Climate as a gatekeeper: Unexpected absence of *Batrachochytrium salamandrivorans* in an Asian Chytrid hotspot suggests a narrow climatic niche for the pathogen

Dan Sun[1], Gajaba Ellepola[1], Jayampathi Herath[1], and Madhava Meegaskumbura[1]

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Abstract

The chytrid fungal pathogens *Batrachochytrium salamandrivorans* (*Bsal*) and *B. dendrobatidis* (*Bd*) are driving amphibian extinctions and population declines worldwide. They are thought to have originated in East/Southeast Asia, and hence Asia remains crucial for understanding the ecology of these pathogens. However, *Bsal* screening is relatively limited in this region, particularly in hotspots where *Bd* lineage diversity is high. To address this gap, we conducted an extensive survey across the Guangxi region of Southern China, now considered a *Bd* hotspot. We examined 1230 individuals from 38 amphibian species and 36 environmental water bodies sampled during mostly the middle spring and summer months of 2019-21. However, PCR testing revealed absence of *Bsal* in our samples. A subsequent niche modeling analysis for *Bsal* suggested that the bioclimatic conditions of much of the region may not be conducive to *Bsal*. Although our findings show absence of *Bsal* in the surveyed habitats, periodic monitoring in amphibians is still needed, particularly across seasons. This is because *Bsal* pathogenicity could increase at relatively lower temperatures, and *Bsal* may be partitioning its niche with *Bd* across seasons. Our results suggest that the climatic conditions of the karstic Guangxi plains and perhaps competition from other *Bd* lineages may suppress *Bsal* establishment in the region. Our study provide interesting insights into *Bsal* niche dynamics and the knowledge generated will facilitate the conservation efforts in amphibian populations devastated by chytrid pathogens across other regions of the world.

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Keywords

Batrachochytrium salamandrivorans ; Amphibians; Asia; Niche; Temperature; Geographic Distribution; Seasonality

Introduction

Amphibians worldwide face considerable threats, including habitat loss, climate change, and disease, which contribute to severe population declines and biodiversity loss (Amphibiaweb, 2023). Chytridiomycosis, a disease caused by the chytrid fungi *Batrachochytrium dendrobatidis* (*Bd*) and *B. salamandrivorans* (*Bsal*), is a major driver of these declines (Longcore et al., 1999; Martel et al., 2013; Scheele et al., 2019). Both *Bd* and *Bsal* are thought to have originated in Asia, with *Bd* portraying multiple lineages in the region (Martel et al., 2014; O'hanlon et al., 2018).*Bd* affects all three amphibian orders and has caused widespread declines, particularly in anuran species across all amphibian-inhabited continents (Scheele et al., 2019). In contrast, although present in Asia, *Bsal* has led to severe declines of native salamanders only in Europe so far (Fisher & Garner, 2020), however, the impending threat for the highly diverse Northern American and Neotropical urodelans is significant (Carter et al., 2020; Crawshaw et al., 2022; García-Rodríguez et al., 2022; Moubarak et al., 2022; North American*Bsal* Task Force, 2022; Yap et al., 2015).

Although *Bsal* primarily infects urodelans, recent studies show that anurans can act as reservoir hosts or as transmitters (Lötters et al., 2020; Nguyen et al., 2017; Schulz et al., 2020; Stegen et al., 2017; Towe et al., 2021). This role increases disease risk to sensitive salamander species and populations. Therefore, identifying reservoir hosts is crucial for understanding infection dynamics and potential occurrences as *Bsal* continues to expand its range and threaten biodiversity (Martel et al., 2020; Spitzen-Van Der Sluijs et al., 2016).

Bsal has restricted distributional areas, co-occurring with*Bd* in several microhabitats (Laking et al., 2017; Lötters et al., 2020). *Bd* -*Bsal* occurrences can potentially generate new genotypes with heightened pathogenicity (Farrer et al., 2011; Fisher & Garner, 2020; Wacker et al., 2023). *Bsal* has stronger pathogenicity compared to *Bd* within a shared host species, leading to more severe infection outcomes (Farrer et al., 2017). Out of documented 67 susceptible host species for *Bsal* , nearly 32 species also can be infected by *Bd* (Castro Monzon et al., 2023; Olson et al., 2021), these shared species could serve as the hyper-reservoirs or gain greater impacts from both pathogens. Importantly, *Bd* -*Bsal* coinfections have been reported in three urodelean species in natural habitats (Lötters et al., 2020; Lötters et al., 2018), and such coinfections are known to increase infection severity and disease risk under the laboratory experimental conditions (Longo et al., 2019; Ribas et al., 2022). These emphasize the importance of *Bsal* screening in natural habitats where *Bd*occurs.

In Southeast Asia (Vietnam), *Bsal* co-occurs together with the globalized genotype *Bd* GPL (Laking et al., 2017). However, knowledge on *Bsal* infection is scarce in other Asian amphibian hotspots where different *Bd* lineages are found. South China, for example, harbors the unique Asian genotype *Bd* Asia3 alongside*Bd* GPL (Byrne et al., 2019).

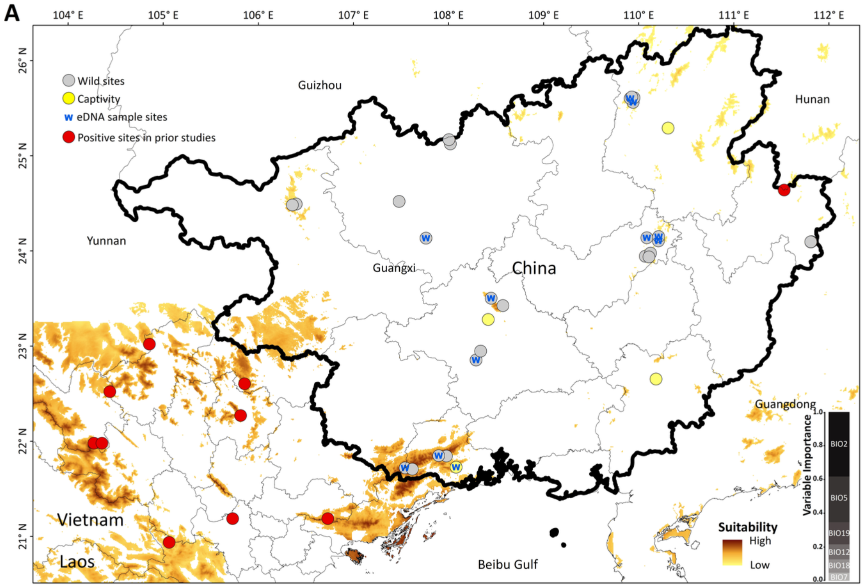
Here, we hypothesize that *Bsal* co-occurs together with *Bd*populations in South China. To investigate this, we screened for *Bsal* in salamanders and potential anuran reservoir hosts within regional amphibian hotspot in South China, which is recognized for its diverse *Bd* genotypes spanning various natural habitats. We also assessed the influence of climatic factors on *Bsal* distribution by estimating its potential range under the current climatic conditions. Analyzing the presence of *Bsal* in areas with high *Bd* diversity will enhance our comprehension of *Bsal* niche dynamics and pathogenicity. This has significant implications for amphibian conservation in the context of pathogen virulence evolution.

Materials and Methods

Sample collection

From spring 2019 to early winter 2021, a total of 31 sites (27 field sites and 4 captive sites) were surveyed throughout the Guangxi region in China (Fig. 1A), which shares its southwestern border with Vietnam, a country known to harbor *Bsal* (Laking et al., 2017). The pathogen was detected in an individual of a salamander species, *Pachytriton wuguanfui* in Guangxi region (Yuan et al., 2018). It is now known that basal Asian and global lineages of *Bd* exist in this region (Fig. 1B, Sun et al., 2023). Occasionally, *Bsal* can spill over from captive populations into wildlife communities (Cunningham et al., 2015; Fitzpatrick et al., 2018; Sabino-Pinto et al., 2015). To account for this, random samples were collected from pet markets and frog farms within the region. Skin swabs were collected following the sampling protocol for chytrid pathogens in amphibians, as described in Hyatt et al. (2007). Water samples were collected from bodies of water for *Bsal* detection in relation to local populations, to be used for environmental DNA (eDNA) analysis; eDNA can be used for pathogen detection in the absence of hosts (Kirshtein et al., 2007; Schulz et al., 2020). For this, approximately 1 L of water was sampled for each water body, then filtered through the 0.40 µm polycarbonate filter membrane using a sterile 100 ml syringe.

Ethical clearance for this study was obtained from the Institutional Animal Care and Use Committee of Guangxi University (GXU2018-048, with an extension of GXU2020-501).



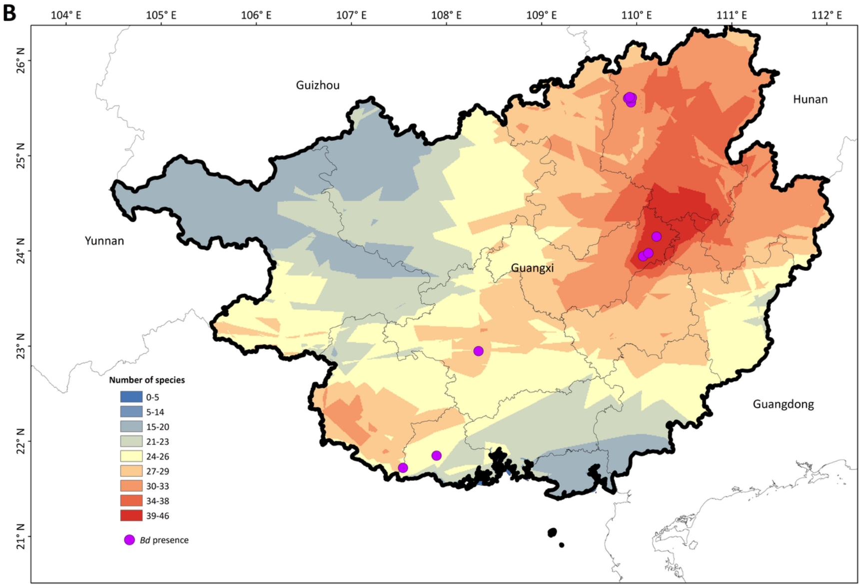


Figure 1. Study region, sampling sites and climatically suitable regions for *Bsal*. (A) Site distribution and climatically suitable habitats for *Bsal* in Guangxi region. **(B)**Documented sites for *Bd* presence in the region (Sun et al., 2023) over a background of amphibian species richness (IUCN 2015) .

Detection of *Bsal* infection

The genomic DNA for skin swabs was extracted using the PreMan Ultra (Applied Biosystems) (Boyle et al., 2004) and Qiagen DNeasy Blood and Tissue Kit, following animal tissue part in the modified manufacturers' protocols (Kosch & Summers, 2012). The environmental DNA for filters was extracted using Qiagen DNeasy PowerSoil Kit.

We used nested PCR to detect *Bsal* on DNA extracts from skin swabs (Gaertner et al., 2009; Zhu et al., 2014). For the first amplification, the primers ITS1f and ITS4 were used which specifically combined the 18S and 28S rRNA genes. The PCR amplification conditions, 4 min at 94°C, followed by 30 cycles of 30 s at 94°C, 30 s at 55°C, and 1 min at 72°C and a final 10 min at 72°C were implemented. For the second amplification, the specific primers (STerF and STerR) for *Bsal* were used to amplify a fragment gene of the ITS-5.8S rRNA region (Martel et al., 2013). The conditions of PCR amplification included 4 min at 94°C, followed by 30 cycles of 30 s at 94°C, 60°C for 30s, and 1 min at 72°C and a final 10 min at 72°C. PCR amplification products were visualized by 1.5% agarose gel electrophoresis.

Environmental samples were tested for *Bsal* using the RT-PCR method described by Blooi *et al* . (2013, 2016). We used a cycle of an initial step at 95°C for 10 min, followed by 50 cycles of 95°C for 10 s and 60°C for 1 min on Light Cycler® 480 System (Roche, Mannheim, Germany). Each water sample was run in duplicate.

We used the synthetic DNA sequences of *Bsal* as positive controls (Pisces Molecular, Boulder, Colorado, USA) and two negative controls in each plate. If nested PCR and RT-PCR products yielded positive results, Sanger sequencing was conducted to verify if the amplified DNA fragments were indeed associated with *Bsal* .

Analyses of *Bsal* prevalence

Bsal prevalence, defined as the ratio of infected amphibians to the total population, was calculated for each species, including 95% binomial confidence intervals (CI). The confidence intervals were derived using the "binom" package (Dorai-Raj, 2022) in R 4.2.2 (R Core Team, 2022).

Climatic suitability for *Bsal*

To understand how environmental conditions affect the distribution of*Bsal* , we used Generalized Linear Modeling (GLM) and Maximum Entropy Modeling (MaxEnt) to estimate its habitat suitability (Breiner et al., 2015; Phillips et al., 2006). If new positive locations of*Bsal* were detected in our study, they were to be combined with the previous verified presence records in native Asia to build the niche model. Previous present records of *Bsal* for Thailand, Vietnam, China and Japan in Asia (n=34), were attained from Basanta et al. (2019), Beukema et al. (2018), Laking et al. (2017), Lötters et al. (2020), and Yuan et al. (2018). We used the ecoregions (Dinerstein et al., 2017) of these *Bsal* occurrences as background to improve model calibration. Nineteen bioclimatic variables representing climatic conditions were download from WorldClim version 2.1 (Fick & Hijmans, 2017) as environmental predictors, at the spatial resolution of 30 seconds (~1 km2). To exclude the effects of high collinearity between predictors, we used the bioclimatic variables with Pearson's $r < 0.7$, where the correlation was calculated in the ENMTools (Warren et al., 2010). The final predictor set included 6 variables: Mean Diurnal Range (BIO2), Maximum Temperature of Warmest Month (BIO5), Temperature Annual Range (BIO7), Annual Precipitation (BIO12), Precipitation of Warmest Quarter (BIO18), and Precipitation of Coldest Quarter (BIO19). To trim duplicate observation records, a single coordinate for each grid cell was retained in our model predictions. The model performance for *Bsal* was evaluated using the AUC (Lobo et al., 2008), which was calculated by splitting the training (70%) and testing (30%) observations. The final ensembled model contained ten replications for each modeling, and were run in "sdm" package (Naimi & Araújo, 2016).

Results

A total of 1230 individuals including 1195 wild individuals and 95 captivities (0% prevalence, 95% CI of 0.00%-0.31%; Table 1), representing 38 amphibian species, were sampled during the study. The thirty-six water bodies sampled were from artificial lakes, natural pools, and slow flow streams (Fig. 1A). However, *Bsal* was not detected in any of the sampled individuals or water bodies.

Table 1 Individual numbers and amphibian species detected in this study in Guangxi Region. Bold fonts represent species which have been recorded positive to *Bd* infection in previous studies from other regions (Bai et al., 2012; Gaertner et al., 2011; Sun et al., 2023; Wang et al., 2018; Zhu et al., 2014) ; * denote samples collected in captivity including a pet market and three frog farms.

Family Fly Genus Species
N 95%CI Ranidae
Amolops Amolops
chunganensis 23
0.00%-14.31% Ranidae
Amolops Amolops
ricketti 272 0.00%-1.39%
Megophryidae
Boulenophrys
Boulenophrys
brachykolos 6
0.00%-39.03%
Megophryidae
Boulenophrys
Boulenophrys mirabilis 1
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Megophryidae
Brachytarsophrys
Brachytarsophrys
carinense 2 0.00%-65.76%
Dicroglossidae Fejervarya
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Hoplobatrachus
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latouchii 4 0.00%-48.99%
Ranidae Hylarana
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guentheri 43 0.00%-8.20%
Microhylidae
Kalophrynus
Kalophrynus
interlineatus 1
0.00%-79.35%
Microhylidae Kaloula
Kaloula pulchra 1
0.00%-79.35%
Rhacophoridae Kurixalus
Kurixalus odontotarsus
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Megophryidae
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Brachytarsophrys
Brachytarsophrys
carinense 2 0.00%-65.76%
Dicroglossidae Fejervarya
Fejervarya multistriata
26 0.00%-12.87%
Dicroglossidae
Hoplobatrachus
Hoplobatrachus chinensis
19 0.00%-16.82% Ranidae
Hylarana Hylarana
latouchii 4 0.00%-48.99%
Ranidae Hylarana
Hylarana maosonensis 17
0.00%-18.43% Ranidae
Hylarana Hylarana
guentheri 43 0.00%-8.20%
Microhylidae
Kalophrynus
Kalophrynus
interlineatus 1
0.00%-79.35%
Microhylidae Kaloula
Kaloula pulchra 1
0.00%-79.35%
Rhacophoridae Kurixalus
Kurixalus odontotarsus
69 0.00%-5.27%
Megophryidae
Leptobrachella
Leptobrachella liui 19
0.00%-16.82%
Megophryidae
Leptobrachella
Leptobrachella alpina 4
0.00%-48.99%
Megophryidae
Leptobrachella
Leptobrachella
shiwandashanensis 7
0.00%-35.43%
Megophryidae
Leptobrachium

Family Fly Genus Species
N 95%CI Ranidae
Amolops Amolops
chunganensis 23
0.00%-14.31% Ranidae
Amolops Amolops
ricketti 272 0.00%-1.39%
Megophryidae
Boulenophrys
Boulenophrys
brachykolos 6
0.00%-39.03%
Megophryidae
Boulenophrys
Boulenophrys mirabilis 1
0.00%-79.35%
Megophryidae
Brachytarsophrys
Brachytarsophrys
carinense 2 0.00%-65.76%
Dicroglossidae Fejervarya
Fejervarya multistriata
26 0.00%-12.87%
Dicroglossidae
Hoplobatrachus
Hoplobatrachus chinensis
19 0.00%-16.82% Ranidae
Hylarana Hylarana
latouchii 4 0.00%-48.99%
Ranidae Hylarana
Hylarana maosonensis 17
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Hylarana Hylarana
guentheri 43 0.00%-8.20%
Microhylidae
Kalophrynus
Kalophrynus
interlineatus 1
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Microhylidae Kaloula
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Rhacophoridae Kurixalus
Kurixalus odontotarsus
69 0.00%-5.27%
Megophryidae
Leptobrachella
Leptobrachella liui 19
0.00%-16.82%
Megophryidae
Leptobrachella
Leptobrachella alpina 4
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Leptobrachella
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Brachytarsophrys
carinense 2 0.00%-65.76%
Dicroglossidae Fejervarya
Fejervarya multistriata
26 0.00%-12.87%
Dicroglossidae
Hoplobatrachus
Hoplobatrachus chinensis
19 0.00%-16.82% Ranidae
Hylarana Hylarana
latouchii 4 0.00%-48.99%
Ranidae Hylarana
Hylarana maosonensis 17
0.00%-18.43% Ranidae
Hylarana Hylarana
guentheri 43 0.00%-8.20%
Microhylidae
Kalophrynus
Kalophrynus
interlineatus 1
0.00%-79.35%
Microhylidae Kaloula
Kaloula pulchra 1
0.00%-79.35%
Rhacophoridae Kurixalus
Kurixalus odontotarsus
69 0.00%-5.27%
Megophryidae
Leptobrachella
Leptobrachella liui 19
0.00%-16.82%
Megophryidae
Leptobrachella
Leptobrachella alpina 4
0.00%-48.99%
Megophryidae
Leptobrachella
Leptobrachella
shiwandashanensis 7
0.00%-35.43%
Megophryidae
Leptobrachium

Family Fly Genus Species N 95%CI Ranidae Amolops Amolops chunganensis 23 0.00%-14.31% Ranidae Amolops Amolops ricketti 272 0.00%-1.39% Megophryidae Boulenophrys Boulenophrys brachykolos 6 0.00%-39.03% Megophryidae Boulenophrys Boulenophrys mirabilis 1 0.00%-79.35% Megophryidae Brachytarsophrys Brachytarsophrys carinense 2 0.00%-65.76% Dicroglossidae Fejervarya Fejervarya multistriata 26 0.00%-12.87% Dicroglossidae Hoplobatrachus Hoplobatrachus chinensis 19 0.00%-16.82% Ranidae Hylarana Hylarana latouchii 4 0.00%-48.99% Ranidae Hylarana Hylarana maosonensis 17 0.00%-18.43% Ranidae Hylarana Hylarana guentheri 43 0.00%-8.20% Microhylidae Kalophrynus Kalophrynus interlineatus 1 0.00%-79.35% Microhylidae Kaloula Kaloula pulchra 1 0.00%-79.35% Rhacophoridae Kurixalus Kurixalus odontotarsus 69 0.00%-5.27% Megophryidae Leptobrachella Leptobrachella liui 19 0.00%-16.82% Megophryidae Leptobrachella Leptobrachella alpina 4 0.00%-48.99% Megophryidae Leptobrachella Leptobrachella shiwandashanensis 7 0.00%-35.43% Megophryidae Leptobrachium

Family Fly Genus Species
N 95%CI Ranidae
Amolops Amolops
chunganensis 23
0.00%-14.31% Ranidae
Amolops Amolops
ricketti 272 0.00%-1.39%
Megophryidae
Boulenophrys
Boulenophrys
brachykolos 6
0.00%-39.03%
Megophryidae
Boulenophrys
Boulenophrys mirabilis 1
0.00%-79.35%
Megophryidae
Brachytarsophrys
Brachytarsophrys
carinense 2 0.00%-65.76%
Dicroglossidae Fejervarya
Fejervarya multistriata
26 0.00%-12.87%
Dicroglossidae
Hoplobatrachus
Hoplobatrachus chinensis
19 0.00%-16.82% Ranidae
Hylarana Hylarana
latouchii 4 0.00%-48.99%
Ranidae Hylarana
Hylarana maosonensis 17
0.00%-18.43% Ranidae
Hylarana Hylarana
guentheri 43 0.00%-8.20%
Microhylidae
Kalophrynus
Kalophrynus
interlineatus 1
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Microhylidae Kaloula
Kaloula pulchra 1
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Rhacophoridae Kurixalus
Kurixalus odontotarsus
69 0.00%-5.27%
Megophryidae
Leptobrachella
Leptobrachella liui 19
0.00%-16.82%
Megophryidae
Leptobrachella
Leptobrachella alpina 4
0.00%-48.99%
Megophryidae
Leptobrachella
Leptobrachella
shiwandashanensis 7
0.00%-35.43%
Megophryidae
Leptobrachium

Family	Fly Genus	Species	N	95%CI
Ranidae	Amolops	Amolops chunganensis	23	0.00%-14.31%
Ranidae	Amolops	Amolops ricketti	272	0.00%-1.39%
Megophryidae	Boulenophrys	Boulenophrys brachykolos	6	0.00%-39.03%
Megophryidae	Boulenophrys	Boulenophrys mirabilis	1	0.00%-79.35%
Megophryidae	Brachytarsophrys	Brachytarsophrys carinense	2	0.00%-65.76%
Dicroglossidae	Fejervarya	Fejervarya multistriata	26	0.00%-12.87%
Dicroglossidae	Hoplobatrachus	Hoplobatrachus chinensis	19	0.00%-16.82%
Ranidae	Hylarana	Hylarana latouchii	4	0.00%-48.99%
Ranidae	Hylarana	Hylarana maosonensis	17	0.00%-18.43%
Ranidae	Hylarana	Hylarana guentheri	43	0.00%-8.20%
Microhylidae	Kalophrynus	Kalophrynus interlineatus	1	0.00%-79.35%
Microhylidae	Kaloula	Kaloula pulchra	1	0.00%-79.35%
Rhacophoridae	Kurixalus	Kurixalus odontotarsus	69	0.00%-5.27%
Megophryidae	Leptobrachella	Leptobrachella liui	19	0.00%-16.82%
Megophryidae	Leptobrachella	Leptobrachella alpina	4	0.00%-48.99%
Megophryidae	Leptobrachella	Leptobrachella shiwandashanensis	7	0.00%-35.43%
Megophryidae	Leptobrachium			

Family Fly Genus Species
N 95%CI Ranidae
Amolops Amolops
chunganensis 23
0.00%-14.31% Ranidae
Amolops Amolops
ricketti 272 0.00%-1.39%
Megophryidae
Boulenophrys
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Megophryidae
Brachytarsophrys
Brachytarsophrys
carinense 2 0.00%-65.76%
Dicroglossidae Fejervarya
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Family Fly Genus Species N 95%CI Ranidae Amolops Amolops chunganensis 23 0.00%-14.31% Ranidae Amolops Amolops ricketti 272 0.00%-1.39% Megophryidae Boulenophrys Boulenophrys brachykolos 6 0.00%-39.03% Megophryidae Boulenophrys Boulenophrys mirabilis 1 0.00%-79.35% Megophryidae Brachytarsophrys Brachytarsophrys carinense 2 0.00%-65.76% Dicroglossidae Fejervarya Fejervarya multistriata 26 0.00%-12.87% Dicroglossidae Hoplobatrachus Hoplobatrachus chinensis 19 0.00%-16.82% Ranidae Hylarana Hylarana latouchii 4 0.00%-48.99% Ranidae Hylarana Hylarana maosonensis 17 0.00%-18.43% Ranidae Hylarana Hylarana guentheri 43 0.00%-8.20% Microhylidae Kalophrynus Kalophrynus interlineatus 1 0.00%-79.35% Microhylidae Kaloula Kaloula pulchra 1 0.00%-79.35% Rhacophoridae Kurixalus Kurixalus odontotarsus 69 0.00%-5.27% Megophryidae Leptobrachella Leptobrachella liui 19 0.00%-16.82% Megophryidae Leptobrachella Leptobrachella alpina 4 0.00%-48.99% Megophryidae Leptobrachella Leptobrachella shiwandashanensis 7 0.00%-35.43% Megophryidae Leptobrachium

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0.00%-18.43% Ranidae
Hylarana Hylarana
guentheri 43 0.00%-8.20%
Microhylidae
Kalophrynus
Kalophrynus
interlineatus 1
0.00%-79.35%
Microhylidae Kaloula
Kaloula pulchra 1
0.00%-79.35%
Rhacophoridae Kurixalus
Kurixalus odontotarsus
69 0.00%-5.27%
Megophryidae
Leptobrachella
Leptobrachella liui 19
0.00%-16.82%
Megophryidae
Leptobrachella
Leptobrachella alpina 4
0.00%-48.99%
Megophryidae
Leptobrachella
Leptobrachella
shiwandashanensis 7
0.00%-35.43%
Megophryidae
Leptobrachium

Family Fly Genus Species
N 95%CI Ranidae
Amolops Amolops
chunganensis 23
0.00%-14.31% Ranidae
Amolops Amolops
ricketti 272 0.00%-1.39%
Megophryidae
Boulenophrys
Boulenophrys
brachykolos 6
0.00%-39.03%
Megophryidae
Boulenophrys
Boulenophrys mirabilis 1
0.00%-79.35%
Megophryidae
Brachytarsophrys
Brachytarsophrys
carinense 2 0.00%-65.76%
Dicroglossidae Fejervarya
Fejervarya multistriata
26 0.00%-12.87%
Dicroglossidae
Hoplobatrachus
Hoplobatrachus chinensis
19 0.00%-16.82% Ranidae
Hylarana Hylarana
latouchii 4 0.00%-48.99%
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guentheri 43 0.00%-8.20%
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Megophryidae
Leptobrachium

Family	Fly Genus	Species	N	95%CI
Ranidae	Amolops	Amolops chunganensis	23	0.00%-14.31%
Ranidae	Amolops	Amolops ricketti	272	0.00%-1.39%
Megophryidae	Boulenophrys	Boulenophrys brachykolos	6	0.00%-39.03%
Megophryidae	Boulenophrys	Boulenophrys mirabilis	1	0.00%-79.35%
Megophryidae	Brachytarsophrys	Brachytarsophrys carinense	2	0.00%-65.76%
Dicroglossidae	Fejervarya	Fejervarya multistriata	26	0.00%-12.87%
Dicroglossidae	Hoplobatrachus	Hoplobatrachus chinensis	19	0.00%-16.82%
Ranidae	Hylarana	Hylarana latouchii	4	0.00%-48.99%
Ranidae	Hylarana	Hylarana maosonensis	17	0.00%-18.43%
Ranidae	Hylarana	Hylarana guentheri	43	0.00%-8.20%
Microhylidae	Kalophrynus	Kalophrynus interlineatus	1	0.00%-79.35%
Microhylidae	Kaloula	Kaloula pulchra	1	0.00%-79.35%
Rhacophoridae	Kurixalus	Kurixalus odontotarsus	69	0.00%-5.27%
Megophryidae	Leptobrachella	Leptobrachella liui	19	0.00%-16.82%
Megophryidae	Leptobrachella	Leptobrachella alpina	4	0.00%-48.99%
Megophryidae	Leptobrachella	Leptobrachella shiwandashanensis	7	0.00%-35.43%
Megophryidae	Leptobrachium			

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Dicroglossidae	Hoplobatrachus	Hoplobatrachus chinensis	19	0.00%-16.82%
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Rhacophoridae	Kurixalus	Kurixalus odontotarsus	69	0.00%-5.27%
Megophryidae	Leptobrachella	Leptobrachella liui	19	0.00%-16.82%
Megophryidae	Leptobrachella	Leptobrachella alpina	4	0.00%-48.99%
Megophryidae	Leptobrachella	Leptobrachella shiwandashanensis	7	0.00%-35.43%
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Dicroglossidae	Fejervarya	Fejervarya multistriata	26	0.00%-12.87%
Dicroglossidae	Hoplobatrachus	Hoplobatrachus chinensis	19	0.00%-16.82%
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Microhylidae	Kalophrynus	Kalophrynus interlineatus	1	0.00%-79.35%
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Rhacophoridae	Kurixalus	Kurixalus odontotarsus	69	0.00%-5.27%
Megophryidae	Leptobrachella	Leptobrachella liui	19	0.00%-16.82%
Megophryidae	Leptobrachella	Leptobrachella alpina	4	0.00%-48.99%
Megophryidae	Leptobrachella	Leptobrachella shiwandashanensis	7	0.00%-35.43%
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Dicroglossidae	Fejervarya	Fejervarya multistriata	26	0.00%-12.87%
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Hoplobatrachus chinensis
19 0.00%-16.82% Ranidae
Hylarana Hylarana
latouchii 4 0.00%-48.99%
Ranidae Hylarana
Hylarana maosonensis 17
0.00%-18.43% Ranidae
Hylarana Hylarana
guentheri 43 0.00%-8.20%
Microhylidae
Kalophrynus
Kalophrynus
interlineatus 1
0.00%-79.35%
Microhylidae Kaloula
Kaloula pulchra 1
0.00%-79.35%
Rhacophoridae Kurixalus
Kurixalus odontotarsus
69 0.00%-5.27%
Megophryidae
Leptobrachella
Leptobrachella liui 19
0.00%-16.82%
Megophryidae
Leptobrachella
Leptobrachella alpina 4
0.00%-48.99%
Megophryidae
Leptobrachella
Leptobrachella
shiwandashanensis 7
0.00%-35.43%
Megophryidae
Leptobrachium

Family	Fly Genus	Species	N	95%CI
Ranidae	Amolops	Amolops chunganensis	23	0.00%-14.31%
Ranidae	Amolops	Amolops ricketti	272	0.00%-1.39%
Megophryidae	Boulenophrys	Boulenophrys brachykolos	6	0.00%-39.03%
Megophryidae	Boulenophrys	Boulenophrys mirabilis	1	0.00%-79.35%
Megophryidae	Brachytarsophrys	Brachytarsophrys carinense	2	0.00%-65.76%
Dicroglossidae	Fejervarya	Fejervarya multistriata	26	0.00%-12.87%
Dicroglossidae	Hoplobatrachus	Hoplobatrachus chinensis	19	0.00%-16.82%
Ranidae	Hylarana	Hylarana latouchii	4	0.00%-48.99%
Ranidae	Hylarana	Hylarana maosonensis	17	0.00%-18.43%
Ranidae	Hylarana	Hylarana guentheri	43	0.00%-8.20%
Microhylidae	Kalophrynus	Kalophrynus interlineatus	1	0.00%-79.35%
Microhylidae	Kaloula	Kaloula pulchra	1	0.00%-79.35%
Rhacophoridae	Kurixalus	Kurixalus odontotarsus	69	0.00%-5.27%
Megophryidae	Leptobrachella	Leptobrachella liui	19	0.00%-16.82%
Megophryidae	Leptobrachella	Leptobrachella alpina	4	0.00%-48.99%
Megophryidae	Leptobrachella	Leptobrachella shiwandashanensis	7	0.00%-35.43%
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The average AUC value for the *Bsal* distribution model was 0.917 (SD ± 0.047), signifying strong model performance. The top three variables for model predictions included mean diurnal range, maximum temperature of the warmest month, and precipitation during the coldest quarter (Fig. 1A).

The modeling predictions estimated that only a small fraction of suitable habitats for *Bsal* occurrences exists under current climate conditions, with patchy distribution in the subtropical evergreen forests of the Guangxi region. (Fig. 1A). The anticipated habitats for *Bsal* occurrence were situated in southwestern areas near the coastlines. Among the 27 wild sampling sites, 14 were deemed suitable for *Bsal* , with suitability levels ranging from low to high.

Discussion

We analyzed a wide range of species and environmental reservoirs across different seasons to evaluate the infection patterns of *Bsal* in relation to geographic and environmental factors in Guangxi region. We did not detect *Bsal* in any of the samples from wild and captive animals or sampled water bodies. Our species distribution model estimated a small fraction of suitable habitats in this region under the current climatic conditions, but with patchy distributions. These results suggest that climate is a potential barrier, limiting*Bsal* spread into the surveyed sites. However, there is a possibility that it could be present at undetectable levels, or occur in specific microhabitats that were not sampled in our study.

Our niche model predicted that climatically suitable areas for*Bsal* in the Guangxi region are less and fragmented, generally low suitability. The model identified mean diurnal range as the most crucial variable in our models. This corroborates the findings from previous*Bsal* distribution models in its native Asian range (Moubarak et al., 2022). The relatively high variations in mean diurnal range within the study area seem to limit the potential distribution of *Bsal* , emphasizing that environmental temperature is a primary factor influencing *Bsal* occurrences (Martel et al., 2013).

Bsal prefer lower thermal conditions for their existence, the temperatures above 22°C adversely affects its growth and diminish its pathogenicity to hosts (Carter et al., 2021; Martel et al., 2013). Previous studies have proposed that temperature is a key factor behind the low prevalence of *Bsal* in Asian amphibians, as the environmental as well as the water temperatures in these regions are generally considered suboptimal ([?] 15degC) for*Bsal* 's survival and growth (Laking et al., 2017; Martel et al., 2013; Yuan et al., 2018). It has also been documented that warmer temperatures can potentially reduce intraspecific transmission rates, especially when temperatures surpass 25degC (Blooi et al., 2015) .

Furthermore, the precipitation of the coldest quarter plays a contributory role in modeling predictions for *Bsal* occurrences in Asia which shows the same pattern as of European *Bsal* presence which requires moist, relatively cool and stable conditions (Beukema et al., 2021), the high fluctuations of precipitation in cool periods weaken its occurrences.

The absence of *Bsal* in northern sites in our study might partly result from competition with other pathogens that share a similar climatic niche, such as *Bd* . It was identified at ten of the surveyed sites (Fig. 1B), displaying a high prevalence in the northern locales of the Guangxi region (Sun et al., 2023). One of 38 species we examined, *A. davidianus* (positive to *Bd* in our subsequent detections), have been reported as *Bsal* -positive species (Fig.1; Laking et al., 2017; Yuan et al., 2018), but it was negative to*Bsal* infection in our present study. These patterns suggest that Asian *Bd* lineages might outcompete *Bsal* when site-specific conditions and species susceptibility enhance the pathogenic performance of *Bd* lineages as pathogenicity of both pathogens varies with species and environmental conditions (Fisher & Garner, 2020; Martel et al., 2014). This competition could occur because *Bd* infection can negatively impact *Bsal* infection under certain circumstances (Direnzo et al., 2021).

Considering the possibility that *Bsal* has not yet been transmitted to the current sampling sites, particularly in highly suitable habitats (e.g., southwestern sites) where *Bd* is present (Fig. 1), the coexistence of *Bd* and *Bsal* in the same microhabitats could result in severe coinfections or reinfections and potentially generate new, highly virulent genotypes within the same host once the pathogen is introduced to these sites (Greenspan et al., 2018). Among the 38 amphibian species tested for *Bsal* , none were found to be infected. However, 16 of these species tested positive for*Bd* infection (Table 1), highlighting the need for further investigation into the potential co-occurrence of these fungal pathogens. Specifically, we recommend investigating predicted suitable areas for *Bsal* where *Bd* is present, in order to better understand the ecological interactions between these pathogens and their impact on amphibian species.

Geographic barriers such as drier plains which prevents the migration of susceptible species could be another potential reasons for absence of*Bsal* (restricted slowly dispersal) in the region. This may inhibit the host-dependent intraspecific and interspecific as well as human-mediated transmissions of this pathogen within landscapes (Malagon et al., 2020; Spitzen-Van Der Sluijs et al., 2018; Tompros et al., 2021). In addition, the negative result of *Bsal* is consistent with previous studies of this pathogen in Asia that primarily detected the fungus in anuran species (Wang et al. 2017; Zhu et al. 2014), which was thought to lead to transient persistence for *Bsal* and decreased transmission rates due to low galactose proportions in host skin (Stegen et al., 2017; Wang et al., 2021). However, it is possible that *Bsal* could be present sub clinically at low prevalence in these studied amphibians, with fungal loads below the thresholds of detection. As growth of *Bsal* could also depend on relevant plant materials in water (Kelly et al., 2021), extending the range of sampling efforts in environmental reservoirs can improve our understanding the existence of *Bsal* in the region.

Seasonality mainly explained by variations in temperature and precipitation, may influence *Bsal* occurrences and host susceptibility (Bozzuto & Canessa, 2019; Carter et al., 2021). Our study primarily surveyed amphibians that are reproductively active during spring and summer, with a limited number of individuals sampled in autumn. We were unable to conduct any sampling of wild host species during winter, which limits our understanding of *Bsal* infection across seasons. Notably, autumn and winter conditions in this subtropical region might be more conducive for *Bsal* prevalence.

It is important to understand the resource partitioning and natural behaviors of amphibians across seasons. One such factor would be overwintering and potential attenuation of defensive mechanisms such as reduced skin bacterial diversity during hibernation (Tong et al., 2019). This would lead the pathogen to cause sub-lethal infections in susceptible amphibians during autumn and winter. Hence, we recommend integrating experimental and field studies in both summer and winter, to enhance our understanding of the effects of *Bsal* infection on amphibians in specific ecological contexts.

In conclusion, the absence of *Bsal* in our study should not undermine the importance of proactive management and conservation strategies aimed at minimizing the risk of *Bsal* transmission in the region. This is due to the limited presence of climatically suitable areas for *Bsal* in this region and the isolated suitable sites within mountains could provide an important refuge for *Bsal*(Beukema et al., 2021; Lotters et al., 2020). Implementing stringent biosecurity measures, such as regulating the trade of amphibians can help reduce the chances of pathogen introduction. Regular monitoring and surveillance programs are crucial for early detection of *Bsal* , which could allow for timely interventions to prevent severe declines in amphibian populations (Thomas et al., 2019). In addition, further research into the ecology, transmission dynamics, and host-pathogen interactions of *Bsal* is essential to generate knowledge that will inform targeted conservation.

Author contributions

Dan Sun: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); resources (equal); software (lead); visualization (lead); writing-original draft (lead); writing-review and editing (lead).**Gajaba Ellepola:** Data curation (supporting); methodology (supporting); visualization (supporting); validation (equal); writing-original draft (supporting); writing-review and editing (equal).**Jayampathi Herath:** Data curation (supporting); methodology (supporting); validation (equal); writing-original draft (supporting); writing-review and editing (equal). **Madhava Meegaskumbura:**Conceptualization (equal); funding acquisition (lead); resources (lead); software (supporting); project administration (lead); supervision (lead), validation (equal); writing-original draft (equal); writing-review and editing (equal).

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Conflict of interest statement

The authors declare no conflict of interest.

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