

Phylogeny and biogeography of an endemic Madagascar rodent

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Background

Understanding regional biodiversity and its causes is a key goal of evolutionary biology, and the island of Madagascar is an ideal setting in which to test hypotheses surrounding diversification. With 12 described species, *Eliurus* is the most species-rich group of rodents in Madagascar, but monophyly of the genus with respect to *Voalavo* has not been established. Species in this clade are widely distributed across the island and occur in both seasonal dry forests and evergreen humid forests. Here, we present a phylogeographic analysis of the group to test whether speciation occurs within habitat zones or accompanies migration between zones. Previous studies have focused primarily on morphological characters to distinguish taxa (1,2); here we use molecular data to reconstruct a phylogenetic tree of the genus. We sequenced five loci from multiple representatives of each species, and we compare their relative utility in reconstructing the phylogeny of these species. We inferred a final tree from all five genes and optimized habitat preference along this tree to test patterns of speciation with respect to habitat type.

Figure 2. Habitat evolution of *Eliurus*. (a) The species tree on the left depicts current and inferred ancestral states of habitat preference for each species sampled. Nodal support values are Bayesian posterior probabilities (5). Grey bars indicate error concerning the relative timing of each speciation event. Yellow lines indicate dry deciduous forest preference while green lines represent humid evergreen forest preference. Colors are matched to (b) the locality map of Madagascar on the right, where yellow also indicates dry forest, and green indicates humid forest. Red dots on the map indicate localities where individuals for this project were sampled. Elevation is depicted in grayscale: darker colors are higher elevation.

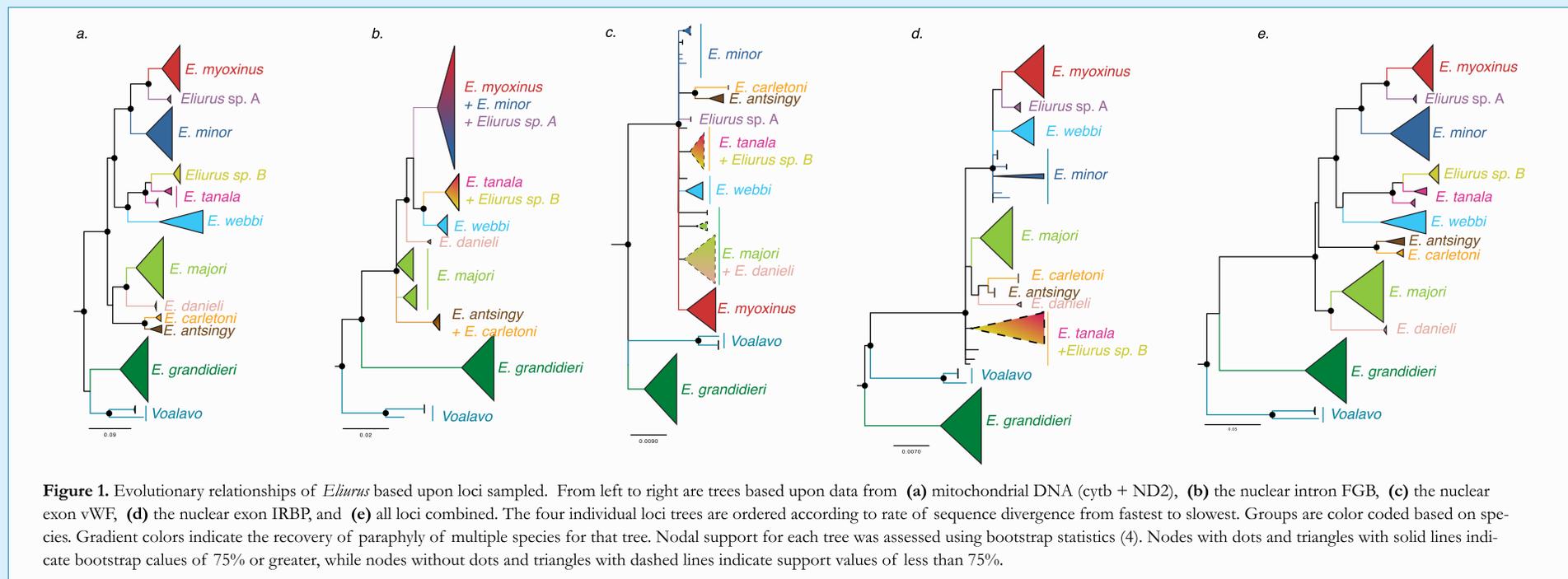
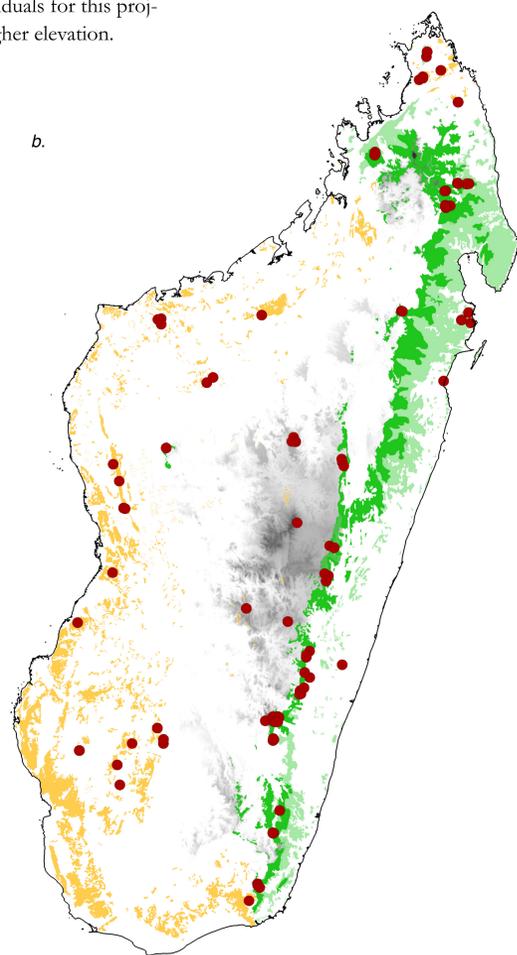
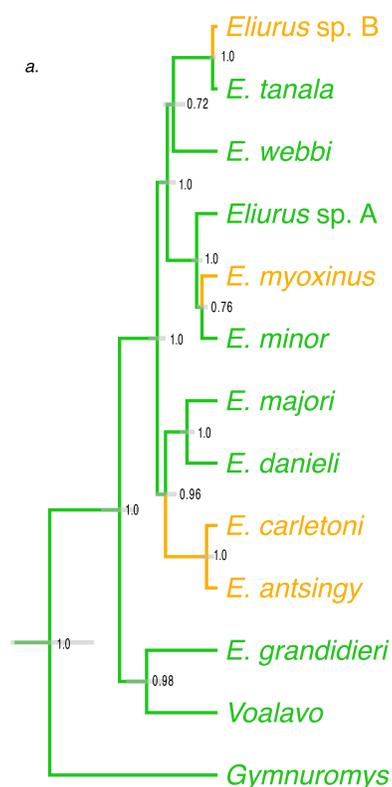


Figure 1. Evolutionary relationships of *Eliurus* based upon loci sampled. From left to right are trees based upon data from (a) mitochondrial DNA (cytb + ND2), (b) the nuclear intron FGB, (c) the nuclear exon vWF, (d) the nuclear exon IRBP, and (e) all loci combined. The four individual loci trees are ordered according to rate of sequence divergence from fastest to slowest. Groups are color coded based on species. Gradient colors indicate the recovery of paraphyly of multiple species for that tree. Nodal support for each tree was assessed using bootstrap statistics (4). Nodes with dots and triangles with solid lines indicate bootstrap values of 75% or greater, while nodes without dots and triangles with dashed lines indicate support values of less than 75%.

Methods

We PCR amplified and sequenced 5 loci for 101 individuals of the genera *Eliurus* and *Voalavo* using methods described in (6). The loci include two nuclear exons (vWF & IRBP), one nuclear intron (FGB), and protein-coding sequences from two mitochondrial genes (ND2 & cytb). Resulting sequences were aligned to each other, and gene trees were inferred using maximum likelihood (3). Loci were concatenated to infer a phylogeny based on information contained in all loci. Habitat diversification patterns were determined by mapping current habitat states onto a species tree and inferring ancestral states, and subsequently determining points of habitat change.

Literature Cited

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Results & Conclusions

Of note in Figure 1 are the different degrees of phylogenetic resolution and support provided by the individual loci. The mitochondrial genes recover (1) monophyly of each species, and (2) a fully resolved phylogeny among species with high bootstrap support at almost all nodes. In contrast, the nuclear genes do not always recover species monophyly, and some species relationships differ among these trees. This is expected as different genes have different evolutionary histories, and mitochondrial genes should, on average, coalesce more rapidly than nuclear genes. Nevertheless, a combined-gene analysis (Figure 1e) recovers a well-resolved, mostly well-supported phylogeny describing relationships among these species. However, despite >5000bp of sequence data, this analysis fails to convincingly resolve whether *Voalavo* and *Eliurus* are reciprocally monophyletic.

In contrast, a species-tree analysis (Figure 2) provides strong support for a non-monophyletic *Eliurus*, because *E. grandidieri* and *Voalavo* are sister taxa. This analysis accounts for different evolutionary histories of the different loci and can be considered the best estimate of phylogenetic relationships among these species. Optimization of habitat type on this phylogeny (Figure 2) suggests that the group originated in humid, evergreen forest and dispersed at least three different times to dry, deciduous forests. This suggests that most speciation in *Eliurus* has occurred in the eastern mountainous regions that contain the island's humid forests, and that dry-forest communities of the western lowlands have been assembled by dispersal rather than *in situ* speciation.