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Single-locus species delimitation: a test of the mixed Yule–coalescent model, with an empirical application to Philippine round-leaf bats

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Prospects for a comprehensive inventory of global biodiversity would be greatly improved by automating methods of species delimitation. The general mixed Yule–coalescent (GMYC) was recently proposed as a potential means of increasing the rate of biodiversity exploration. We tested this method with simulated data and applied it to a group of poorly known bats (*Hipposideros*) from the Philippines. We then used echolocation call characteristics to evaluate the plausibility of species boundaries suggested by GMYC. In our simulations, GMYC performed relatively well (errors in estimated species diversity less than 25%) when the product of the haploid effective population size (N_e) and speciation rate (SR; per lineage per million years) was less than or equal to 10^3 , while interspecific variation in N_e was twofold or less. However, at higher but also biologically relevant values of $N_e \times SR$ and when N_e varied tenfold among species, performance was very poor. GMYC analyses of mitochondrial DNA sequences from Philippine *Hipposideros* suggest actual diversity may be approximately twice the current estimate, and available echolocation call data are mostly consistent with GMYC delimitations. In conclusion, we consider the GMYC model useful under some conditions, but additional information on N_e , SR and/or corroboration from independent character data are needed to allow meaningful interpretation of results.

Keywords: biodiversity discovery; cryptic species; echolocation; *Hipposideros*; species delimitation; taxonomy

1. INTRODUCTION

Achieving a taxonomy that reflects evolutionary history is critical for effective conservation [1], projecting responses of biodiversity to climate change [2], and illuminating the underlying evolutionary and ecological forces that generate biotic communities [3,4]. Thus, rapid and accurate methods of species delimitation are urgently needed to expedite biodiversity discovery and documentation [5,6]. Recently, new species delimitation methods have been developed that are relatively automated and take advantage of DNA sequence datasets [7–10]. These methods offer the promise of making species delimitation both more efficient and less subjective. One example is the general mixed Yule–coalescent (GMYC) [7] that uses maximum-likelihood statistics and a time-calibrated gene tree to delimit species. GMYC analyses typically involve the collection of DNA sequences from a single locus (often mitochondrial) for a sample of closely related organisms. An ultrametric phylogeny is estimated from

the sequences, and the GMYC aims to identify a time in the tree when the branching rate shifts (in forward time) from a Yule (species) to a coalescent (population) process. The GMYC originally estimated the time of a single threshold [7], but was later extended to allow independent transition times on different branches of the phylogeny [11]. GMYC has been used to delimit species in several poorly known groups of organisms [11–14], but few studies have tested its efficacy using either simulated data or by analysing clades with well-established species boundaries. Two studies have explored GMYC performance in the context of an island system, focusing on the effects of migration and sampling density [15,16]. However, a more general test of GMYC on gene trees simulated under a range of biologically relevant conditions has not been undertaken.

Here, we assess GMYC performance using simulated data, and apply the same method to an empirical system from the Philippines: round-leaf bats of the genus *Hipposideros*. The Philippine archipelago is an astounding centre of biodiversity with nearly 1200 species of terrestrial vertebrates [17]. Many new species have been described recently [18–21], and an unknown portion of the country's biodiversity may be threatened with extinction before it is discovered [22]. Several recent phylogeographic studies of Philippine vertebrates

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