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Ecological niche overlap of two allopatric karst-adapted tiger geckos (*Goniurosaurus*) from northern Vietnam: microhabitat use and implications for conservation

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ABSTRACT

Anthropogenic pressures have caused a substantial decline of global biodiversity and have been further reported to strongly affect the ecological performance of species in their habitat, especially reptiles. Understanding the ecology of species and how species respond to habitat alterations is basic knowledge needed to develop conservation programmes and address issues of biodiversity loss. All five species of tiger geckos (*Goniurosaurus*) in Vietnam are known to be threatened by extinction due to anthropogenic impacts such as habitat degradation and harvesting for the international pet trade. However, conservation actions have only been initiated for the better-studied species. This study provides detailed basic data on microhabitat use of two allopatric sister species, namely *Goniurosaurus huuliensis* and *G. luii*. In total, 145 geckos (including 59 records of *G. huuliensis* and 86 records of *G. luii*) were observed during field surveys. All *Goniurosaurus* individuals were mostly recorded in the forest on karst formations, covered with evergreen broad-leaved woody trees, intermixed with ferns, shrubs and vines. Microhabitats of the two species were relatively similar in other traits, such as high vegetation coverage, high humidity, stable ambient temperature and dry-rock substrates. A multiple factor analysis supported that the ecological niche spaces of the two species highly overlap, even though their distribution ranges are geographically separated. We further found no intraspecific niche segregation in both species. The present data provide baseline knowledge for both *in situ* and *ex situ* conservation measures to protect species in the genus *Goniurosaurus*.

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Introduction

A species' distribution range is limited by multiple constraints of species' physiological tolerances, biotic interactions and dispersal barriers. Within the distribution range, the

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realised niche space of a species contains the necessary resources to maintain a stable population density and allow reproduction (Grinnel 1917; Schoener 1974; Toft 1985; van Buskirk 2005; Bowles et al. 2006; Indemaur et al. 2010; Menin et al. 2011). A non-equilibrium of ecosystems due to past and ongoing human impacts may strongly affect the ecological performances of species, especially of ectotherms, and may consequently lead to a substantial decline in the species' abundance or even to species loss (Huey 1991; Sunday et al. 2014). Monastersky (2014) indicated that habitat loss/degradation and climate change have been regarded as the most severe threats to the global biodiversity and it is assumed they will become worse over time. Understanding the ecology of species and how species respond to natural alterations under human impacts are highly necessary to propose adequate conservation measures to protect species and ecosystems more effectively (Lichstein et al. 2002; Amo et al. 2007; Pelegrin et al. 2009).

Karst and granite formations from the Ryukyu Archipelago, Japan, southwards through southern China (including the Hainan Archipelago) to northern Vietnam (including the Gulf of Tonkin) provide various natural habitats for a total of 24 *Goniurosaurus* (i.e. 'tiger gecko') species (Grismer et al. 1999; Orlov et al. 2008; Ziegler et al. 2008; Nguyen et al. 2009; Yang and Chan 2015; Honda and Ota 2017; Zhou et al. 2018; Qi et al. 2020a, 2020b; Zhu et al. 2020a, 2020b; Grismer et al. 2021; Ngo et al. 2021b; Uetz et al. 2022). Owing to restricted geographic ranges and small population sizes, all species of *Goniurosaurus* are considered to be susceptible and vulnerable to anthropogenic impacts, such as habitat degradation and climate change (Yang and Chan 2015; Ngo et al. 2016, 2019b, 2021a, 2022). Furthermore, several tiger gecko species have been over-exploited to supply the international pet trade (Ngo et al. 2019b), which has already led to local extirpations in a few areas in China and Vietnam (Grismer et al. 1999; Stuart et al. 2006; Yang and Chan 2015; Ngo et al. 2016, 2019b). Consequently, all species of *Goniurosaurus* have been recently listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to regulate the international trade (Ngo et al. 2019b; CITES Notification No. 2020/068), whereof 17 species have been evaluated to be threatened [listed as Vulnerable (VU), Endangered (EN) and Critically Endangered (CR)] in the IUCN Red List (IUCN 2021).

In Vietnam, four tiger gecko species, namely *G. araneus*, *G. catbaensis*, *G. huuliensis* and *G. luyi*, have been found exclusively in evergreen forests on karstic formations, and *G. lichtenfelderi* has been only found in granitic-stream habitats (Nguyen et al. 2009; Nguyen 2011; Grismer et al. 2021; Ngo et al. 2021b). Due to their small population sizes and high rates of exploitation for the pet trade, all Vietnamese tiger geckos are further nationally protected by the Governmental Decree 06/2019/ND-CP (Management of endangered, precious and rare species of forest fauna and flora in Vietnam) Group IIB; thus, exploitation and trade in wild animals of these species are not allowed without permits proved by relevant national authorities (Ngo et al. 2019b). Based on studies of the population status and the species ecology, *in situ* conservation measures have been implemented to protect wild populations of *G. catbaensis* in Ha Long Bay and Cat Ba National Park in northern Vietnam (see Ngo et al. 2016, 2019a). Using species distribution models (SDMs), Ngo et al. (2021a) predicted the potential distribution and identified the core refugia for *G. lichtenfelderi*. Ngo et al. (2022) used these SDMs results, coupled with detailed descriptions of microhabitat use, as science-based information to kick off conservation activities for this species. In the case of *G. araneus*, despite extensive surveys

over the last two decades, its distribution in Vietnam is uncertain (Grismer et al. 1999; Ngo et al. 2021b). For the two remaining species, *G. luyi* and *G. huuliensis*, their ecology and habitat use have been poorly studied so far.

The Huulien tiger gecko, *G. huuliensis*, was considered endemic to its type locality in Huu Lien Nature Reserve (NR), Lang Son Province, northern Vietnam (Figures 1, 2(c)) (Orlov et al. 2008; Nguyen et al. 2009; Nguyen 2011). Recently, new populations of *G. huuliensis* were discovered outside of Huu Lien NR, in Than Sa – Phuong Hoang Nature Reserve in Thai Nguyen Province (Figure 1; Ngo et al. 2021b). The Lui tiger gecko, *G. luyi*, was first discovered in southern China and afterwards found in northern Vietnam (Figures 1, 2(d)) (Grismer et al. 1999; Vu et al. 2006). Based on morphological and phylogenetic analyses, the two tiger gecko species are considered sister taxa in the *G. luyi* group, which includes seven more relatives (Orlov et al. 2008; Grismer et al. 2021; Ngo et al. 2021b).

Due to the small area of occupancy, wild populations of the two species are assumed to be relatively small and highly susceptible to anthropogenic impacts (Ngo et al. 2016, 2019b, 2021a). A preliminary population size estimation for *G. luyi* indicated that its wild populations are indeed rather small, with only a few individuals per locality (Ngo et al. 2016). For *G. huuliensis*, it was predicted that the potential distribution will be diminished or even will be completely vanished by the 2070s due to climate change (Ngo et al. 2021a). Recently, *G. huuliensis* (CR) and *G. luyi* (VU) were assessed in the IUCN Red List (Nguyen 2018; Nguyen et al. 2021).

The present study aimed to provide insights on the microhabitat characteristics of the two less studied tiger gecko species and assess intraspecific and interspecific differences in their habitat use. Despite their geographical distribution being contiguous, the two tiger gecko species occur in allopatry (Ngo et al. 2021b). We herein assess whether there is niche partitioning between *G. huuliensis* and *G. luyi* pointing to a non-physical barrier. This ecological knowledge will provide a basis for *in situ* and *ex situ* measures for the conservation of tiger geckos and their habitats.

Materials and methods

Study sites

Study sites were selected based on previous observations, literature and interviews with local people and rangers in northern Vietnam. *Goniurosaurus huuliensis* is known from its type locality in Huu Lien NR, Lang Son Province, northern Vietnam, at elevations from 300 to 370 m a.s.l. (Figures 1, 2(a)) (Orlov et al. 2008). The landscape of Huu Lien Nature Reserve is predominantly covered by evergreen forests on karst formations. In particular, 9734 ha or 91% of the nature reserve is limestone karst, of which 9082 ha (93% of the total) is forested (Anon 1990). In Vietnam, *G. luyi* has been found from Ha Lang and Trung Khanh districts of Cao Bang Province along the border between China and Vietnam (Grismer et al. 1999; Vu et al. 2006), and was afterwards recorded in Trang Dinh District of Lang Son Province (Ngo et al. 2021b), in close proximity to its type locality in China (Figures 1, 2(b)).

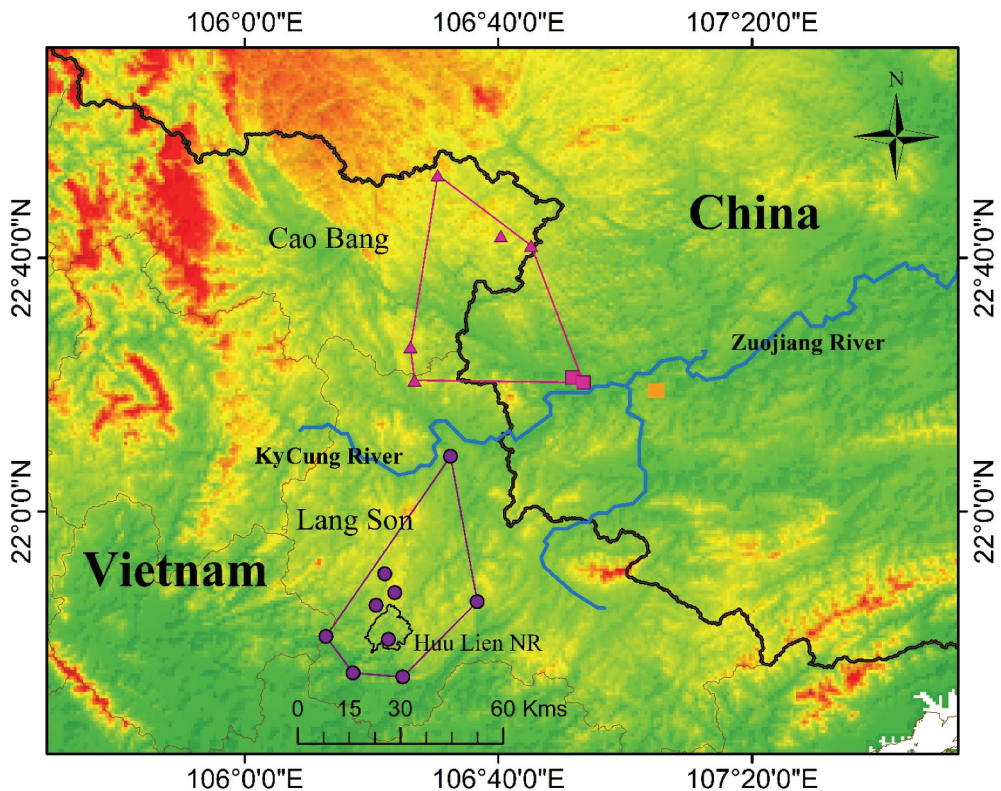


Figure 1. Geographic distribution of *Goniurosaurus huuliensis* (violet circles enclosed by a violet line) and *Goniurosaurus luyi* (pink triangles – northern Vietnam; pink squares – southern China – enclosed by a pink line). The orange square represents the distribution of another tiger gecko species, namely *Goniurosaurus araneus*, in China.

Field surveys

Field surveys were conducted to collect data on microhabitat parameters for *G. luyi* in June 2014, May, July and September 2019, September 2020 and April 2021, and for *G. huuliensis* in April and August 2019 as well as in June 2020. We carried out a few daytime excursions to interview local people for potential unknown sites of occurrence and to assess the presence of human impacts in the forest. A total of 17 survey transects, comprising five transects in the area of occupancy of *G. huuliensis* and 12 in the area of occupancy of *G. luyi*, were set up along forest paths or patrolling trails of forest rangers, selected based on evidence of the presence of the species in the area. Crop hills in close proximity to the survey transects were also checked for the occurrence of tiger geckos. Night excursions were conducted between 20:00 and 05:00 of the next day, since the target species are nocturnal and spend the daytime hidden in rocky crevices (Grismer et al. 1999; Werner et al. 2005; Vu et al. 2006; Orlov et al. 2008; Nguyen 2011). During the few daytime surveys, no animals were recorded. Animals were captured by hand and subsequently released at their collecting site after taking measurements of snout-vent length (SVL) and body temperature and after sexual identification.

Microhabitat characterisation

Regarding microclimatic parameters, the air temperature (°C) and relative air humidity (%) were measured with a digital thermometer (TFA Dostmann/Wertheim Kat. No. 30.5015) at each location where animals were captured. We used an infrared thermometer (Measupro IRT20) to measure temperatures (°C) at the substrate surface and at the body surface of animals (on the belly). We further documented the weather conditions of each surveyed day (raining or not).

The following microhabitat characteristics were also recorded: substrate type [classified as rock (bare rock), rock – moss (rock covered with moss), rock – vines – leaves (rock covered with vines and leaves), wood, soil, rock on ground], substrate condition (dry or wet), substrate angle (between the substrate surface axis and the horizontal axis, ranging from 0° to 90°), height (vertical distance from the ground to the animal, in m), exposure (outside or inside cave/crevice) and canopy (percentage of vegetation coverage above each animal – estimated by direct observation). The activity status of each animal was recorded as resting, feeding or moving. In addition, the time of observation was recorded. Coordinates of captured individuals, together with elevation values, were recorded with a Garmin 64 GPS. The specific coordinate data will be shared by the authors only upon request.

To identify intraspecific differences in microhabitat use, the sex of each captured individual was determined based on the presence (in males) or absence (in females) of large, swollen hemipenial bulges. Each individual was assigned to an age class by measuring the body length (SVL < 85 mm = juveniles, SVL ≥ 85 mm = adults; see Ngo et al. 2021b).

Statistical analyses

Statistical analyses were performed using R v. 3.1.2 (RStudio Team 2018). A Shapiro–Wilk test was used to check the assumption of normality. A Kruskal–Wallis test, combined with a Mann–Whitney pairwise test, was performed to determine differences in microhabitat parameters among age and sex classes. A Wilcoxon test was used to identify the difference in habitat use between *G. huuliensis* and *G. luyi*. Additionally, we used a Chi-square test to examine intra- and interspecific differences of categorical variables. A linear regression was computed to test for the linear relationship between body and air/substrate temperatures. For these tests, we applied a significance level of $P = 0.05$.

We performed a multiple factor analysis (MFA) using the collected ecological data set, comprising two qualitative groups – ‘species’ and ‘habitat’ (e.g. activity status, occupied position, substrate type, substrate condition) – and four quantitative groups – ‘canopy’, ‘climate’ (e.g. humidity and air temperature), ‘elevation’ and ‘micro-position’ (e.g. occupied height). This ordination test was performed using the packages ‘factoextra’ (Kassambara and Mundt 2020) and ‘FactoMinerR’ (Le et al. 2008) in the software R. The approach was applied to identify active groups and variables that account most for the variation within the data set. Similar coded colours in the MFA scatter plot, surrounded with convex hulls, were presented to visualise the ecological niche spaces of *G. huuliensis* and *G. luyi*. Their ecological spaces were showed within two different spatial coordinates of dimension axes (Dim1 and Dim2; Dim3 and Dim4 – showing the highest eigenvalues).

To evaluate the overlap, the first four Dim values of each tiger gecko individual were extracted to identify the difference between the two species using the Wilcoxon test.

Results

Microhabitat use

The microhabitat characterisation for the two species was based on an ecological data set of 145 individuals of *Goniurosaurus* observed during field surveys. Among them, 59 individuals (1 juvenile, 34 females, 20 males, 4 unsexed adults) were identified as *G. huuliensis*, and 86 individuals (11 juveniles, 41 females, 30 males, 4 unsexed adults) were assigned as *G. luyi*. *Goniurosaurus huuliensis* was found at various elevations from 176 to 500 m a.s.l. (384 ± 9.6 m), whereas *G. luyi* was documented at higher elevations from 338 to 719 m a.s.l. (465 ± 8.9 m) (Figure 3(h); Table 1; Wilcoxon test, $W = 740$, P value < 0.001). Individuals of the two species were mainly recorded in the forest on limestone formations, covered with evergreen broad-leaved woody trees, intermixed with ferns, shrubs and vines (Figure 2(a,b)). Only three individuals of *G. luyi* were found on single rocks, in two crop hills in Cao Bang Province. Usually, the two species were not evenly distributed along the transects; rather, we usually found them clumped at a few sites, often around large cave formations.

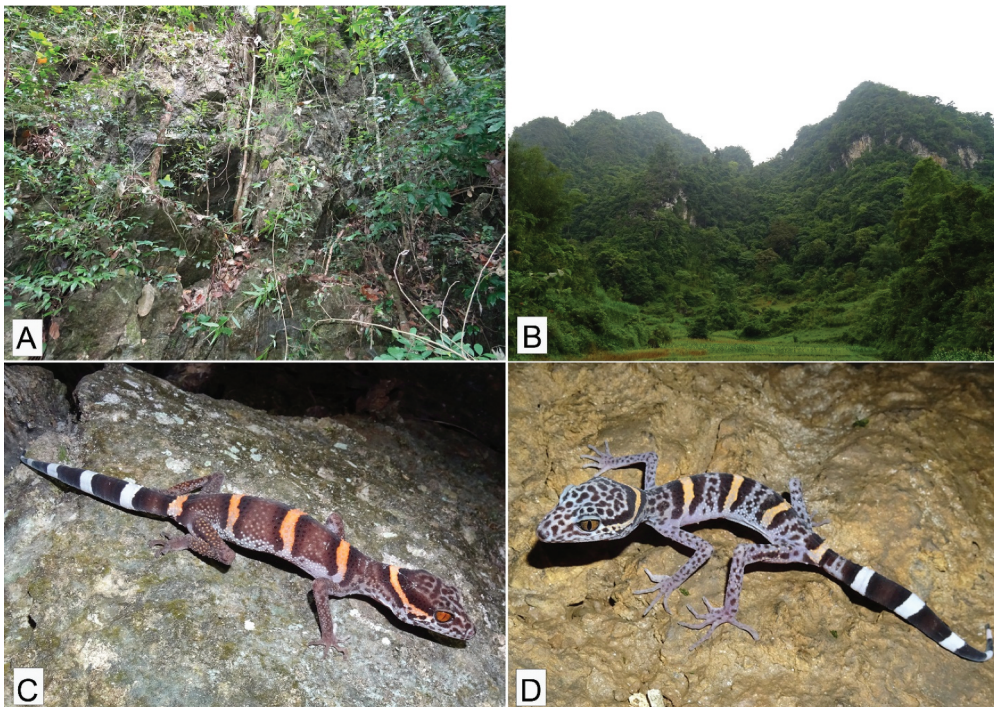


Figure 2. (a) Karst mountain inhabited by *Goniurosaurus huuliensis*; (b) Microhabitat of *Goniurosaurus luyi*; (c) *G. huuliensis*; and (d) *G. luyi* on rock substrate. (Photographed by Hai N. Ngo.)

The mean ambient air temperature in habitats of *G. huuliensis* was $26.7 \pm 0.2^\circ\text{C}$ (22.7–28.9°C, $n = 58$), slightly higher than that in habitats of *G. luii* ($25.6 \pm 0.2^\circ\text{C}$, 21.9–28.6°C, $n = 71$) (Figure 3(a); Table 1; Wilcoxon test, $W = 2984$, P value < 0.001). A difference was also documented for substrate and body temperatures, with significantly higher values for *G. huuliensis* (Figure 3(b,c); Table 1; Wilcoxon tests, P values < 0.05). The body temperature was positively correlated with the ambient air temperature as well as the substrate temperature (linear regression, $r_s > 0$, P values < 0.001). The relative humidity was similar in the habitats of both species and ranged between 58% and 100% (Figure 3(d); Table 1; Wilcoxon test, $W = 2205$, P value $= 0.7 > 0.05$).

With regard to the substrate type, the majority of individuals of both species were found on bare rock (at least 72.9%), while *G. luii* was never found on rocks on the ground (Figure 4(a)). Both species were rarely observed on other substrates such as wood or the forest floor (Figure 4(a1,a2)). Individuals of *G. luii* were generally found sitting on more steeply angled surfaces (mean 68.3° , $n = 24$) than *G. huuliensis* (mean 55.3° , $n = 34$) (Figure 3(e); Table 1; Wilcoxon test, $W = 451$, P value < 0.05). The majority (at least 75%) of animals in both species were found outside, but in the close vicinity, of caves and rocky crevices as well as on dry substrates (Figure 4(b1,b2,d1,d2); Chi-square tests, P values > 0.05). The canopy coverage was relatively less dense in microhabitats of *G. huuliensis* ($65.18 \pm 4.0\%$; 5–100%, $n = 59$) compared to *G. luii* ($83.73 \pm 2.9\%$; 0–100, $n = 71$) (Figure 3(g); Table 1; Wilcoxon test, $W = 1347$, P value < 0.001). We found *G. huuliensis* at an average height above the ground of 0.7 ± 0.2 m (0–2.5 m, $n = 59$), which was relatively lower than *G. luii* (0.9 ± 0.1 m, 0–3.0 m, $n = 86$) (Figure 3(f); Table 1; Wilcoxon test, $W = 1440$, P value < 0.001). During night surveys, the majority of animals were found resting (*G. huuliensis*: 67.8% – 40 individuals; *G. luii*: 85.9% – 61 individuals), whereas a few individuals of both species were found actively foraging and feeding (Chi-square test, $\text{Chi}^2 = 4.89$, $\text{df} = 2$, P value > 0.05). An individual of *G. luii* was observed feeding on a large cave cricket. Regarding intraspecific comparisons, we did not find any significant differences in microhabitat use between sexes or age classes (Chi² tests and Kruskal–Wallis tests, P values > 0.05).

No individual of either species was encountered during the daytime surveys. At night, both species were observed to be active from approximately 20:00 h to 03:00 h, with the exception of one individual of *G. luii*, which was observed between 03:00 h and 05:00 h (Figure 5). The recorded time of highest activity in both species was between 21:00 h and 01:00 h ($n = 103$; Figure 5).

Table 1. Environmental parameters characterising the microhabitat of *Goniurosaurus huuliensis* and *Goniurosaurus luii*. SE: standard error.

Parameters	<i>Goniurosaurus huuliensis</i>	<i>Goniurosaurus luii</i>
	Min – max (mean \pm SE)	Min – max (mean \pm SE)
Elevation (m)	176–500 (384 ± 9.6 , $n = 59$)	338–719 (465 ± 8.9 , $n = 71$)
Humidity (%)	58–100 (75.2 ± 1.5 , $n = 58$)	59–85 (74.0 ± 0.9 , $n = 71$)
Air temp. (°C)	22.7–28.9 (26.7 ± 0.2 , $n = 58$)	21.9–28.6 (25.6 ± 0.2 , $n = 71$)
Substrate temp. (°C)	20.4–26.8 (24.0 ± 0.3 , $n = 32$)	17.7–28.2 (23.0 ± 0.2 , $n = 64$)
Body temp. (°C)	20.2–27.1 (24.2 ± 0.3 , $n = 32$)	17.5–28.5 (23.3 ± 0.2 , $n = 64$)
Canopy coverage (%)	5–100 (65.18 ± 4.0 , $n = 59$)	0–100 (83.73 ± 2.9 , $n = 71$)
Height (m)	0–2.5 (0.7 ± 0.2 , $n = 59$)	0–3.0 (0.9 ± 0.1 , $n = 86$)
Position angle (°)	0–90 (55.3 ± 5.4 , $n = 34$)	20–90 (68.3 ± 3.9 , $n = 24$)

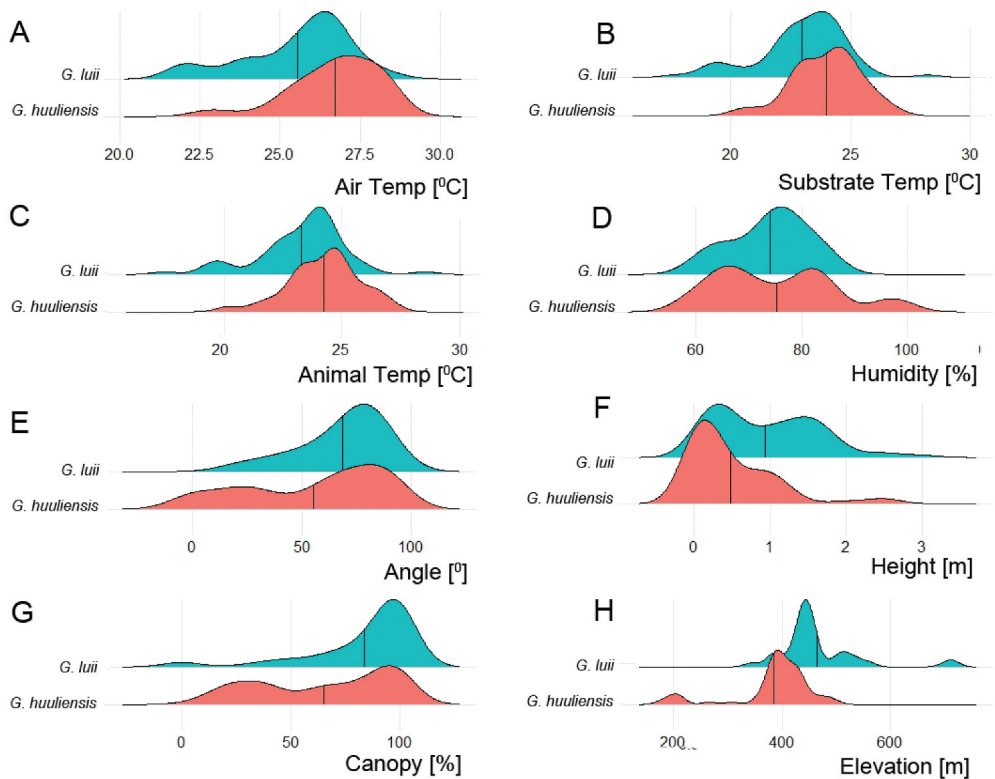


Figure 3. Microhabitat characters of *Goniurosaurus huuliensis* and *Goniurosaurus luii*. (a) Air temperature; (b) substrate surface temperature; (c) animal temperature; (d) relative air humidity; (e) substrate angle; (f) occupied height; (g) canopy coverage; (h) elevation.

The MFA identified ecological sets of habitat, climate, canopy and elevation as active groups (Figure 6(a)), and the first four important dimensions (Dim1–4) accounted for 50.3% of the variation in the data set (Figure 6(c)). In particular, Dim1 accounted for 17.1% of the variation, and was loaded most heavily by canopy coverage, elevation and two climatic variables (air temperature and humidity). Three remaining dimensions accounted for slightly lower percentages of the observed variation and were loaded primarily by elevation (Dim2), canopy (Dim3) and humidity (Dim4) (Figure 6(b)). The MFA further showed that the ecological space of *G. huuliensis* highly overlaps with that of *G. luii* according to axes Dim1, Dim3 and Dim4 (Figure 6(c); Wilcoxon tests, P values > 0.05). However, Dim2 is significantly different between the two tiger gecko species (Figure 6(c1); Wilcoxon test, $W = 594$, P value < 0.001).

Habitat degradation

Limestone mountains, the habitat of the two tiger gecko species, have been destroyed and quarried to extract materials for cement production, and to expand road construction and infrastructure associated with urbanisation (Figure 7(a)). Furthermore, a large area of the protected forests was found to be strongly fragmented due to timber logging

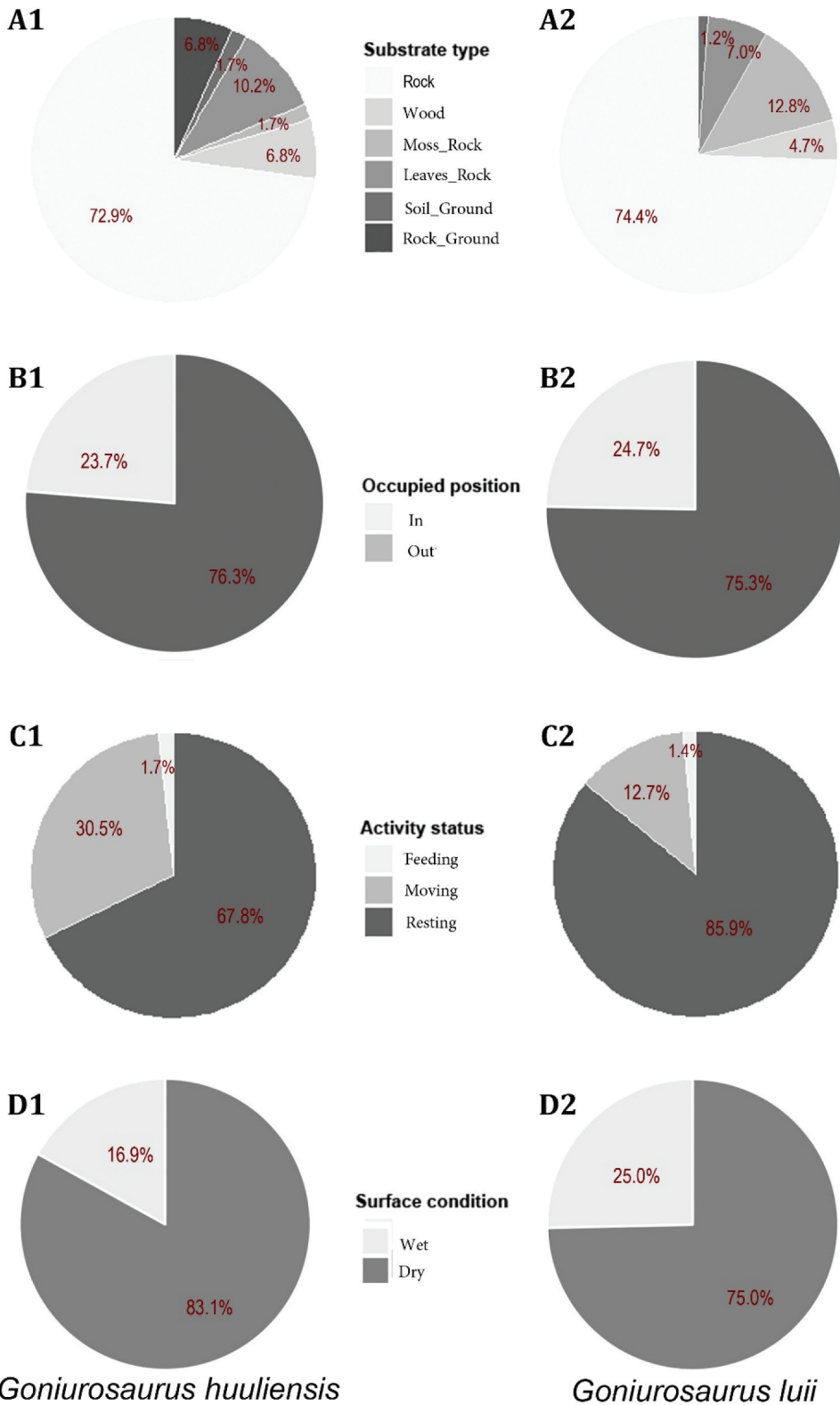


Figure 4. Microhabitat parameters and activity of *Goniurosaurus huuliensis* (1) and *Goniurosaurus luii* (2): (a) substrate type; (b) position to cave/ crevice; (c) activity status; (d) substrate moisture.

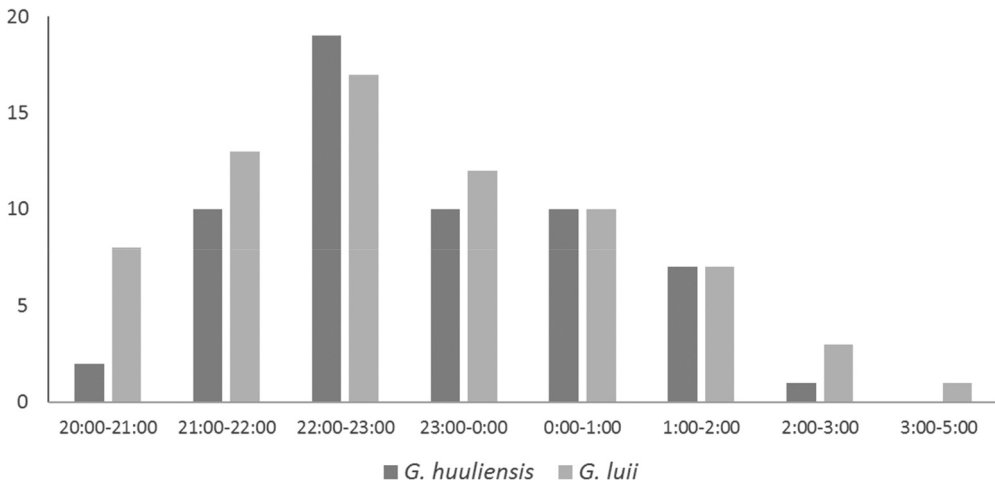


Figure 5. The number of observed individuals of *Goniurosaurus huuliensis* and *Goniurosaurus luyi* at different time intervals.

activities, and those areas were gradually replaced with industrial crops or became grassy hills (Figure 7(b)).

Discussion

Microhabitat characterisation

The present microhabitat characterisation confirmed previous observations that *G. huuliensis* and *G. luyi* are indeed limestone karst-dwelling lizards in evergreen forests (Grismer et al. 1999, 2021; Orlov et al. 2008; Nguyen 2011; Ngo et al. 2021b). Only three individuals of *G. luyi* were found on single rocks in crop hills, in close proximity to the forest, which might be only temporary sites, visited during foraging. In general, the microhabitats of the two species were highly similar, characterised by high vegetation coverage, high humidity, stable ambient temperature and the presence of dry rocks. Rock crevices of open caves, as well as single karstic rocks, were identified as shelters for *G. huuliensis* and *G. luyi* to escape from predators and to hide during the day. These characteristics are relatively similar to those of a karst-dwelling sister species, namely *G. catbaensis*, which occurs on isolated islands in northern Vietnam (Ngo et al. 2019a). However, the MFA ordination test of niche spaces for *G. huuliensis* and *G. luyi* revealed that their slight discordance is mainly related to the elevation segregation (Figure 6(c)).

Not surprisingly, the body temperature of each species was positively correlated with the environmental temperature, confirming that their physiological functions are inter-linked with environmental conditions, as for most ectothermic species (van Schingen et al. 2015; Ngo et al. 2018, 2019a; Vicente et al. 2019). Single tests documented interspecific differences in air and substrate temperatures between microhabitats of the two species. These differences might be explained by naturally varying weather conditions among the relatively short survey periods. Therefore, we recommend long-term monitoring to assess potential effects of environmental conditions on the adaptation of the two tiger geckos.

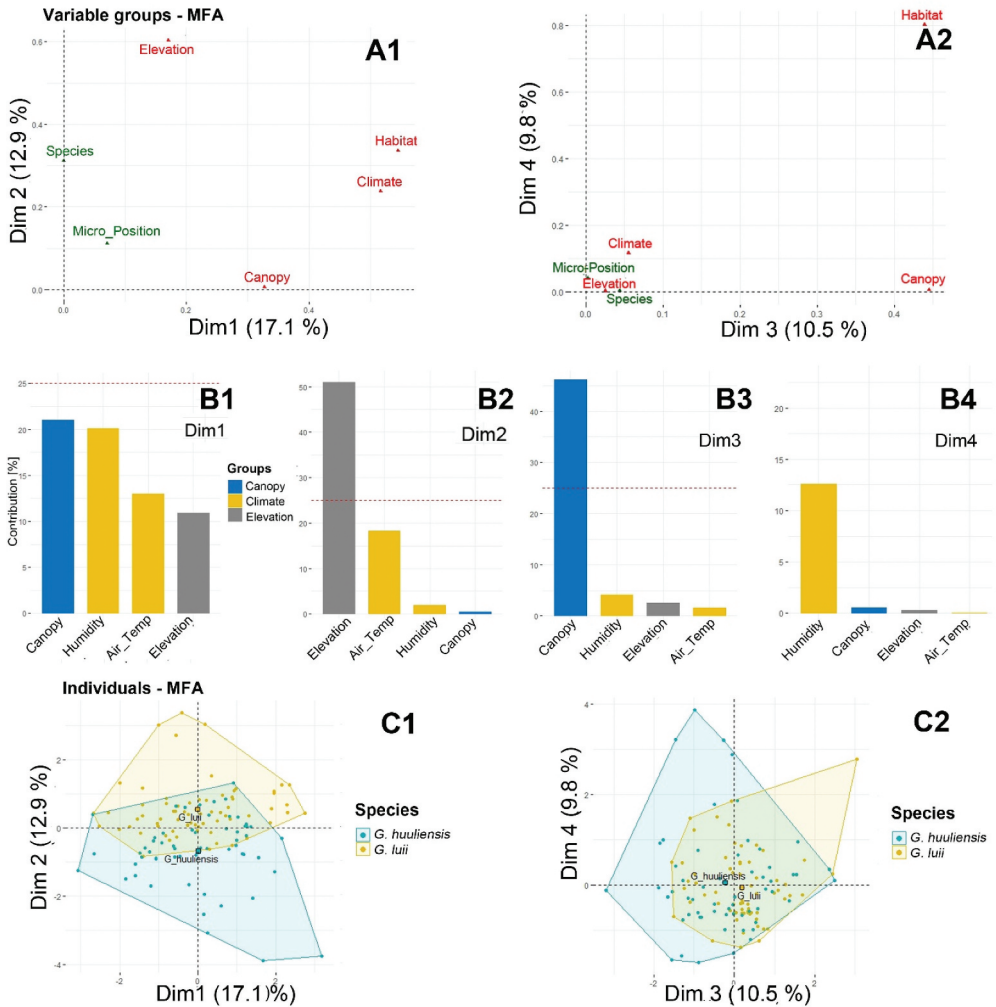


Figure 6. (a) Scatterplots of all variable groups on coordinates of (1) Dim1–Dim2, (2) Dim3–Dim4 axes in the multiple factor analysis (MFA); (b) the first four important variables contributing to (1) Dim1, (2) Dim2, (3) Dim3, (4) Dim4; (c) scatter diagrams illustrating ecological spaces of *Goniurosaurus huuliensis* and *Goniurosaurus luii* on coordinates of (1) Dim1–Dim2, (2) Dim3–Dim4 axes.

We further noted a wide range in humidity (58–100%) in habitats of both tiger gecko species, whereof the lowest values (humidity < 65%, n = 29) were mostly recorded before 0:00 h (about 86%). Probably, the different times of day and weather events, such as rain, cause this high range in humidity.

Intraspecific competition has frequently been reported for high-density populations that share resources, such as mating sites and nest sites, especially when the optimal space is limited (Irschick et al. 2005; van Schingen et al. 2015; Ngo et al. 2016). Niche partitioning can reduce the pressure of intraspecific competition and has been documented in other Vietnamese lizards regarding the height of the resting position from the ground, which differed between age classes (e.g. in *G. catbaensis*, *Cnemaspis psychedelica* and *Shinisaurus crocodilurus*) (van Schingen et al. 2015; Ngo et al. 2018, 2019a). In the

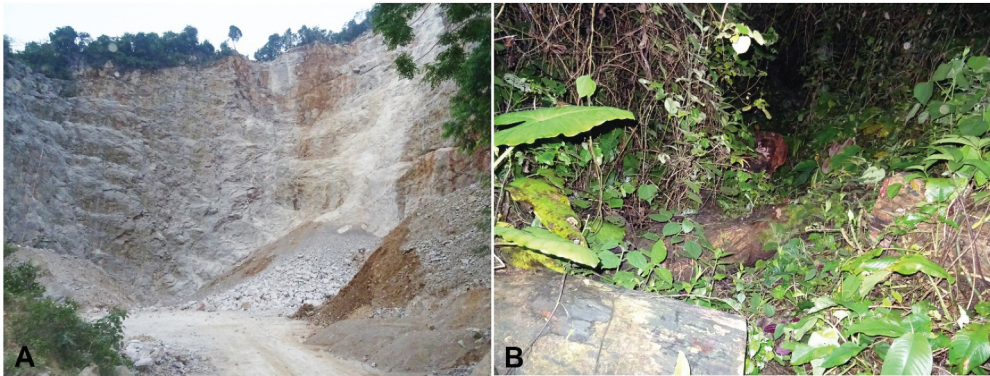


Figure 7. Anthropogenic impacts in natural habitats of *Goniurosaurus huuliensis* and *Goniurosaurus luyi*: (a) quarrying for cement production; (b) timber logging. (Photographed by Hai N. Ngo.)

present study, we did not record any significant difference in the microhabitat characteristics among age or sex classes in either species. This could be due to the low observed population densities, which might mitigate the frequency of encounters (e.g. male–male) and thus limit the intraspecific competition.

Allopatric speciation

Previous studies and our observations have never documented *G. luyi* and *G. huuliensis* at the same locality (Vu et al. 2006; Orlov et al. 2008; Ngo et al. 2016); thus, they are considered to be allopatric in northern Vietnam. In particular, *G. luyi* is currently known from areas stretching across the North of Lang Son Province, northwards of Cao Bang provinces, from northern Vietnam to southern China. *Goniurosaurus huuliensis* has been recorded in similar karstic formations, but only in isolated areas in the South of Lang Son Province (Figure 1) (Grismer et al. 1999; Orlov et al. 2008; Nguyen 2011; Ngo et al. 2021b). Ecological conditions are considered the major factors of non-physical barriers that determine range limits, as well as being a driver of speciation (MacArthur 1984; Orr and Smith 1998; Schluter 2009; Glor and Warren 2011). Disjunct karst formations along the elevation gradient can facilitate the existence of isolated microhabitats in close proximity with one another, which can promote allopatric speciation as a result of long-term reproductive isolation and genetic drift (Lichstein Körner 2004; Clements et al. 2006; Hoorn et al. 2018). Although the species' occurrences are geographically separated and differ in elevation (from 176 to 719 m a.s.l.), we found that their micro-niche space highly overlapped and that microhabitat characteristics are similar between the two species, which indicates a high level of niche conservatism (Wiens and Graham 2005; Wiens et al. 2010; Pyron et al. 2014). That would be in line with the morphological and genetic similarities between the two phylogenetic sister species (Grismer et al. 2021; Ngo et al. 2021b). Recent studies have highlighted the role of large rivers and canyons as potential barriers among *Goniurosaurus* sister taxa in continental sites from China and Vietnam (Chen et al. 2014; Qi et al. 2020a; Zhu et al. 2020a; Ngo et al. 2021b). The cladogenesis (viz. the allopatric speciation of *G. huuliensis* and *G. luyi*) could be explained by the emergence

of a local river (Ky Cung River) in Lang Son Province (Figure 1), which might have limited interbreeding populations. Notably, distribution ranges of *G. luyi* and *G. araneus* in China are separated by the Zuojiang River (Chen et al. 2014), which is coupled with the Ky Cung River and has likely established the continuous eastern distribution boundary of *G. luyi* (Figure 1).

Conservation

The present microhabitat characterisation of *G. huuliensis* and *G. luyi* is intended to assist conservationists in collaboration with local rangers and other relevant authorities to carry out conservation actions more effectively. Typically, karst formations in undisturbed forests provide key habitats for these two species of *Goniurosaurus*. However, as we documented in interviews with local communities and by direct observations in the field, several of these unique habitats have been dramatically degraded or destroyed by human disturbances. The less dense coverage of vegetation recorded in wild populations of *G. huuliensis* from Huu Lien NR may be due to timber logging activities. Thus, we recommend greater protection of the species' core refugia by local rangers to ensure the long-term persistence of range-restricted populations and the integrity of their natural habitats. Recently, species distribution models have been applied to predict the potential distribution of *G. huuliensis* and identify the core refugia (Ngo et al. 2021a). Based on these models, coupled with ecological findings, a proposed plan to establish a protected area for conservation of *G. huuliensis* (Ngo et al. 2021a) promises success in the future. Due to the similarity in their microhabitat use, one-size-fits-all conservation measures can be applied between the two species, and can even be expanded to other karst-dwelling *Goniurosaurus* species.

The basic understanding of the microhabitat use of tiger geckos contributes to improve husbandry conditions and thereby also enhances the potential success of future reintroductions. In particular, the slight differences in microhabitat characteristics (e.g. lower air and substrate temperatures, steeper angle of substrates, higher perch sites and more dense coverage observed for *G. luyi* compared to *G. huuliensis*) should be considered for *ex situ* measures. Recently, *ex situ* conservation breeding programmes for all Vietnamese tiger gecko species have been established at the Me Linh Station for Biodiversity, Vietnam and Cologne Zoo, Germany, which resulted in the first, and continuing, breeding success (Pham et al. 2019, 2021; Ziegler and Rauhaus 2022). The establishment of a conservation breeding network is planned, which already includes several European zoos and is expanding into the USA (Ziegler and Rauhaus 2022). Having both in-country and foreign breeding programmes assures that reserve populations can be developed, which could facilitate future repatriation/restocking if required for disturbed wild populations to recover.

This study emphasised the importance of studying the natural history of species to enhance conservation activities. While more species are continually being described, data on their ecology and threat status are lacking in many cases. During the last decade, many reptile species have been further discovered in the study sites, for example *Gekko canhi* (Rösler et al. 2010), *Oligodon nagao* (David et al. 2012), *Gekko adleri* (Nguyen et al. 2013b), *Hemiphyllodactylus zugi* (Nguyen et al. 2013a) and *Achalinus juliani* (Ziegler et al. 2019). Especially considering the ongoing anthropogenic impacts, such as over-exploitation

(Ngo et al. 2019b), climate change (Ngo et al. 2021a) and habitat degradation, ecological studies on other species are needed to better understand the different roles and interactions of species in their habitats to better protect remaining ecosystems as a whole.

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