Microhabitat segregation of two coexisting tadpole species on Emei Mountain

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Abstract. Understanding mechanisms determining the coexistence between different species is one of the key issues in community ecology and biodiversity conservation. Microhabitat segregation is a way for species to coexist, which reflects the specific habitat selection of coexisting species in a finer spatial scale. Despite quantitative studies have been conducted to investigate the microhabitat segregation of coexisting species, this type of studies was not often performed on tadpoles. In this study, we assessed the habitat selection of two coexisting tadpoles (*Quasipaa boulengeri* and *Leptobrachium boringii*) in a stream on Emei Mountain, China. Our results demonstrated that *L. boringii* and *Q. boulengeri* tadpoles occupied different microhabitats. Specifically, *Q. boulengeri* tadpoles preferred deep, narrow, and weak acid stream segments with slow current velocity and low value of conductivity, while *L. boringii* tadpoles tended to occur in a wide, shallow water bodies with relatively higher pH, conductivity, and current velocity. Overall, our study supported the Hutchinson's niche concept, showing that at least one dimension of niche differentiation (i.e., microhabitat) occurred between coexisting tadpole species.

Keywords. Microhabitat selection, species coexistence, niche differentiation, environmental variables.

INTRODUCTION

Understanding mechanisms determining the coexistence between different species is one of the key issues in community ecology and biodiversity conservation (Adler et al., 2010; Hanane, 2015). Previous studies indicated that coexisting species should occupy specific ecological niche (e.g., microhabitat niche, trophic niche; Grinnell, 1917) to evade competition based on the limiting similarity theory (Macarthur and Levins, 1967). As ecological niche is an *n*-dimensional ecological space satisfying all the essential conditions that support the organisms (Hutchinson, 1957), coexisting species exhibit at

least one dimension of niche differentiation in the same ecosystem (Caceres and Machado, 2013; Hanane, 2015). This phenomenon can be referred to as niche partitioning involved in several facets, such as temporal or spatial distribution, as well as the trophic habits (Baker and Ross, 1981; de Andrade et al., 2014; Schoener, 1974). Therefore, Hutchinson's niche concept primarily focuses on habitats and resources utilization of sympatric species, as well as their environmental tolerances (Rosenfeld, 2002). Accordingly, the segregation of habitats can be considered as one of the important niche partitioning forms allowing the coexistence of species (Melo et al., 2013; Schoener, 1974; Wei et al., 2000). For instance,

Guo et al. (2012) indicated that two species of goby fish (*Rhinogobius giurinus* and *Rhinogobius cliffordpopei*) were introduced into Lake Erhai, China in 1961. They eventually had to adapt to a different ecological niche in order to coexist in the ecosystem.

At a mesohabitat scale, habitat segregation is usually tested in physiognomically homogeneous units (Heggenes and Saltveit, 2007; Kano et al., 2013; Rezende et al., 2010). However, when focusing on species at a finer spatial scale, habitat segregation is usually assessed by measuring a set of environmental parameters (Rincon, 1999). This can reflect exact habitat utilization of coexisting species in the same ecosystem, particularly in the aquatic ecosystems (Jackson et al., 2001; Jorgensen, 2004; Leger et al., 1983; Leitao et al., 2015). For instance, two turtle species coexist in freshwater streams in Southwest of Iberian Peninsula due to their divergence in habitat selection. Specifically, the European pond turtle (*Emys orbicularis*) shows a preference for temporary, shallow, well vegetated, and sandy stream segment, while the Mediterranean pond turtle (*Mauremys leprosa*) tends to occupy deeper stream segment with more rocks (Segurado and Figueiredo, 2007). Similar situation is also observed in two coexisting fish species in Anizacate River. In this ecosystem, current velocity is the key factor that facilitates the coexistence of the stream catfish (*Trichomycterus corduvense*) and the eel catfish (*Heptaterus mustelinus*), who prefers the high-velocity and the low-velocity water flows, respectively (Hued and Bistoni, 2006). Despite quantitative studies have been conducted to investigate the microhabitat segregation of coexisting species in different ecosystems (e.g., invertebrates, Mammola et al., 2016; fish, Horinouchi, 2008; Kessler and Thorp, 1993; and amphibian adults, Ayala et al., 2018), empirical studies are still relatively rare in anuran tadpoles.

Tadpoles can exhibit plasticity in terms of functional traits (Jordani et al., 2019; Zhao et al., 2019), behavior (Freitas et al., 2019; Zhao et al., 2019), and metabolism (Freitas et al., 2019; Wang et al., 2019) in response to environmental change. In addition, tadpoles could influence the composition and abundance of plankton and periphyton, which has cascading effects on primary productivity in aquatic ecosystems (Alford and Wilbur, 1985; Seale, 1980; Strauss et al., 2010). More importantly, tadpoles are the larval stage of amphibian adults, which face multiple threats (e.g., habitat loss, climate change, and pollution, Alford, 2011). Therefore, identifying the microhabitat selection of coexisting tadpoles may bring important insights to tadpole biodiversity conservation, and suggest priorities for the improved management of mountain stream ecosystems.

In the present study, we evaluated the habitat selection of two coexisting tadpoles, *Quasipaa boulengeri* and *Leptobrachium boringii* in a mountain stream. Specifically, we first compared the difference of variables of microhabitat occupied by *L. boringii* and *Q. boulengeri* tadpoles. We then explored the distribution pattern of the two tadpoles in the stream. Based on previous studies (e.g., Winston, 1995; Xu et al., 2020), we predict that the coexisting tadpoles of two different species occupy different microhabitat.

MATERIAL AND METHODS

Study area and species description

Field work was carried out in Heilongjiang stream, Qingyinge of Emei Mountain, Sichuan Province, China (Fig. 1). The vegetation of this area is mostly composed by evergreen broad-leaved forest. The elevation of this region is about 680m a.s.l., and the weather is characterized by subtropical monsoon climate. The mean annual temperature and the mean annual precipitation is about 17.29 °C and 1555.3 mm (Gu and Li, 2008; Ling, 2005). Several tadpoles belonging to different species were detected during our field work in this stream (e.g., *Megophrys omeimontis*, *Megophrys minor*, *Odorrana graminea*, *Q. boulengeri*, *L. boringii*, *Leptobrachella oshanensis*, and *Odorrana schmackeri*). The dominant species were *L. boringii* and *Q. boulengeri*, which occupied 90% of the proportion of the individuals. We focused on the divergences in habitat selection occurring between these two dominant species, as it would be more physiological than that showing how non-dominant species can coexist (Lyons et al., 2005; Barrett et al., 2008).

Data collection

Based on the distribution of target tadpoles and accessible for the sampling, one kilometer of the segment of the stream was selected as the transect. The transect was fixed and extended through a gorge, with strong variability in its physical variables due to the complex terrain and different vegetation cover rate. We divided this transect into three parts based on the blocking of rocks (i.e., approximate 200m of the upstream transect, 450 m of the medium-stream transect, and 350 m of the downstream transect). Tadpole sampling was carried out after sunset (between 20:30 and 23:00) from 22nd to 27th in August 2018. We searched at the both edges (about 1m from the bank) of the stream where the tadpoles distributed, with one part of one side being sampled per night. Specifically, we divided each side of the transect into 1000 squares (1 × 1 m), and two persons searched these plots of 1 m² intensively from downstream to upstream using torch (220 lm). Once the target tadpoles were detected, the related square was recorded as one valid quadrat. After that, all the tadpoles located in the quadrat were collected by sweeping all potential microhabitats for tadpoles (i.e., water column and edge of rocks with and without vegetation) using hand nets (mesh size: 2 mm). We assumed that tadpoles likely did not have chances to move from one side to the other
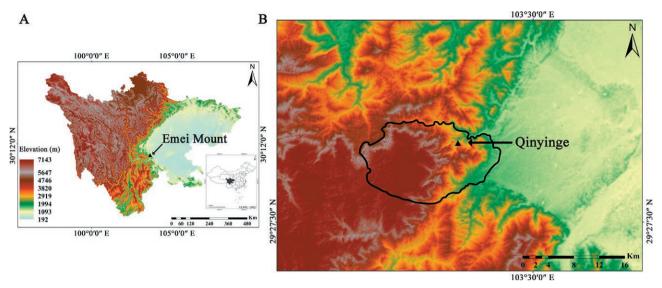
Fig. 1. Geographical location of the study area. The solid line describes the range of Emei Mountain.

of the river, or to cross the rocks limiting the sections during the survey period. The two target tadpoles can be easily identified based on their external morphology. Specifically, there is a light "*Y*" symbol at the back of *L. boringii* tadpole, while *Q. boulengeri* tadpole has flat head and back, thick caudal muscle, and I:4+4/1+1:II labial tooth row (Fei et al., 2012, Fig. S1). Collected tadpoles were kept in 500 ml plastic bottles with freshwater from the stream separately. The stage of each tadpole was determined based on Gosner (1960).

In each quadrat where we found tadpoles, a set of eight environmental factors were measured. Details of the factors and the related measurement approaches are as follows: substrate type was divided into two groups (i.e., gravel and a mix of gravel and humus, associating with different food resources in the quadrats), water temperature was measured to the nearest 0.1 °C by a thermometer (KTJ - TA318, China, Shenzhen), river width was measured to the nearest 0.1 m using a tape meter, the maximum depth of the quadrat was measured to the nearest 0.1 cm with a ruler, current velocity was measured to the nearness 0.1 m/s using a portable current meter (LS1206B, China, Nanjing), pH, conductivity (to the nearest 0.1μS/cm) and dissolved oxygen (to the nearest 0.1 mg/l) were measured using a portable fluorescence photometer (Star A, 520M - 01A, Thermo Fisher Scientific, USA). During the measurements, the researcher remained outside the stream to do not affect the recorded parameters (Ferreira et al., 2015).

Statistical analyses

Shapiro-Wilk test was used to test the normality of the seven environmental variables of microhabitats. In order to compare the difference of variables of microhabitat occupied by *L. boringii* and *Q. boulengeri* tadpoles, we conducted Student's t tests for variables which followed a normal distribution, or Mann-Whitney U test for those were not normal distributed.

After that, we used detrended correspondence analysis (DCA) to explore the distribution pattern of the two tadpoles (linear model or single peak model). Considering the DCA axis lengths is less than 3 (i.e., the species distribution was fitted well with the linear model), we finally chose redundancy analyses (RDA) to quantify the environmental determinants of the distribution of the two target tadpoles. All statistical analyses were performed in R version 3.6.1 (R development core team 2020) using the packages *stats*, *spaa*, and *vegan*.

RESULTS

In total, 27 quadrats were sampled and measured for environmental variables, in which 13 quadrats were occupied by *L. boringii* tadpoles, and 14 quadrats were occupied by *Q. boulengeri* tadpoles. These two tadpoles were not detected at the same time in each of the sampled quadrat. We overall captured 74 individuals of *L. boringii* from stage 24 to 37 and 193 individuals of *Q. boulengeri* from stage 25 to 43.

Student's t test indicated that there was no significant difference of dissolved oxygen ($t = -1.674$, $P = 0.107$) in the microhabitats that were occupied by *L. boringii* and *Q. boulengeri* tadpoles. Mann-Whitney U tests revealed that pH, conductivity, river width, water depth, and current velocity were significantly different ($P < 0.05$; Fig. 2; substrate type cannot be tested as it was a categorical variable). Specifically, *L. boringii* tadpoles occupied quadrats that had higher values of pH, conductivity, river width, and current velocity, but lower values of water depth. In contrast, *Q. boulengeri* tadpoles occupied quadrats that had lower values of pH, conductivity, river width,
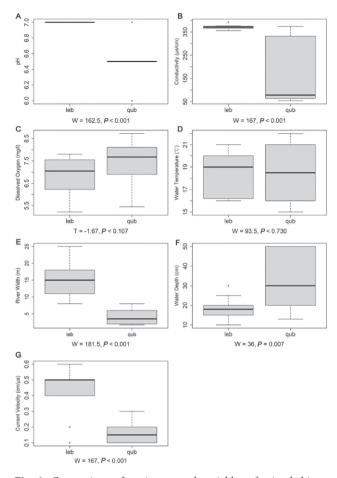
Fig. 2. Comparison of environmental variables of microhabitats between *L. boringii* tadpoles and *Q. boulengeri* tadpoles. "leb": *L. boringii* tadpoles, "qub": *Q. boulengeri* tadpoles.

Table 1. The influence of eight environmental factors tested by RDA analyses on the two tadpole species.

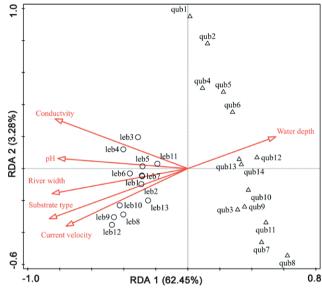| Environmental Variables	RDA1	RDA2	r^2	P
pH	-0.918	0.397	0.524	**0.001**
Conductivity	-0.968	0.252	0.573	**0.001**
Dissolved oxygen	0.997	0.082	0.139	0.160
Water temperature	-0.650	0.760	0.012	0.869
River width	-0.847	0.531	0.596	**0.001**
Water depth	0.793	-0.609	0.266	**0.014**
Current velocity	-0.737	0.676	0.600	**0.001**
Substrate type	-0.799	0.600	0.632	**0.001**

Significant effects are indicated in bold.

Fig. 3. Redundancy analyses of the relationships between environmental factors and the distributions of model tadpoles. The length of an environmental vector indicates the degree of correlations. Only significant variables are depicted ($P < 0.05$), "leb": *L. boringii* tadpoles, "qub": *Q. boulengeri* tadpoles.

and current velocity, but higher values of water depth. In addition, no significant difference existed in terms of water temperature values ($W = 93.5$; $P > 0.05$).

The RDA model was significant when testing the environmental determinants of the distribution of *L. boringii* and *Q. boulengeri* tadpoles ($P = 0.001$). The first two axes accounted for 65.75% of the variation (62.45% and 3.28%, respectively). Our results revealed that five environmental factors including substrate type, river width, current velocity, pH, and conductivity had highly significant effects on the distribution of *L. boringii* tadpoles and *Q. boulengeri* tadpoles ($P = 0.001$, Table 1), and the influence of water depth was significant ($P < 0.05$, Table 1). Obvious dissimilarity of the distribution of *L. boringii* and *Q. boulengeri* tadpoles could be observed in the RDA sequence diagram (Fig. 3). Specifically, most of the quadrats occupied by *L. boringii* tadpoles were distributed in the second and third quadrant densely, which were positively associated with current velocity, river width, pH, conductivity, and sub-

strate type. However, they were negatively correlated with water depth. In contrast, most of the quadrats occupied by *Q. boulengeri* tadpoles exhibited opposite distribution pattern, which were positively correlated with water depth, and negatively associated with current velocity, river width, pH, conductivity, and substrate type.

DISCUSSION

Discrepant preferences for microhabitat utilization on a small scale is often considered to be responsible for the

coexistence of sympatric species (Dammhahn and Goodman, 2014; Dammhahn et al., 2013; Escoriza et al., 2018; Wei et al., 2000; Yang et al., 2019). Our results demonstrated that despite *Q. boulengeri* and *L. boringii* tadpoles co-occurred in the same stream, microhabitat segregation existed between them. Specifically, *L. boringii* tadpoles tended to occur in a wide, shallow water bodies with relatively higher pH, conductivity, and current velocity, which was consistent with previous study (Wei et al., 2017). In contrast, *Q. boulengeri* tadpoles were apt to occupy deep, narrow stream segments with low pH, conductivity and current velocity. Therefore, our results indicated that these two tadpoles occupied totally different microhabitat in this stream. Indeed, due to the poor movement ability, tadpoles' microhabitats are largely determined by the selection of breeding habitats by breeding adults (Biesterfeldt et al., 1993). Therefore, the occupation of the microhabitat of the two tadpole species were in accordance with previous observation showing that female *Q. boulengeri* spawned in puddles under the stream waterfall, while female *L. boringii* spawned at streams segments with more rocks and slow water flow (Fei et al., 2012).

It has been recognized that tadpole functional traits were correlated with their selection of microhabitats in water bodies (Fatorelli et al., 2015; Glos et al., 2017), as well as other factors (e.g., predatory occurrence and strategy, Mogali et al., 2020). Based on our previous study (Xu et al., 2020), these two tadpole species have distinct phenotypic functional traits, which also reflected their adaptation of different environment in the water bodies (Zhao et al., 2017). Specifically, *Q. boulengeri* tadpoles have flattened bodies and stubby tails, associating with their selection of deep and slow flowing water bodies. *L. boringii* tadpoles have long and muscular tails, which can be useful for them to swim when water velocity is high. These external functional traits reflect the food acquisition and locomotion of tadpoles, which are critical for them to obtain nutrients to survive, and to facilitate the movement in water bodies (Schoenfuss and Blob 2007). In the present study, substrate type was one of the main environmental factors determining the distribution of the two tadpoles, which probably related to their feeding preferences. That is, *Q. boulengeri* tadpoles tended to choose a substrate with gravels which can provide them adherent algae and benthos. In contrast, *L. boringii* tadpoles preferred a mixture of humus and gravels where organic detritus and invertebrates are more abundant. However, more work such as stable isotope analyses are needed to verify our inferences.

Overall, the present study evaluated the microhabitat segregation of two sympatric tadpole species in a mountain stream. Our observations supported Hutchinson's niche theory demonstrating that the existence of at least one dimension of niche differentiation between coexisting species. Therefore, specific microhabitat features should be incorporated into the conservation strategies for different species. Beyond our studies, future work could focus on the roles that coexisting species played in communities and ecosystems. Furthermore, as mountain streams are vulnerable to anthropogenic disturbance, how increasing fishing pressure on tadpoles from tourists may affect ecosystem functioning can be also tested.

SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at <htttp://www.unipv.it/webshi/appendix> manuscript number 9758

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