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Short Communication

Archipelago colonization by ecologically dissimilar amphibians: Evaluating the expectation of common evolutionary history of geographical diffusion in co-distributed rainforest tree frogs in islands of Southeast Asia



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ABSTRACT

Widespread, co-distributed species with limited relative dispersal abilities represent compelling focal taxa for comparative phylogeography. Forest vertebrates in island archipelagos often exhibit pronounced population structure resulting from limited dispersal abilities or capacity to overcome marine barriers to dispersal. The exceptionally diverse Old World tree frogs of the family Rhacophoridae have colonized the forested island archipelagos of Southeast Asia on multiple occasions, entering the islands of Indonesia and the Philippines via a “stepping stone” mode of dispersal along elongate island chains, separated by a series of marine channels. Here we evaluate the prediction that two tightly co-distributed Philippine rhacophorids colonized the archipelago during concomitant timescales and in the same, linear, “island-hopping” progression. We use a new multilocus dataset, utilize dense genetic sampling from the eastern arc of the Philippines, and we take a model-based phylogeographic approach to examining the two species for similar topological patterns of diversification, genetic structure, and timescales of diversification. Our results support some common mechanistic predictions (a general south-to-north polarity of colonization) but not others (timescale for colonization and manner and degree of lineage diversification), suggesting differing biogeographic scenarios of geographical diffusion through the archipelago and unique and idiosyncratic ecological capacities and evolutionary histories of each species.

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1. Introduction

Understanding of the evolutionary and biogeographic processes that have facilitated colonization of island archipelagos is of fundamental interest to biodiversity specialists focused on the global conservation hotspots of Southeast Asia and the Pacific (Lohman et al., 2011; Brown et al., 2013), where rates of forest destruction has been higher than anywhere else in the world (Whitmore and Sayer, 1992; Brooks et al., 2002). In the Philippine biodiversity hotspot, high levels of land vertebrate diversity and soaring rates of

endemism (Brown and Diesmos, 2009) have fueled the search for common mechanisms of diversification, and piqued biogeographers' interest in population substructuring, evolutionary partitioning, and maintenance of biodiversity (Evans et al., 2003; Esselstyn and Brown, 2009; Oaks et al., 2013; Brown et al., 2013). Although the application of molecular data and rigorous statistical tools has greatly enhanced biogeographers' ability to address questions of diversification in a hypothesis-testing framework (Oaks et al., 2013; Brown et al., 2013), these efforts have been hampered by a lack of comprehensive biodiversity surveys, logistical obstacles to field work, and a prevailing focus on fine-scale patterns of diversification associated with widespread microendemism (Brown and Diesmos, 2009; Brown et al., 2013). As a result, biogeographers have only recently begun to identify more widespread, co-distributed groups of species, suitable for hypothesis-testing with a multi-taxon approach (Roberts, 2006; Esselstyn et al., 2010; Siler et al., 2010; Brown et al., 2010; Oaks et al., 2013).

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One group of amphibians intimately tied to the geographical template as a result of their variable natural history and ecological tolerances are the Old World tree frogs of the family Rhacophoridae (Brown and Alcalá, 1994; Li et al., 2013). Two such unrelated species, *Kurixalus appendiculatus* and *Rhacophorus bimaculatus* are widely (but patchily) distributed throughout the eastern island arc of the Philippines (Brown and Alcalá, 1970, 1994), with separate origins in the Philippines via presumed colonization from the islands of the Sunda Shelf (e.g., Borneo; Li et al., 2013; Yu et al., 2013). *Kurixalus appendiculatus* is a forest floor, stagnant ephemeral pool or swamp-breeding species, and *R. bimaculatus* is a streamside vegetation-inhabiting species (Inger, 1954; Brown and Alcalá, 1994) most commonly encountered perched in vegetation above spray zones and high-gradient cascading waterfalls (RMB, personal observation). *Rhacophorus bimaculatus* exhibits vegetation-suspended larval development via foam-nest construction; the reproductive biology and larval ontogeny of Philippine populations of *K. appendiculatus* have not been well studied (Alcalá and Brown, 1982; Brown and Alcalá, 1994). Because of their differing ecological and life-history strategies and their partially co-distributed ranges (overlapping five or six major hypothesized barriers to dispersal; Fig. 1), we were motivated to evaluate the prediction that they share a common history of archipelago colonization and similar evolutionary consequences of dispersal and isolation, possibly within similar timescales for diversification. Although other studies have shown species-specific individual colonization histories (Evans et al., 2003; Brown et al., 2010; Brown and Siler, 2013) the near-perfect co-distributed known occurrences of these

two species (Brown and Alcalá, 1994) along the eastern Philippine island arc lays the foundation for a simple biogeographic prediction of concomitant pattern and history of colonization, which can be tested phylogeny.

Our surprising results are consistent with the prediction of similar initial routes of colonization in both taxa (entryway into the Southwestern portions of the archipelago, presumably via colonization from the Sunda Shelf island of Borneo via the elongate Sulu Archipelago, and a general south-to-north diffusion into the remaining Philippines), emphasizing the linear nature of the Philippines' eastern island arc, but include exceptions to the pure expectation of stepwise colonization. Additionally, pronounced phylogeographic and population-genetic differences among populations of both taxa suggest different colonization histories and disparate patterns of geographically based genetic variation, consistent with variable natural history and microhabitat preferences of each respective species.

2. Materials and methods

2.1. Taxon sampling and data collection

Sampling included individuals collected over the past two decades from localities throughout the eastern island arc of the Philippines in an effort to target sampling from extreme southwestern Mindanao (adjacent to Borneo) to the northern portions of the northern most island of Luzon (Fig. 1; Appendix 1). To

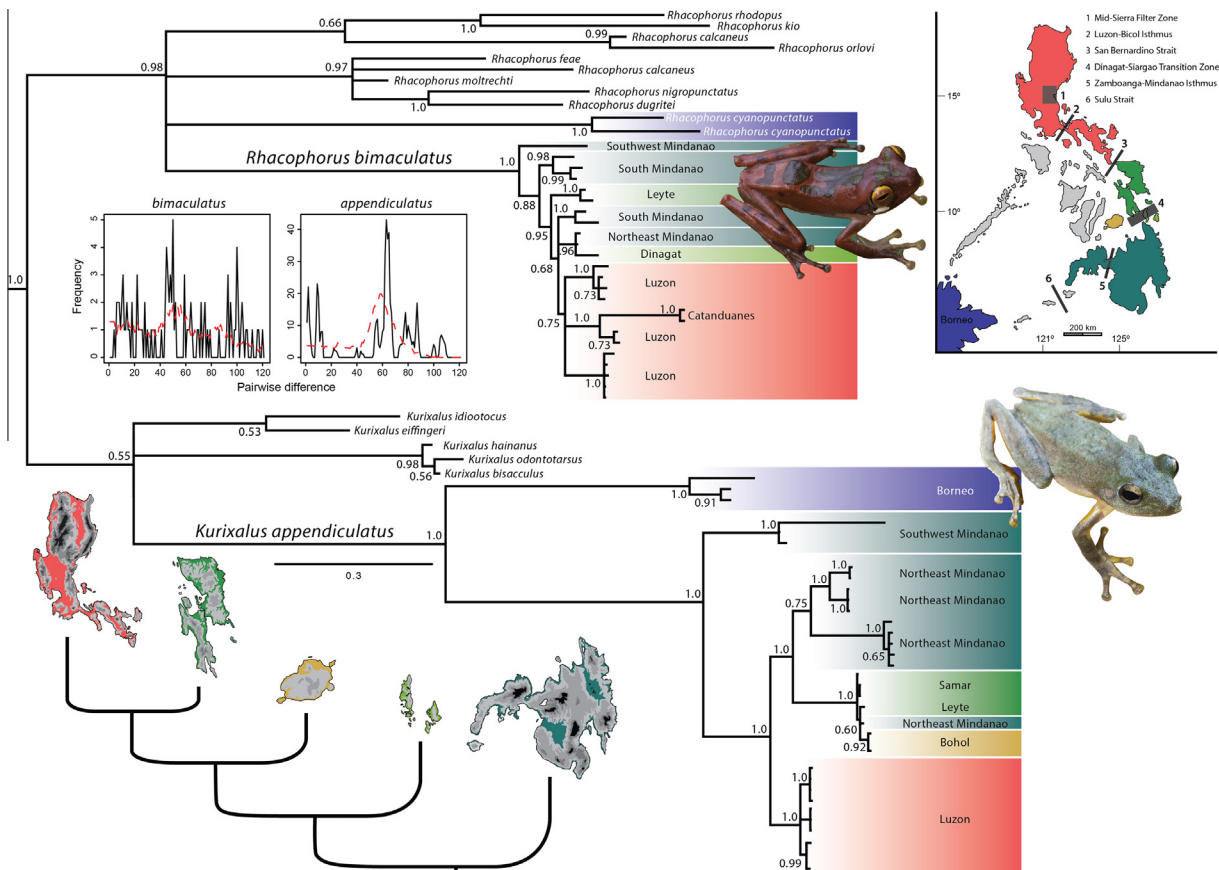


Fig. 1. Hypothesized relationships of rhacophorid frogs related to *R. bimaculatus* and *K. appendiculatus*, illustrated by the maximum clade credibility tree resulting from Bayesian analyses. Nodes supported by ≥ 0.95 Bayesian PP were considered highly supported. Terminals are labeled with taxonomic names of outgroups, and localities within the two focal species. The expected topology stepwise colonization across the eastern arc is depicted at lower left, and a color-coded key to general localities and tree tip labels is presented at upper right, with hypothesized barriers to dispersal indicated for reference; these include: (1) the Mid-Sierra Filter Zone, (2) the Bicol-Luzon Isthmus, (3) the San Bernardino Strait, (4) the Dinagat-Siargao Transition Zone, (5) the Zamboanga-Mindanao Isthmus, and (6) the Sulu Strait.

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