### Ecomorphological correlates of microhabitat selection in two sympatric Asian box turtle species (Geoemydidae: Cuora)

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Ecomorphological correlates of microhabitat selection in two sympatric Asian box turtle species (Geoemydidae: *Cuora*)

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Ecomorphological correlates of microhabitat selection in two sympatric Asian box turtle species (Geoemydidae: Cuora)


Abstract: Closely related species that co-occur in homogeneous environments often possess differing morphologies, which can result in niche divergence that minimizes interspecific competition. In the present study, we examined the relationship between the ecomorphological characteristics and microhabitat selection of two Asian box turtle species, the keeled box turtle Cuora mouhotii (Gray, 1862) and Indochinese box turtle C. galbinifrons (Bourret, 1939), which have sympatric distributions in the rainforest of Hainan, China. We found that C. mouhotii had a relatively flat shell and preferred microhabitats with rock crevices and steep slopes in the field, whereas C. galbinifrons had a domed shell and was restricted to microhabitats of deciduous leaves under bamboo growing on gentle slopes. We conclude that morphological divergence allows the two Cuora spp. to use different microhabitats and, thereby, to successfully co-occur.

Key words: keeled box turtle, Cuora mouhotii, Indochinese box turtle, Cuora galbinifrons, leaf litter, microhabitat, rock crevice.
Introduction

One of the most important objectives of ecomorphology is to determine the underlying mechanisms of species co-occurrence in relation to their morphological and ecological characteristics, both in the present and over evolutionary time (Motta and Kotrschal 1992; Vanhooydonck et al. 2000). Generally, co-occurring species either possess similar morphologies, owing to convergent evolution from adaptation to the same habitat (Grant 1972), or divergent morphologies that result in niche divergence and minimize interspecific competition (Hutchinson 1959; Brown and Bowers 1985). In particular, closely related species that co-occur in homogeneous environments should be morphologically distinct to partition limited resources, such as microhabitats, and, thus, to reduce competitive interactions and, ultimately, achieve co-occurrence. Numerous studies on vertebrate taxa have shown that ecomorphology correlates with habitat selection among sympatric species (e.g., mammals: Davies et al. 2007; birds: Guillemain 2002; reptiles: Pounds 1988; Lindeman 2000; Vanhooydonck et al. 2000; Higham and Russell 2010; and fish: Robinson and Wilson 1994). However, such studies have typically correlated morphological features with habitat classes, and only a few have quantified ecological characteristics, such as microhabitat (Lindeman 2000; Vanhooydonck et al. 2000).

Both the keeled box turtle (*C. mouhotii* Gray, 1862; formerly *Pyxidea mouhotii*) and Indochinese box turtle (*C. galbinifrons* Bourret, 1939) are distributed in south China, including Hainan Province (Zhao and Adler 1993). *C. mouhotii* is typically found in moist evergreen forests at low altitude (Wang et al. 2011a; Wangyal et al. 2011b).
(2012; Struijk et al. 2016), whereas *C. galbinifrons* is found in similar forests but at high altitude (Wang et al. 2011b). Previous studies have reported the occurrence of natural hybrids in Hainan Province (Shi et al. 2005), which implies that, in some areas, the distributions of the two species overlap, and the species have since been reported to co-occur at 700–914 m in the Hainan Diaoluoshan Natural Reserve by Wang et al. (2011a,b).

Interestingly, the morphology of *C. mouhotii* is extremely divergent from its sympatric species, *C. galbinifrons*, as well as from all other species in the genus. For example, *C. mouhotii* possesses a relatively flat carapace for a member of *Cuora*, with a flattened top, whereas *C. galbinifrons* has a highly domed carapace. In general, carapace shape is correlated with the habitat preference of turtles: aquatic turtles have flattened carapaces, whereas terrestrial turtles have highly domed carapaces, and semiaquatic turtles have carapaces with intermediate morphology (Romer 1967; Claude et al. 2003; Bonnet et al. 2010; Benson et al. 2011). However, previous studies about the microhabitat preference of flat-topped turtle species remain scarce, such as *C. mouhotii*. Additionally, although *C. galbinifrons* has been considered to exhibit a semiaquatic habit (Ernst and Barbour 1989), Wang (2007) and Wang (2008) tracked nine individuals in Diaoluoshan Natural Reserve for two years, using radio telemetry, and found that the species never entered the water. Therefore, the ecological function of the two species’ divergent morphologies has been unclear.

Recently, one individual of *C. mouhotii* was found in a rock crevice at the Deo Ca Protected Forest, Phu Yen Province, Vietnam (Ly et al. 2013). In contrast, *C.
*galbinifrons* is more frequently observed in microhabitats of deciduous leaves under dense bamboo (Wang et al. 2011b). Therefore, in the present study, we quantified the microhabitat use of co-occurring *C. mouhotii* and *C. galbinifrons* at Diaoluoshan Natural Reserve. We hypothesized that the two species would occupy different microhabitats, owing to their divergent shell morphology.

**Materials and methods**

**Ethics statement**

This study was approved by the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (HNECEE-2014-002), and was carried out in strict accordance with the institutional guidelines. Fieldwork was carried out with permission from the Diaoluoshan Forest Bureau. No turtles were sacrificed for this study or incurred injury or death while in the traps.

**Microhabitat selection**

We studied the microhabitat selection of *C. mouhotii* and *C. galbinifrons* at the Diaoluoshan Natural Reserve in Hainan Province, China (18°43’53”N, 109°52’10”E) from April 2015 to February 2016. The field site was located in a rainforest between 860 and 914 m in altitude, where the average highest temperature is 28 °C in July, the average lowest temperature is 15.4 °C in January, and the annual rainfall ranges from 1870 to 2760 mm.
The turtles were captured in traps baited with salty fish or rancid pork skin; thereafter, a radio-tracking transmitter (RI-2B, 216.000–216.999 MHz; Holohil Systems, Ltd., Caro Ontario, Canada) was fitted to the last costal scute of each turtle. The size (diameter × height = 21 × 8 mm), mass (6 g), and location of the transmitters would not have prevented turtles from using any of the microhabitats. Then the turtles were released at the site of capture. The turtles were tracked daily from 09:00 to 16:00, using a handheld receiver (TRX-1000S, 216.000–216.999 MHz; Wildlife Materials International, Inc., Murphysboro, Illinois, USA) with a three-element folding antenna (Wildlife Materials, Inc.), and the locations were recorded using a handheld Magellan Triton 400 Global Positioning System (Magellan Navigation, Inc., Santa Clara, USA). Radio-tracked turtles were tracked for an average of 164 days. All radio-tracking transmitters were carefully removed from the turtles’ shells when the tracking study was complete.

We hypothesized that the locations at which the turtles remained for >3 d indicated preferred microhabitats and quantified 14 microhabitat characteristics within two different-sized quadrats (10 × 10 m and 1 × 1 m) at each preferred site. In the large quadrats, we quantified (1) slope gradient (°), (2) slope position (1 = upper slope, 2 = middle slope, 3 = lower slope; slope position refers to the location of slope occupied by turtle in the mountain, which was classified as upper slope, middle slope or lower slope when the turtle occur near peak, middle or low position of the mountain, respectively), (3) canopy cover (%), (4) number of fallen logs, (5) number of bamboo clumps, (6) number of tree holes, and (7) number of rock crevices; and in
the small quadrats, we quantified (8) bamboo density (plants/m²), (9) herbage height (cm), (10) herbage density (plants/m²), (11) deciduous leaf cover (%), (12) deciduous leaf thickness (cm), (13) stone cover (%), and (14) type of concealment (1 = rock crevice, 2 = tree hole, 3 = fallen log, 4 = grass, 5 = bamboo clump, 6 = deciduous leaves, 7 = bare ground). In total, we collected data from 44 preferred sites from seven *C. mouhotii* individuals and from 27 preferred sites from five *C. galbinifrons* individuals.

Chi-squared tests (SPSS 16.0; SPSS, Inc., Chicago, IL, USA; same below) were used to assess whether the two species differed in their preference of slope position and type of concealment. The Kolmogorov-Smirnov test was performed to test the normality of the 12 numeric microhabitat variables. One-way analysis of variance (ANOVA) was subsequently used to test whether the two species differed in slope gradient, herbage height, and deciduous leaf cover, and the Mann-Whitney U test was used to determine whether the two species differed in any of the nine remaining microhabitat variables. Furthermore, discriminant function analysis (DFA) was performed to assess the differences in the 12 numeric microhabitat variables between the two species. The stepwise method of DFA was performed to determine the best variables significantly separating the two species.

In addition, we measured the slope gradient at stopover sites at which the turtles remained for <1 d, using a clinometer. Whether the two species differed in slope gradient was examined using one-way ANOVA.
Morphological measurements

Morphological measurements were taken from all the experimental individuals (\( n = 9 \) for *C. mouhotii*, \( n = 8 \) for *C. galbinifrons*), as well as from other individuals that were more recently encountered in the field (nine individuals for *C. mouhotii* and five individuals for *C. galbinifrons*), using a Vernier caliper (accuracy to 0.02 mm). For each individual, we measured carapace length, carapace width (measured at the sixth marginal scute), and carapace height (measured at the sixth marginal scute). In addition, we also calculated the ratio of carapace height to width (R) as a measure of shell contour (Domokos and Várkonyi 2008).

After the normality and homogeneity of variance were tested for all morphological measurements, one-way ANOVA was used to test whether the two species differed in carapace length, and to remove the effect of body size, one-way analysis of covariance (ANCOVA; carapace length as the covariate) was performed to test whether the two species differed in any of the other morphological variables.

Results

Microhabitat selection

No individuals of either *C. mouhotii* or *C. galbinifrons* were found in the water during the field study. Among the 14 microhabitat variables, slope gradient, number of rock crevices, deciduous leaf cover, deciduous leaf thickness, stone cover (Table 1), and type of concealment \( (\chi^2 = 69.69, \ df = 6, \ P < 0.0001) \) significantly differed
between the two species. This finding indicates that *C. mouhotii* was more commonly observed on rocky substrates and steep slopes (Table 1) and typically selected rock crevices for concealment (56.82%; Fig. 1B), whereas *C. galbinifrons* was usually observed in deciduous leaves on gentle slopes (Table 1) and selected deciduous leaves for concealment (93.93%; Fig. 1C).

The stepwise DFA indicated that three variables were selected which significantly discriminate *C. mouhotii* and *C. galbinifrons* (stone cover, slope gradient, and bamboo density; Table 2), and the efficiency of the analysis was high (62 of 71 quadrats - 87.3% were correctly classified). The distribution of the quadrats on the DFA axis showed that the microhabitats selected by *C. mouhotii* were mostly distinct from those selected by *C. galbinifrons*, and only a small overlap between the two species (Fig. 2). For instance, both *C. mouhotii* and *C. galbinifrons* selected the same terrestrial habitat with high-canopy cover (Table 1; Fig. 1A).

In addition, the slope gradients of the stopover sites of the two species differed significantly (one-way ANOVA; $F_{1, 324} = 128.214; P < 0.0001$), with *C. mouhotii* (mean ± SD: 30.3 ± 8.7°, range: 5 – 60°) occurring on steeper slopes than *C. galbinifrons* (22.3 ± 7.5°, 5 – 40). This result was in accordance with the slope gradients from the preferred sites.

**Morphological measurements**

The carapace length of the two species did not differ significantly (one-way ANOVA; Table 3). However, one-way ANCOVA, with carapace length as the
covariate, indicated that the carapace height and ratio of carapace height to width of the two species all differed significantly, whereas the carapace width of the two species was similar (Table 3). These findings indicated that *C. mouhotii* had a relatively flat shell, whereas *C. galbinifrons* had a highly domed one. In addition, the plastron hinge of *C. mouhotii* only allowed the shell to close partially, whereas that of *C. galbinifrons* allowed the shell to close completely; and *C. mouhotii* also possessed a carapace with serrated posterior edges and a flattened top, whereas *C. galbinifrons* possessed a carapace with smooth edges.

**Discussion**

In agreement with previous studies, we found that both adult *C. mouhotii* and *C. galbinifrons* were terrestrial species and selected the same high-canopy cover habitat (Wang 2007; Lian 2009); however, we also observed that the microhabitats of the two species were significantly different. Notably, *C. mouhotii* individuals were mostly observed in areas with greater stone cover and often selected rock crevices for concealment, where they hid for up to 20 d, whereas *C. galbinifrons* individuals were mostly observed in deciduous leaf litter under bamboos, where they often hid for long periods, as well. In addition, *C. mouhotii* also occupied microhabitats with slopes that were much steeper than those of the microhabitats occupied by *C. galbinifrons*. This suggests that the two species co-occur by occupying different niches.

Understanding the relationship between microhabitat selection and morphology is critical for understanding ecomorphological adaption (Vanhooydonck et al. 2000;
Rivera 2008; Rivera et al. 2014). In the present study, we found that body size (carapace length) did not differ between *C. mouhotii* and *C. galbinifrons*, but the shell of *C. mouhotii* was significantly more flat than that of *C. galbinifrons*. Our microhabitat experiment confirmed that *C. mouhotii* prefers and selects microhabitats with rock crevices, and since flattened bodies often allow animals to fit into narrow crevices (Miles 1994) and because previous studies have reported that terrestrial turtles with flat carapaces, such as the African pancake tortoise (*Malacochersus tornieri* Siebenrock, 1903), are adapted to lifestyles in rocky crevices (Ireland and Gans 1972; Malonza 2003), we believe that the relatively flat shell of *C. mouhotii* is an adaptation for using microhabitats with rock crevices. In addition to possessing a flatter shell than *C. galbinifrons*, the flat-topped carapace of *C. mouhotii* was important in its adaptation to the rock crevice microhabitats, as in several species of the genus *Homopus* Duméril and Bibron, 1835 (Ernst and Barbour 1989; Bonin et al. 2006).

We also observed that *C. mouhotii* has a posteriorly serrated carapace, which might help prevent the turtles from being dragged out of rocky crevice by predators. In addition, *C. mouhotii* occupied microhabitats with slopes that were much steeper than those of the microhabitats occupied by *C. galbinifrons*. This difference may be correlated with the shell shapes of the two species. Since flat shells impart a lower center of gravity (Domokos and Várkonyi 2008) and thus increase stability on steeper surfaces, the relatively flat shell of *C. mouhotii* could also be an adaptation for climbing on smooth rocks and inclined substrates; however, this morphofunctional
hypothesis should be confirmed by further investigation.

In contrast to the relatively flat shell of *C. mouhotii*, the highly domed shell of *C. galbinifrons* is typical of terrestrial turtles, and both the present and previous studies (Wang 2007) have reported that *C. galbinifrons* inhabits terrestrial habitats. Indeed, the species is well adapted to terrestrial environments, since its shell can tolerate much stronger mechanical forces, such as those from terrestrial predators (Greene 1988; Stayton 2011); and although the highly domed shell may also restrict the species to hiding in soft leaves and to microhabitats with relatively gentle slopes, the species possesses several alternative defensive features. For example, *C. galbinifrons* also has a single transverse hinge across the middle of its plastron that allows complete retraction and protection of its extremities from predators (Pritchard 2008), and the color and pattern of the species’ carapace is similar to that of deciduous leaves, which may function to reduce predator detection via camouflage (Fig. 1C; Stevens and Merilaita 2009; Xiao et al. 2016). Moreover, the smooth marginal scutes of *C. galbinifrons* allow it to burrow deeper than *C. mouhotii* under deciduous leaves.

Notably, we found that *C. galbinifrons* was a leaf-dwelling species. However, many terrestrial species that hide under leaf litter, such as the black-breasted leaf turtle (*Geoemyda spengleri* Gmelin, 1789; R = 0.54; Benson et al. 2011), forest cane turtle (*Vijayachelys silvatica* Henderson, 1912; R = 0.51; Whitaker and Vijaya 2009), and spiny turtle (*Heosemys spinosa* Gray, 1831; R = 0.53; Spinks et al. 2012), have flat shells. Therefore, it is actually quite surprising that the highly domed *C. galbinifrons* also uses this microhabitat. One possible way in which *C. galbinifrons*
can mitigate the disadvantage of its tall shell is that the coloration of *C. galbinifrons* is somewhat similar to that of other leaf-dwelling species, as well as to that of leaves (i.e., camouflage). It is also possible that the leaf litter in the habitat of *C. galbinifrons* affords high cover and is thick enough to hide its highly domed shell.

Intriguingly, other *Cuora* spp. possess different shell morphologies and occupy diverse habitats. For example, both *C. galbinifrons* (*R* = 0.70) and the yellow-margined box turtle (*C. flavomarginata* Gray, 1863; *R* = 0.65; Benson et al. 2011) have highly domed shells and occupy terrestrial habitats, i.e., evergreen forests (Lue and Chen 1999), whereas the Malayan box turtle (*C. amboinensis* Daudin, 1802), which also has a relatively domed shell (*R* = 0.61; Benson et al. 2011), is aquatic (Ernst 1989; Joyce and Gauthier 2004). Similarly, *C. mouhotii*, which has a relatively flat shell (*R* = 0.58), occupies terrestrial environments with rocky crevices; whereas, the Chinese three-striped box turtle (*C. trifasciata* Bell, 1825), golden-headed box turtle (*C. aurocapitata* Luo and Zong, 1988), and Pan’s box turtle (*C. pani* Song, 1984), which are morphologically similar and possess very flat and streamlined shells (*R* = 0.48, 0.45, and 0.47, respectively; Zhang et al. 1998) that are typical of aquatic species (*R* under approx. 0.6; Domokos and Várkonyi 2008), are completely aquatic (Zhang et al. 1998; Cheung 2007). Phylogenetic analysis will be needed to elucidate the patterns of shell evolution and habitat diversification of *Cuora* spp. in the future.

In summary, we found that the two species occupy different niches. *C. mouhotii* prefers microhabitats with rock crevices and was more commonly observed on slopes with steep inclines in the field, for which its flattened shell is well suited, whereas the
dome-shelled of *C. galbinifrons* restricts the species to hiding in deciduous leaves with bamboos and to microhabitats with relatively gentle slopes. Therefore, we conclude that morphological divergence allows the two *Cuora* spp. to partition the available microhabitats, and, thereby, to successfully co-occur.

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Table 1 Characteristics of microhabitat used by C. mouhotii and C. galbinifrons. Values indicate the mean ± SD measurements for each species, as well as the statistical significance of their difference.

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<th>Quadrat size</th>
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<th>C. galbinifrons</th>
<th>one-way ANOVA</th>
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<tr>
<td>Slope gradient (°)</td>
<td>10 × 10 m</td>
<td>33.55 ± 8.5</td>
<td>26.81 ± 6.25</td>
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<tr>
<td>Canopy (%)</td>
<td>10 × 10 m</td>
<td>75.45 ± 10.39</td>
<td>80.19 ± 6.12</td>
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<tr>
<td>No. fallen logs</td>
<td>10 × 10 m</td>
<td>2.84 ± 1.78</td>
<td>2.85 ± 1.23</td>
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<tr>
<td>No. bamboo clumps</td>
<td>10 × 10 m</td>
<td>4.95 ± 2.47</td>
<td>4.00 ± 2.62</td>
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<tr>
<td>No. tree holes</td>
<td>10 × 10 m</td>
<td>1.25 ± 0.87</td>
<td>0.89 ± 0.75</td>
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<tr>
<td>No. rock crevices</td>
<td>10 × 10 m</td>
<td>5.45 ± 4.81</td>
<td>0.19 ± 0.48</td>
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<td>Bamboo density (plants/m²)</td>
<td>1 × 1 m</td>
<td>4.43 ± 4.37</td>
<td>3.85 ± 5.19</td>
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<td>Herbage height (cm)</td>
<td>1 × 1 m</td>
<td>41.01 ± 23.59</td>
<td>38.70 ± 16.68</td>
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<tr>
<td>Herbage density (plants/m²)</td>
<td>1 × 1 m</td>
<td>4.41 ± 2.49</td>
<td>4.33 ± 2.97</td>
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<tr>
<td>Decid. leaf cover (%)</td>
<td>1 × 1 m</td>
<td>48.07 ± 20.78</td>
<td>80.93 ± 14.08</td>
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<tr>
<td>Decid. leaf thickness (cm)</td>
<td>1 × 1 m</td>
<td>6.18 ± 3.38</td>
<td>17.56 ± 24.88</td>
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<tr>
<td>Stone cover (%)</td>
<td>1 × 1 m</td>
<td>58.48 ± 35.21</td>
<td>2.78 ± 2.25</td>
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Table 2 Stepwise discriminant analysis of microhabitat variables of two Cuora spp.

<table>
<thead>
<tr>
<th>Variable No.</th>
<th>Variables</th>
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<th>Wilk’s λ</th>
<th>F</th>
<th>P</th>
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<tr>
<td>1</td>
<td>Stone cover</td>
<td>0.962</td>
<td>0.51</td>
<td>66.29</td>
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<tr>
<td>2</td>
<td>Slope gradient</td>
<td>0.424</td>
<td>0.463</td>
<td>39.429</td>
<td>&lt;0.0001</td>
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<tr>
<td>3</td>
<td>Bamboo density</td>
<td>0.36</td>
<td>0.432</td>
<td>29.382</td>
<td>&lt;0.0001</td>
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Table 3 Difference in the morphology of two *Cuora* spp. Values indicate the mean ± SD measurements for each species, as well as the statistical significance of their difference (one-way ANOVA for carapace length and one-way ANCOVA for the remaining parameters, with carapace length as the covariate).

<table>
<thead>
<tr>
<th></th>
<th><em>C. mouhotii</em></th>
<th><em>C. galbinifrons</em></th>
<th>$F$</th>
<th>$P$</th>
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<tbody>
<tr>
<td>Sample size</td>
<td>18</td>
<td>13</td>
<td></td>
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<tr>
<td>Carapace length (mm)</td>
<td>162.91 ± 18.47</td>
<td>168.77 ± 8.61</td>
<td>1.12</td>
<td>0.298</td>
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<tr>
<td>Carapace width (mm)</td>
<td>114.24 ± 7.82</td>
<td>113.98 ± 4.73</td>
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<tr>
<td>Carapace height (mm)</td>
<td>65.81 ± 4.19</td>
<td>79.26 ± 3.67</td>
<td>101.53</td>
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<td>Carapace height / width</td>
<td>0.58 ± 0.03</td>
<td>0.70 ± 0.03</td>
<td>113.65</td>
<td>&lt; 0.0001</td>
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**Figure Legends**

**Fig. 1** The shared macrohabitat and divergent preferred microhabitats of two sympatric *Cuora* spp. in Hainan, China. A, the high-canopy cover habitat shared by both *C. mouhotii* and *C. galbinifrons*. B, the preferred microhabitat of *C. mouhotii* (rock crevices), with a turtle visible in the crevice (arrow). C, the preferred microhabitat of *C. galbinifrons* (deciduous leaf litter under bamboo clumps), with a turtle visible under the leaf litter (arrow). All photos were taken by F. Xiao.

**Fig. 2** Distribution of the quadrats on the DFA axis.
Fig. 1 The shared macrohabitat and divergent preferred microhabitats of two sympatric Cuora spp. in Hainan, China.

382x821mm (300 x 300 DPI)
Fig. 2 Distribution of the quadrats on the DFA axis

105x75mm (300 x 300 DPI)