



Within-island speciation with an exceptional case of distinct separation between two sibling lizard species divided by a narrow stream [☆]



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ARTICLE INFO

Article history:

Received 5 August 2014

Revised 24 February 2015

Accepted 22 April 2015

Available online 14 May 2015

Keywords:

Ancestral range reconstruction

Contact zone

Fine-scale differentiation

Genetic introgression

Hybridisation

Parapatric speciation

ABSTRACT

Delimitation of genetic and geographic boundaries between species is a focus of evolutionary biology. In this study, we demonstrated fine-scale differentiation of *Takydromus formosanus* species complex comprising four insular endemics on Taiwan Island. Phylogeny and ancestral range reconstruction based on mitochondrial DNA sequences of 430 *Takydromus* lizards (405 lizards of this complex throughout their distribution range, and 25 lizards from 11 other species) indicated that the major branching process occurred within Taiwan, which represented a solid evidence of within-island speciation on this small island. We further demonstrated an exceptional case of a pair of sister species, *T. viridipunctatus* and *T. luyeanus*, that were separated by a narrow stream with a width of only 15 m. This pattern might be one of the narrowest contact zones ever documented in terrestrial vertebrates. To evaluate the level of genetic introgression between these sister species, a fine-scale collection of another 382 lizards was conducted along a transect line across the stream. A total of 13 microsatellite markers and mtDNA genotyping was used to detect a low proportion of hybrids (5.7–9.9% from STRUCTURE, and 2.3% from DAPC). Our results indicated that the two clades are highly differentiated across this extremely short distance.

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1. Introduction

Islands have been recognised as natural laboratories for studying the processes of species diversification (Johnson, 2003; Losos and Ricklefs, 2009). Various factors, including dispersal, vicariance and ecological adaptations, are involved in the formation of island biota (Paulay and Meyer, 2002; Cowie and Holland, 2006; Ryan et al., 2007). Owing to the obvious isolation by oceans, traditional research related to insular endemism has focused on the evolutionary process of inter-island speciation. However, within-island speciation has gained increasing attention in recent decades (Kisel and Barraclough, 2010; Rosindell and Phillimore, 2011). Several well-studied cases have been presented, especially in tropical islands such as the West Indies and Madagascar, where within-island speciation has been shown to play an important role in increasing the biodiversity on these islands (Losos et al., 1998; Rabemananjara et al., 2007; Townsend et al., 2009). However, research in other regions of the world is comparatively limited. Islands located near the eastern and northeastern Asian coastline are among the regions with relatively few studies concerning this issue.

Taiwan, a medium-sized island (36,000 km²) located offshore from mainland Asia, is suitable for the study of evolutionary events between continents and islands because of its geographic location connecting mainland Asia and the Ryukyu Archipelago. Due to its steep topography among adjacent regions, this island served as a refugium for both high-latitude and high-altitude species during the repetitive fluctuation of global climate in past glaciations (Wu et al., 2006; Yuan et al., 2006). A number of published studies collectively indicated that the biodiversity on this island was created by three major factors: (1) a complicated and repetitive colonisation history from mainland Asia (Lin et al., 2002; Ota et al., 2002; Jang-Liaw et al., 2008; Jang-Liaw and Chou, 2011), (2) inter-island dispersals from adjacent islands (Ota, 1997, 2000), and (3) genetic differentiation shaped by high landscape heterogeneity across the island (Lin et al., 2012). Although the first two factors have been thoroughly addressed from biogeographic or phylogenetic perspectives, the last model has not yet received much attention.

In this study, we aim to demonstrate a case of speciation occurring on the island and an extremely narrow contact zone across a stream. The *Takydromus* lizards (Squamata: Lacertidae) are widely distributed in the Oriental and eastern Palaearctic regions, with the greatest diversity in Taiwan (Arnold, 1997; Lue and Lin, 2008). In most cases, lizards of this genus rarely occur sympatrically, possibly due to their overlapping ecological requirements and niche

[☆] This paper has been recommended for acceptance by J.A. Schulte.

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competition. Taiwan Island represents a unique case of coexistence of multiple *Takydromus* species, which rarely occurs in any other place in the world (Arnold, 1997; Lin et al., 2002; Lue and Lin, 2008). In 2008, *T. formosanus*, which is widely distributed throughout the island, was identified as a complex of three sibling species owing to their differences in morphology and courtship colourations. This discovery increased the species number on the island to seven, including six endemics. According to current taxonomy, *T. formosanus* (Boulenger, 1894), with no sexual dichromatism, occurs only in southwestern Taiwan. *Takydromus viridipunctatus* and *T. lueyanus* Lue and Lin, 2008 are distributed in northern and eastern Taiwan, with nuptial colouration of green and yellow spots, respectively. The other two species in this clade are *T. hshuehshanensis* Lin and Cheng, 1981, which is unique as it is the only alpine species in this genus occurring exclusively in montane grasslands, and *T. wolteri* (Fischer, 1885), which is distributed in mid-northern China, Korean peninsula, and southernmost Russian Far East thus forming a disjunctive distribution from other closely related species. With their well-defined and parapatric distribution pattern, this group of lizards provides an ideal target to investigate the tempo and mode of the speciation process in East Asian islands.

Discussing distributional and genetic boundaries among these closely related species is the second goal of this study. The boundary between sister species, usually known as contact zones or hybrid zones (Barton and Hewitt, 1985; Harrison, 1993), have long been recognised as “windows on the evolutionary process” (Harrison, 1990), which provide valuable chances to detect selective adaptation and gene flow between newly evolving taxa (Abbott et al., 2013; Hoskin and Higgie, 2013). The formation and maintenance of a contact zone relies on a number of mechanisms that are related to ecological differentiation or reproductive isolation. If hybridisation does not increase fitness of offspring, a species will tend to avoid mating with other species to reduce energy costs. Reproductive character displacement or reinforcement, referred to as the strengthened performance of courtship signals, will have a chance to evolve from the contact region between sister taxa (Howard, 1993; Noor, 1999; Servedio and Noor, 2003). In contrast, hybridisation and subsequent genetic introgression contribute to homogenise their differences (Rieseberg et al., 1999; Pfennig, 2003; Turner et al., 2005). The future of such a contact zone may have several possibilities: extinction of one of the two populations, stable coexistence with hybridisation, fusion of the two populations, or an increase in premating divergence that facilitates the formation of distinct species (Barton and Hewitt, 1985). Research across the contact region has the potential to provide insights into speciation processes, including the process of differentiation and maintenance of this barrier (Abbott et al., 2013; Hoskin and Higgie, 2013).

This study focuses on three major issues among this group of lizards: within island speciation, fine-scale genetic differentiation, and the detection of hybridisation. The specific purposes of this study were as follows: (1) to provide evidence for within-island speciation using molecular phylogeny and ancestral range reconstruction; (2) to reveal fine-scale differentiation between *T. viridipunctatus* and *T. lueyanus* that are separated by a narrow stream; (3) to evaluate the ratio of hybrids and the level of genetic introgression in this sister pair; and (4) to discuss this contact zone from geographic and genetic viewpoints.

2. Materials and methods

2.1. Sample collection and DNA extraction

During 2002–2003, 402 samples belonging to the *Takydromus formosanus* species complex were collected from 34 localities throughout Taiwan (Fig. 1B; Table S1). This large-scale collection

regime comprised 178 *T. viridipunctatus*, 87 *T. lueyanus*, 99 *T. formosanus*, and 38 *T. hshuehshanensis* (Table S2). To approach the distribution boundary between *T. viridipunctatus* and *T. lueyanus*, a comparatively intense collection was conducted across the Qingshui Cliff, in specific localities (8–15, Fig. 1C). Two *T. wolteri* collected from eastern China (Fig. 1A), as well as another complete mitochondrial genome sequence (GenBank Accession No. JX181764, Yu and Ji, 2013), were also included in this study.

Mitochondrial DNA sequencing of three genes from the large-scale sampling led us to focus on a narrow contact zone along the Liwu River, a montane river that flows in an eastward direction (Fig. 1D). In non-raining seasons, the major water body of the river is less than 15 m and is sometimes shallow enough to wade across. To detect the fine-scale genetic differentiation across this stream, another intense fine-scale collection was conducted along the river banks from 2004 to 2005. Seven (N1–N7) and eight (S1–S8) sites were chosen from the northern and southern banks of the stream (Fig. 1D), respectively, yielding a total of 263 lizards consisting of 125 northern and 138 southern individuals, respectively. The collection sites of all of the specimens were precisely located using a handheld GPS device (Oregon 550t, GARMIN Ltd., Taiwan). To represent the spatial distribution of possible hybrids, samples from this contact zone were aligned from north to south according to their distance from the stream in the following analyses.

Outgroup included 25 individuals from 11 other *Takydromus* (Table S3), and this study covered a total of 16 species among the 22 currently recognised *Takydromus* spp. Sequences of three closely related lacertids (Fu, 2000) were downloaded from GenBank and were used to root the phylogenetic trees. Genomic DNA of all these specimens was isolated using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) following the manufacturer's instructions and stored at -20°C .

2.2. Mitochondrial DNA sequencing

Mitochondrial DNA sequencing was applied to all the *Takydromus* individuals in the large-scale sampling. Partial cytochrome *b* (*cytb*, 702 base pairs after alignment), partial cytochrome *c* oxidase subunit I (COI, 789 bp) and full-length 12S rRNA (1014 bp) were amplified using the following primers designed in this study: CYTB-L: 5'-CGAGAYGTYCAAYAYGGMTGRYTYATYCG-3'; CYTB-H: 5'-ACAATAAGGTTTGAGAGAGTGGGCG-3'; COI-L: 5'-GCTGGTACYG GCTGAAGTGTCTACCC-3'; COI-H: 5'-CARTGNACRAATCCRCCATRA TTGC-3'; 12S-L: 5'-AGTCTGCTCAAAAAGATTAATGTAA-3'; 12S-H: 5'-TCTTGGTCTGAAACCTCAGTTACCTA-3'. Reactions were conducted in a 20- μl reaction volume containing 1 \times PCR buffer (10 mM Tris-HCl, pH 9.0; 50 mM KCl, 0.01% (w/v) gelatine and 0.1% Triton X-100), 0.8 U of Taq DNA polymerase (Amersham Bioscience, New Jersey, USA), 0.5 mM dNTP, 0.2 mM each primer and 50 ng of template DNA. The PCR conditions consisted of denaturation at 94 $^{\circ}\text{C}$ for 3 min, followed by 35 cycles of 94 $^{\circ}\text{C}$ for 30 s, 52 $^{\circ}\text{C}$ for 40 s and 72 $^{\circ}\text{C}$ for 90 s, with a final extension at 72 $^{\circ}\text{C}$ for 10 min using an iCycler Thermal Cycler (Bio-Rad). PCR products were purified with the PCR Product Pre-Sequencing Kit (USB Corp., Cleveland, OH, USA) and subsequently used as the template for direct DNA sequencing reactions with the DYEnamic ETDye Terminator Cycle Sequencing Kit (Amersham Pharmacia Biotech). The primers used for PCR were also used for the sequencing reactions. Sequencing products were run on a MegaBACE 1000 automated DNA sequencer (Amersham Bioscience, New Jersey, USA). The sequences were determined in both directions, and the original signals were proofread using SEQUENCHER 4.7 software (Gene Codes Corp., MI, USA). Sequences were aligned by SEQUENCHER 4.7 software with the default settings. All the haplotypes were submitted to GenBank (AY248482–AY248604, KM487140–KM487188).

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