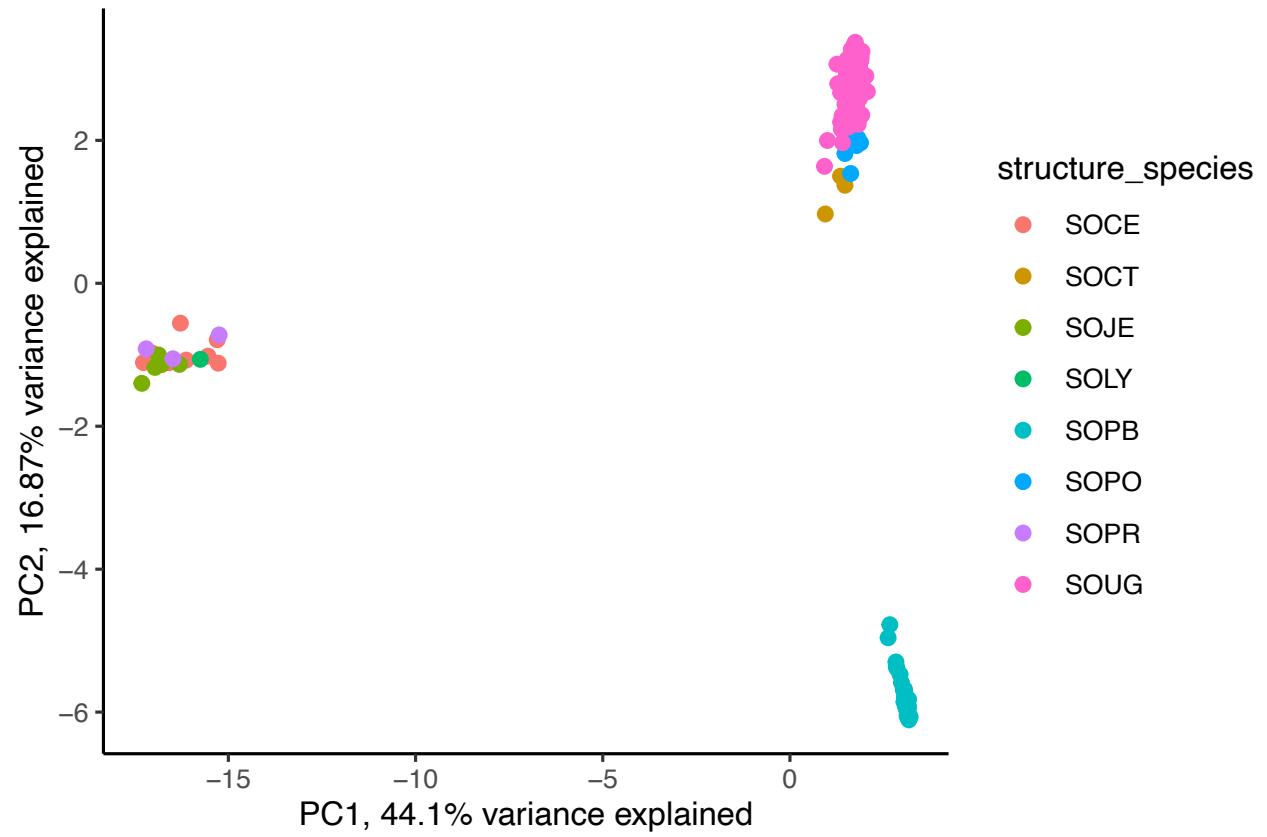
noun: **complex**

/,käm'pleks, kəm'pleks, 'käm,pleks/

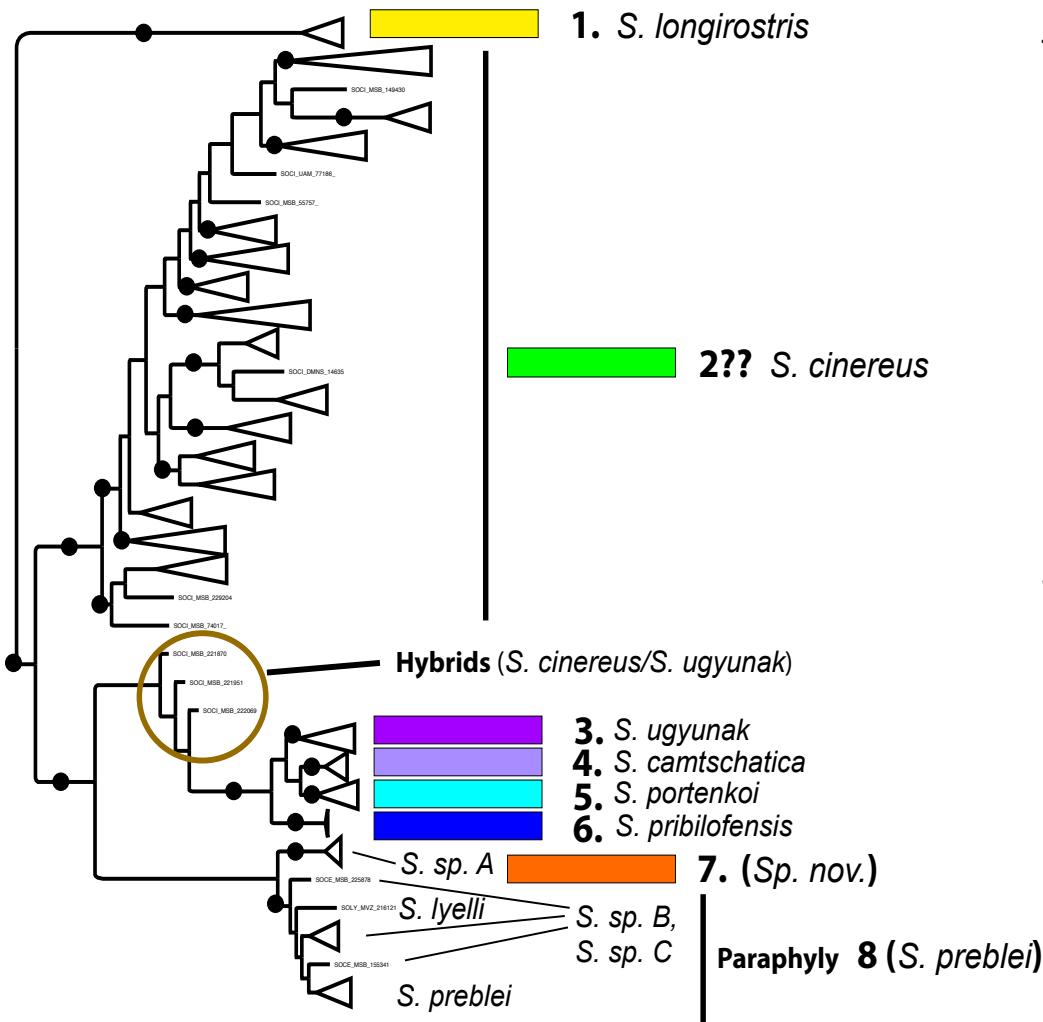
1. a group or system of **different things** that are linked in a close or complicated way.



- Without refining focal groups before delimiting species, it is difficult to resolve potentially diagnosable taxa



Conclusions



To Be Determined:

S. milleri
S. emarginatus
S. jacksoni
S. leucogaster
S. haydeni

No Good Samples

At least one new species:
San Juan Mtns. (NM/CO)

Subsumed taxa:

S. preblei should include:
S. lyelli
S. sp. B
S. sp. C
(All intermountain west)