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The natural and human-mediated expansion of a human-commensal lizard into the fringes of Southeast Asia

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Abstract

Background Human-commensal species often display deep ancestral genetic structure within their native range and founder-effects and/or evidence of multiple introductions and admixture in newly established areas. We investigated the phylogeography of *Eutropis multifasciata*, an abundant human-commensal scincid lizard that occurs across Southeast Asia, to determine the extent of its native range and to assess the sources and signatures of human introduction outside of the native range. We sequenced over 350 samples of *E. multifasciata* for the mitochondrial ND2 gene and reanalyzed a previous RADseq population genetic dataset in a phylogenetic framework.

Results Nuclear and mitochondrial trees are concordant and show that *E. multifasciata* has retained high levels of genetic structure across Southeast Asia despite being frequently moved by humans. Lineage boundaries in the native range roughly correspond to several major biogeographic barriers, including Wallace's Line and the Isthmus of Kra. Islands at the outer fringe of the range show evidence of founder-effects and multiple introductions.

Conclusions Most of enormous range of *E. multifasciata* across Southeast Asia is native and it only displays signs of human-introduction or recent expansion along the eastern and northern fringe of its range. There were at least three events of human-introductions to Taiwan and offshore islands, and several oceanic islands in eastern Indonesia show a similar pattern. In Myanmar and Hainan, there is a founder-effect consistent with post-warming expansion after the last glacial maxima or human introduction.

Keywords Phylogeography, Biogeography, Invasive species, Scincidae, Southeast Asia, *Eutropis multifasciata*

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Introduction

Determining the extent of a species' native versus introduced range is often difficult due to lack of records and extreme human modification to landscapes and transportation [1, 2]. Of these so-called cryptogenic species, widespread human-commensals that are good at dispersing both naturally and through human-movements are particularly difficult to decipher [3]. As the introduction of these species can lead to cascading ecological consequences, understanding the native range of species is important to conservation [4]. Phylogeographic and population genetic methods are critical tools to assessing if populations are native versus introduced, but they require comprehensive sampling of range-wide genetic diversity, and different invasion scenarios can lead to very different resulting patterns [5–7]. While single introductions to new areas show a classical founder-effect of extremely low genetic diversity in the new populations, multiple introductions are likely to instead produce high genetic diversity with divergent mitochondrial haplotypes in close proximity and admixture in nuclear DNA [5, 8–11]. Gene flow between introduced divergent lineages can restore genetic diversity to bottlenecked populations and provide the basis for adaptation that can worsen invasions [12–14]. Inside the native range, however, genetic structure is often preserved due to a combination of evolutionary and ecological processes [15–17]. Together these patterns can be used to understand the geographic extent of the native range and important biogeographic forces within it, and to pinpoint introduced populations.

The Many-lined Sun Skink, *Eutropis multifasciata* (Kuhl, 1820), is perhaps the most-commonly encountered diurnal lizard in Southeast Asia and possesses an incredibly large range from Bangladesh [18] through Indonesia [19]. It is an abundant inhabitant of urban areas, human-settlements, and forest edges, and is found from sea level to 1800 m in tropical areas [20] and 500 m at its northern extent in Taiwan [21]. Due to its abundance and relatively simple maintenance in a lab, it has become a model system for studying niche plasticity and thermal physiology, including its relationship with viviparity [21–27]. There are documented introductions to Florida [28, 29], Australia [30], New Guinea [31], and Taiwan (including nearby Luda and Lanyu) [32, 33] due to frequent human-transportation including reports on airport luggage [34], ferries (J. McGuire, pers. obsv.), and international cargo shipments [35]. On Taiwan, Luda, and Lanyu, *E. multifasciata* rapidly invaded and poses a significant conservation threat [32, 36, 37]. We used a geographically comprehensive genetic dataset of *E. multifasciata* to investigate its biogeographic history, the extent of its invasion, and the processes causing

phylogeographic structure to be maintained or eroded. Together, these results can be utilized for conservation management in areas that have been recently invaded.

The phylogeography of *E. multifasciata* has been studied to some extent but still remains poorly understood. Barley et al. [38] investigated the population genomics of *E. multifasciata* with RADseq data, demonstrating that *E. multifasciata* has moderate levels of genome-wide genetic variation. Barley et al. observed higher genetic differentiation on islands relative to the mainland, recovering three Philippine lineages (southern; central/west; northern) and two weakly-differentiated continental populations (Myanmar; remainder of Indochina). They included only a few samples from Sundaland and Wallacea, limiting the scope of the phylogeographic analysis. The Philippine populations could be allied with Borneo, Sulawesi, or Indochina, or divided indicating multiple invasions of the Philippines [39]. Due to its random nature, RADseq data may encompass signatures of local adaptation, and this may be relevant when introduced populations have divergent environmental conditions to the source. For our study, the use of mitochondrial data may provide unique power to elucidate spatial patterns. The genome-wide data provides an interesting backdrop for our study, allowing us to understand the fine-scale mitochondrial structure we uncover given rates of nuclear gene flow estimated by Barley et al.

Since *E. multifasciata* is found in four major biogeographic regions: Indochina, Sundaland, the Philippines, and Wallacea [40], it is an interesting system to investigate how it is impacted by barriers that restrict many other species. We investigate if these regions are part of the native range, and if so, is there genetic structuring associated with the common biogeographic barriers that separate them? Mabuyine skinks are excellent dispersers that have crossed expansive marine barriers to distant islands [41–43], leaving the relative roles of natural vs. human-mediated dispersal in *E. multifasciata* an open question. An early phylogenetic study that included a few *E. multifasciata* samples recovered two major clades: one from Borneo, Myanmar, and China, and another from Java, Bali, Seram, and the Philippines [44], providing some indication that clades in *E. multifasciata* may not follow standard biogeographic area predictions (i.e. the Sunda Shelf not forming a clade). In another study, genetic structure across the Lesser Sunda Archipelago was substantial enough to reflect natural dispersal, and a clade on Bali and Timor was divergent from the remaining Lesser Sundas [19].

With comprehensive geographic sampling from over 350 samples, we investigated the biogeographic history of *E. multifasciata* to understand the extent of its native range and assessed the sources and signatures of human