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Research poster: Quaternary biogeography of Neotoma cinerea: Linking genetic patterns with environmental change

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Quaternary biogeography of *Neotoma cinerea*: Linking genetic patterns with environmental change

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① Introduction

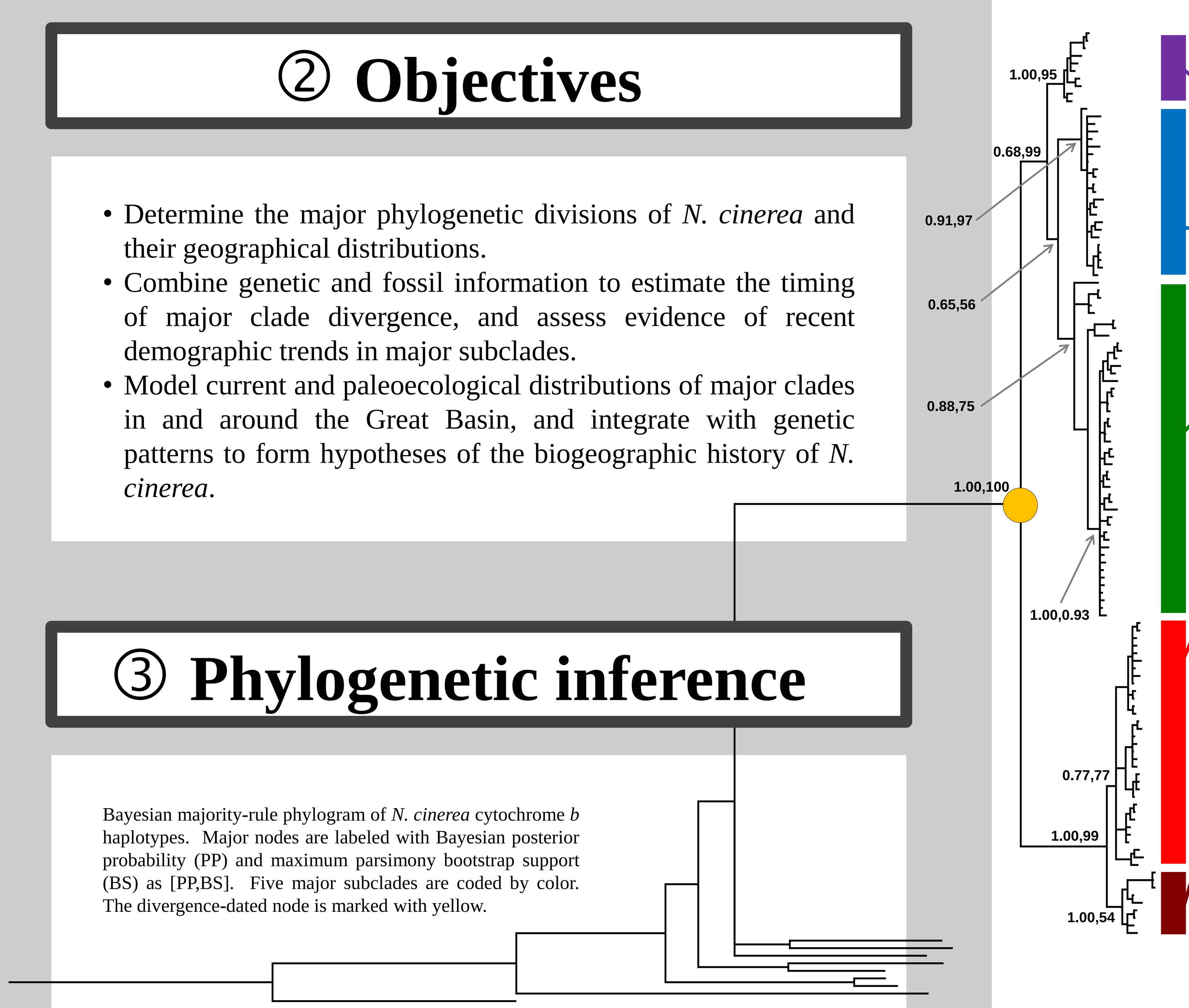
Our understanding of the development and maintenance of phylogeographical structure is aided by integrating information from genetics, subfossil assemblages, and models of ecological niche distributions through the late Quaternary. The bushy-tailed woodrat, *Neotoma cinerea*, offers an interesting study case for several reasons:

- Molecular work in *Neotoma* has prompted the elevation of several groups to species status in recent years; given the wide ranges of occupied environments and morphological variation in this species, it is plausible that divisions in *N. cinerea* are similarly deeper than currently reflected by taxonomy.
- Parts of the current *N. cinerea* range were previously restricted by Pleistocene glaciers and pluvial lakes, offering the potential for different regional histories and patterns of colonization since the last glacial maximum *ca.* 21,000 years ago (21 ka).
- Subfossil paleomidden assemblages have provided extensive historical information for numerous taxa; as one of the primary builders of these middens, *N. cinerea* has an almost unparalleled Quaternary record which has made it a model organism for investigating species' reactions to past climate change[1] and has helped form and assess hypotheses regarding Great Basin biogeographic history[2,3].

② Objectives

- Determine the major phylogenetic divisions of *N. cinerea* and their geographical distributions.
- Combine genetic and fossil information to estimate the timing of major clade divergence, and assess evidence of recent demographic trends in major subclades.
- Model current and paleoecological distributions of major clades in and around the Great Basin, and integrate with genetic patterns to form hypotheses of the biogeographic history of *N. cinerea*.

③ Phylogenetic inference



Bayesian majority-rule phylogram of *N. cinerea* cytochrome *b* haplotypes. Major nodes are labeled with Bayesian posterior probability (PP) and maximum parsimony bootstrap support (BS) as [PP,BS]. Five major subclades are coded by color. The divergence-dated node is marked with yellow.

Methods

We reconstructed phylogenetic relationships using complete mitochondrial cytochrome *b* sequences (1,143 bp). Bayesian inference with the GTR+I+Γ model was performed in MrBayes v3.1.2 through 2 runs of 4 chains with 5,000,000 generations, and a heuristic maximum parsimony search was performed in MEGA v4.1 with 1,000 bootstraps.

Results

Reconstructions of 120 unique haplotypes representing 182 specimens yielded largely consistent topologies including 2 major clades and 5 subclades. Average uncorrected sequence difference between the 2 major clades was 6.5% (max = 7.6%, min = 5.4%) while distances within averaged East: 1.7% (max = 3.5%) and West: 2.6% (max = 4.6%).

④ Genetic patterns

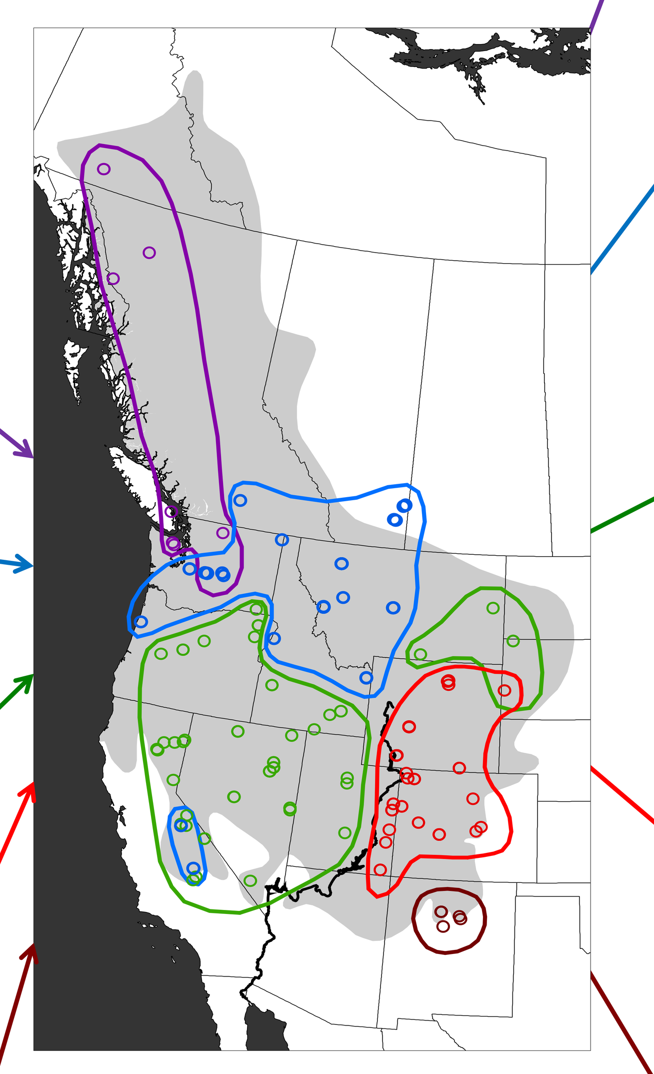
Divergence dating

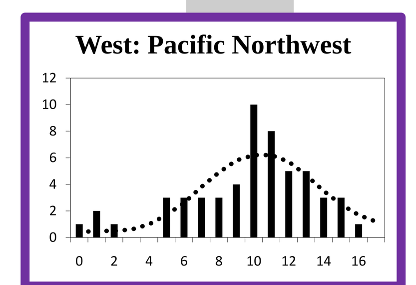
Methods

We estimated divergence time of the 2 major clades using BEAST v1.4.8. Unique *N. cinerea* haplotypes and Cricetid outgroup taxa were analyzed assuming the GTR+I+Γ model, an intraspecific tree prior, and uncorrelated lognormal clock. Tribe Neotomini (woodrats and relatives in genera *Neotoma*, *Hodomys*, and *Xenomys*) was restricted to monophyly with a uniform divergence age prior of 6.6 +/- 0.8 million years ago (Ma) representing the oldest known woodrat fossil[4].

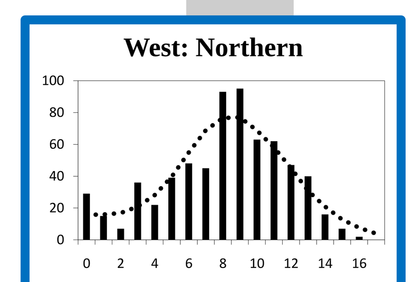
Results

The divergence time between the 2 major clades was estimated at a mean 1.82 Ma with a 95% highest posterior density interval of 1.29 to 2.37 Ma.

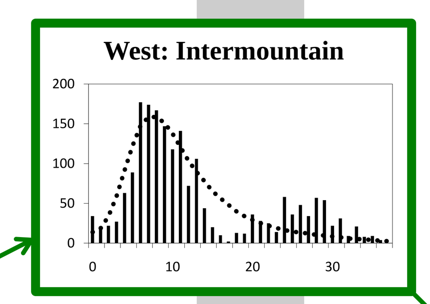




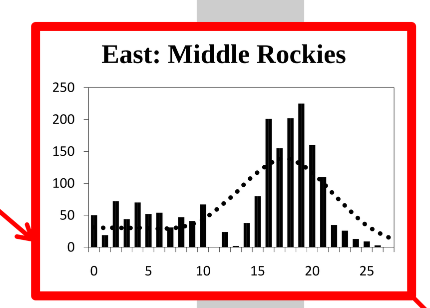
D = -0.51741, P = 0.325
F_S = -2.31281, P = 0.093
Mismatch P = 0.676



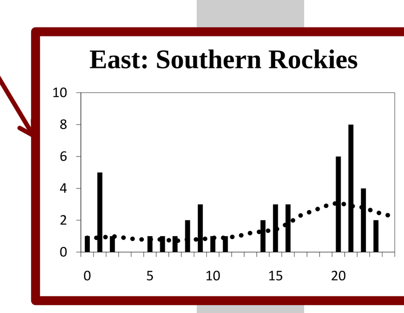
D = -1.86993, $\mathbf{P = 0.01}$
F_S = -6.55849, $\mathbf{P = 0.015}$
Mismatch P = 0.454



D = -1.8363, $\mathbf{P = 0.008}$
F_S = -19.84677, $\mathbf{P = 0.000}$
Mismatch P = 0.676



D = -0.53463, P = 0.309
F_S = -4.71952, P = 0.112
Mismatch $\mathbf{P = 0.026}$



D = 0.2208, P = 0.641
F_S = -0.87122, P = 0.259
Mismatch P = 0.120

Above: Distribution of the 5 major subclades, coded by color. Open circles show collection locations of tissues used for analyses, and heavy lines delineate subclade ranges. The current distribution of *N. cinerea* is shaded gray, and the Green and Colorado Rivers are shown as a heavy black line.

Right: Mismatch distributions and demographic test outcomes. X-axes show the number of differences in pairwise sequence comparisons, and y-axes show frequency. Bars represent observed data and dotted lines represent the expectations of the null expansion model. Significant outcomes of D, F_S, and mismatch analyses are bolded.

Demographic tests

Methods

We performed 3 tests in Arlequin 3.1.1 to assess evidence of recent population expansion: Tajima's D, Fu's F_S with 1,000 simulated samples, and mismatch distribution analyses with 500 bootstraps These tests were conducted for each of the 5 major subclades.

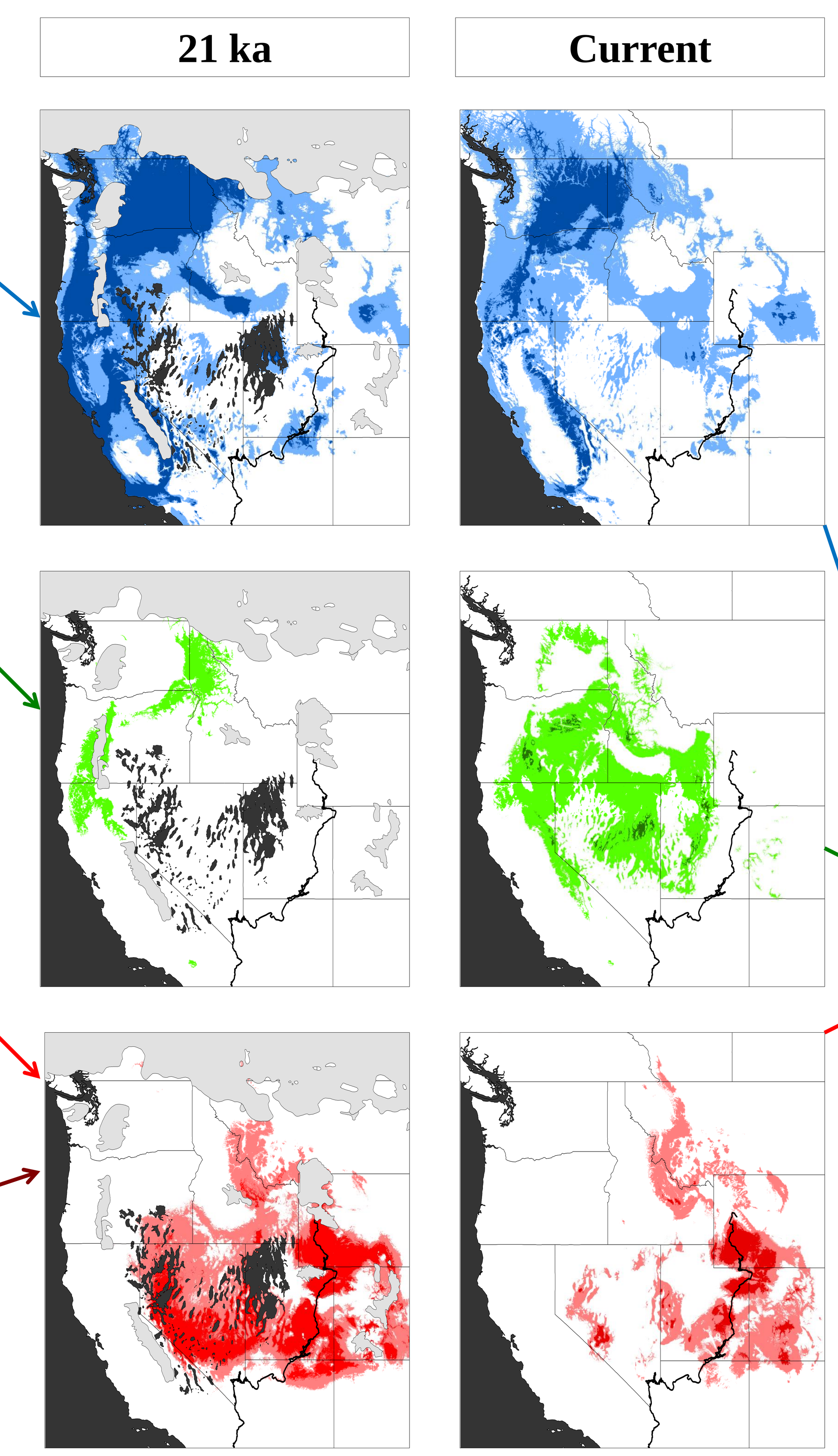
Results

Significant negative values of D and F_S for the Northern and Intermountain subclades indicate recent population expansion, supported by non-significant deviations from the mismatch distribution null model of population expansion. In contrast, the Middle Rockies distribution differed significantly from the null, indicating population stability or contraction.

⑤ Ecological niche modeling

Methods

We used 30 arc-second resolution grid files for 19 bioclimatic variables representing current (WorldClim[5]) and 21 ka (ECHAM3[6]) time periods. *Neotoma cinerea* records were acquired through MaNIS, Arctos, and individual museum databases, and clade identities were determined genetically or by proximity to characterized samples. Bioclimatic values were checked for correlation and discarded until no relationships exceeded R^2 = 0.7. Models of the current ecological niche distribution were developed in Maxent[7] v3.3.1 and projected onto the 21 ka climate grids.



Ecological niche models for 3 clades and subclades at 21 ka and current time periods. Dark coloration shows high probability of habitation (75-100%), and light coloration shows moderate probability (50-75%). Pluvial lakes are shown in dark gray, Pleistocene glaciers are shown in light gray, and the Green and Colorado Rivers are shown as a heavy black line.

Results

Models of the species-wide current and 21 ka niche distributions (not shown) were largely consistent with previous modeling efforts[3]. This study further introduced models specific to clades and subclades, which showed marked differences. For instance, the Intermountain subclade appears to have greatly expanded its predicted niche area over time, particularly in the Great Basin, while the Eastern clade area appears to have contracted severely in the same region.

⑥ Conclusions

The estimated divergence time of the 2 major *N. cinerea* clades is consistent with the onset of the Pleistocene glacial epoch *ca.* 1.8 Ma. The current phylogeographical distribution additionally suggests that the Green and Colorado Rivers may be sufficient barriers to dispersal. Only one point of sympatry (western South Dakota) was detected between the 2 major clades, likely representing a secondary contact zone.

Despite the Eastern clade's wide predicted niche area in the Great Basin at 21 ka, this group may have never inhabited this region due to river barriers. Great Basin populations of *N. cinerea* may instead have been comprised of Northern clade members in the late Pleistocene, and later Intermountain clade members in the Holocene. This potentially recent colonization of the Great Basin by the Intermountain clade is supported by strong demographic evidence suggesting population expansion.

Reasons for potential clade replacement are speculative but may be related to hypothesized local extinctions in the arid mid-Holocene[2]. The Northern clade may have been supplanted by the Intermountain clade through chance, competition, or otherwise; whether, when, and why this occurred has yet to be determined, but hold implications for understanding the reaction of this species to past and future climate changes.

⑦ Future work

Hundreds of paleomiddens have been collected and characterized through the efforts of other researchers. It may be possible to analyze ancient DNA from the copious fecal material or bones, which would allow us to describe chronological phylogenetic patterns in the Great Basin and test new hypotheses of the habitation and colonization of *N. cinerea* clades through periods of past climate change.

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