Gene flow creates a mirage of cryptic species in a Southeast Asian spotted stream frog complex

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Abstract

Most new cryptic species are described using conventional tree- and distance-based species delimitation methods (SDMs), which rely on phylogenetic arrangements and measures of genetic divergence. However, although numerous factors such as population structure and gene flow are known to confound phylogenetic inference and species delimitation, the influence of these processes is not frequently evaluated. Using large numbers of exons, introns, and ultraconserved elements obtained using the FrogCap sequence-capture protocol, we compared conventional SDMs with more robust genomic analyses that assess population structure and gene flow to characterize species boundaries in a Southeast Asian frog complex (Pulchrana picturata). Our results showed that gene flow and introgression can produce phylogenetic patterns and levels of divergence that resemble distinct species (up to 10% divergence in mitochondrial DNA). Hybrid populations were inferred as independent (singleton) clades that were highly divergent from adjacent populations (7%-10%) and unusually similar (<3%) to allopatric populations. Such anomalous patterns are not uncommon in Southeast Asian amphibians, which brings into question whether the high levels of cryptic diversity observed in other amphibian groups reflect distinct cryptic species-or, instead, highly admixed and structured metapopulation lineages. Our results also provide an alternative explanation to the conundrum of divergent (sometimes nonsister) sympatric lineages-a pattern that has been celebrated as indicative of true cryptic speciation. Based on these findings, we recommend that species delimitation of continuously distributed "cryptic" groups should not rely solely on conventional SDMs, but should necessarily examine population structure and gene flow to avoid taxonomic inflation.

KEYWORDS

FrogCap, gene flow, hybridization, HYDE, phylogenetic network, PHYLONET, population genetics

1 | INTRODUCTION

Species delimitation plays a pivotal role in biodiversity research, with potential cascading effects in conservation and other applied sciences (Devitt, Wright, Cannatella, & Hillis, 2019; Stanton et al., 2019).

While lineages that are obviously distinct can be easily diagnosed, the delimitation of cryptic species can be controversial. The rise in cryptic species discoveries has largely been driven by the expansive use of molecular data and new methods for analyses of increasingly large data sets, which have enabled us to elucidate genetic structure at an