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Chytridiomycosis in Sri Lanka: Predicting the future of a global amphibian hotspot

Ruvinda K. de Mel[1,2] | H. G. Salindra K. Dayananda[3,4,5] | G. A. Sanoj Wijayasekara[6] | Tharindu Ranasinghe[7] | Amila P. Sumanapala[8] | Surendranie Judith Cabral de Mel[2,9] | Edward Narayan[10] | Dinesh E. Gabadage[11] | Kanishka D. B. Ukuwela[12]

[1]Centre for Behavioural and Physiological Ecology, University of New England, Armidale, New South Wales, Australia

[2]National Institute of Fundamental Studies, Kandy, Sri Lanka

[3]Guangxi Key Laboratory of Forest Ecology and Conservation, Guangxi University, Nanning, China

[4]Field Ornithology Group of Sri Lanka, Department of Zoology and Environment Science, University of Colombo, Colombo, Sri Lanka

[5]Foundation for Ecology & Research on Nature, Panadura, Sri Lanka

[6]Faculty of Medicine, University of Colombo, Colombo, Sri Lanka

[7]Butterfly Conservation Society of Sri Lanka, Malwana, Sri Lanka

[8]Department of Zoology and Environment Sciences, University of Colombo, Colombo, Sri Lanka

[9]Institute for Life Sciences and the Environment, University of Southern Queensland, Toowoomba, Queensland, Australia

[10]School of Agriculture and Food Sciences, The University of Queensland, Gatton, Queensland, Australia

[11]Biodiversity Conservation Society, Nugegoda, Sri Lanka

[12]Department of Biological Sciences, Rajarata University, Mihinthale, Sri Lanka

Correspondence
Ruvinda K. de Mel, Centre for Behavioural and Physiological Ecology, Zoology, University of New England, Armidale, NSW 2351, Australia.
Email: ruvinda_demel@hotmail.com

Abstract

1. Chytridiomycosis, caused by *Batrachochytrium dendrobatidis* (*Bd*), constitutes a major threat to many amphibian species worldwide. Predicting the species and regions of highest geographical risk is critical for the early detection and mitigation of chytrid emergence.
2. In this study, using a niche modelling approach, the most conducive habitat for *Bd* within Sri Lanka (a high-risk zone) was modelled. The distribution of 69 amphibian species was then modelled and their overlap with the high-risk zone ($area_{Bd}$) was calculated.
3. Using $area_{Bd}$ and a biotic index (BI), created using ecological traits of each species, a risk index (RI) was calculated. Using this RI, a high-risk species index (HRSI) was developed to identify the species most at risk.
4. The results indicate that the high elevations of Sri Lanka (>600 m a.s.l.) are highly conducive for *Bd*. The HRSI includes 35 species, with *Minervarya greenii* being the species most at risk. All species in the HRSI are globally Critically Endangered ($n = 14$) or Endangered ($n = 21$).
5. We propose active conservation measures such as the routine monitoring of HRSI species and other proactive measures to identify and prevent the spread of *Bd*. We believe our findings would promote the establishment of pre-emptive mitigation measures both within Sri Lanka and elsewhere, to counter the threat of chytridiomycosis and to conserve amphibian species.

KEYWORDS

amphibians, *Batrachochytrium dendrobatidis*, conservation, disease, herpetofauna, modelling, species distribution modelling

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1 | INTRODUCTION

The world's amphibian species are currently facing a myriad of threats that challenge their survival. These include habitat loss and degradation (Davidson, Shaffer & Jennings, 2002; Gallant et al., 2007), the presence of pernicious chemicals in the environment (Hayes et al., 2006; Wolmarans et al., 2021), and infectious diseases (Leroy, 2004; Berger et al., 2005). Among the diseases that threaten global amphibian populations, unarguably the greatest risk is posed by chytridiomycosis, a disease caused by the fungal agent *Batrachochytrium dendrobatidis* (*Bd*) (Bosch, Martínez-Solano & García-París, 2001; Scheele et al., 2019; Fisher & Garner, 2020).

Since it first came under scientific scrutiny (Berger et al., 1998; Longcore, Pessier & Nichols, 1999; Morell, 1999), *Bd* has been detected from 1,375 species of amphibians (Olson et al., 2021) and is responsible for the decimation of many amphibian populations around the world (La Marca et al., 2005; Pounds et al., 2006; Fisher & Garner, 2020). Given the virulence of the pathogen, it has the ability to extirpate entire populations of amphibians (Lips, Reeve & Witters, 2003; Muths et al., 2003) and has even driven certain species, such as *Eleutherodactylus jasperi* and *Eleutherodactylus karlschmidti*, to extinction (Burrowes, Joglar & Green, 2004; Scheele et al., 2017). To date, the *Bd*-induced mass mortality of amphibian populations has been recorded from countries such as Puerto Rico (Burrowes, Joglar & Green, 2004), Spain (Bosch, Martínez-Solano & García-París, 2001), Costa Rica (Lips, Reeve & Witters, 2003), USA (Muths et al., 2003), and Australia (Retallick, McCallum & Speare, 2004; Hero, Williams & Magnusson, 2005).

Although these events have been reported since the late 1990s, the prevalence and effects of *Bd* in Asia has only been investigated since the late 2000s (McLeod et al., 2008; Une et al., 2008). Although *Bd* is Asian in origin (O'Hanlon et al., 2018), biodiverse islands surrounding the main continent, such as Sri Lanka, may be highly susceptible to the threat posed by chytridiomycosis. Sri Lanka has been separated from India for approximately 10,000 years (Pethiyagoda & Sudasinghe, 2021), and the speciation of amphibians has resulted in 86% endemism in frog species and 25% endemism in frog genera. Home to 112 species of amphibians (Ellepola et al., 2021), the species richness in the country, during recent times, has led to studies that describe multiple species at a time (Meegaskumbura, Manamendra-Arachchi & Pethiyagoda, 2009; Wickramasinghe et al., 2013b). The remarkably high endemism within the island has led some authors to raise concern over considering Sri Lanka and the Western Ghats as a single biodiversity entity (Bossuyt et al., 2004). However, juxtaposed on Sri Lanka's high amphibian diversity is a high rate of extinction with 18 species already considered recently extinct (Manamendra-Arachchi & Meegaskumbura, 2012; Meegaskumbura et al., 2012; de Silva, Ukuwela & Chathuranga, 2022).

Given the recently accelerated rate of extinction within Sri Lanka, the spread of *Bd* could be catastrophic. Despite this veritable risk, there is a paucity of information on the status of chytridiomycosis in Sri Lanka and the dynamics of a potential outbreak, except for a study that identified a few infected individuals (Swei et al., 2011). The present study aimed to answer two questions that are critical to devise future screening processes and risk mitigation efforts.

1. Which areas within Sri Lanka would constitute the ideal habitat for the establishment and spread of *Bd* (i.e. the high-risk zone)?
2. Which Sri Lankan amphibian species are at a higher risk of contracting *Bd* and manifesting its subsequent effects (i.e. the high-risk species index)?

The answers to these questions are of value for establishing pragmatic and pre-emptive measures against a potential future outbreak of chytridiomycosis in Sri Lanka.

2 | METHODS

A niche modelling approach was used to evaluate potential areas within Sri Lanka that would constitute the ideal habitat for the establishment and spread of *Bd* (i.e. the high-risk zone). The distribution of 69 species of frogs (see below for a justification of their selection) in Sri Lanka was then modelled to determine their risk of contracting *Bd* and manifesting its subsequent effects (risk index, RI). The percentage overlap of the high-risk zone and amphibian species ranges ($area_{Bd}$) were calculated. A biotic index (BI) – incorporating both life history and elevation to predict the susceptibility of Sri Lankan frogs to *Bd* infection – was then calculated. Finally, to evaluate the risk of a given species being infected by *Bd*, the 'risk factor' was calculated using the BI and $area_{Bd}$. The RI was assigned according to the risk factor.

2.1 | Modelling of the most conducive environmental range of *Bd* (high-risk zone) within Sri Lanka (methods discussed in detail in Appendix S1)

Climate information from six bioclimatic variables was obtained, based on Rödder et al. (2009): 'annual mean temperature', 'maximum temperature of the warmest month', 'minimum temperature of the coldest month', 'annual precipitation',

'precipitation of wettest month', and 'precipitation of driest month' (data downloaded on 15 May 2020 from https://worldclim.org). In addition, the relevant 'elevation' data were also obtained (http://www.diva-gis.org/Data). Through a literature survey of 11 publications, 32 locations were identified in Asia where *Bd* has been reported in the wild (Appendix S1; Figure S1; Table S1). The maximum entropy algorithm available in MaxEnt 3.4 (all variable layers were at 1 km × 1 km resolution on WGS84 longitude–latitude projections) was used to model the distribution, and an occurrence probability of >0.5 was used to model the high-risk zone for *Bd* within Sri Lanka.

2.2 | Developing risk index for Sri Lankan amphibians (methods discussed in detail in Appendix S1)

2.2.1 | Species distribution modelling for frogs

Of the 112 frog species recorded in Sri Lanka (Ellepola et al., 2021), the 93 extant species were considered in this study. The 18 extinct species were discounted as their distributional ranges have not been well documented (de Silva, Ukuwela & Chathuranga, 2022), whereas *Hoplobatrachus tigerinus* was discounted as its occurrence is now refuted (Dutta, 1997; Batuwita et al., 2019). Occurrence data over a 30-year period (1990–2020) was collected and supplemented with data from the literature. For the first analysis, species with more than seven distinct location records were used based on Hernandez et al. (2006) and van Proosdij et al. (2016), which resulted in 69 species being selected. The species with fewer than seven location records were all range-restricted species (de Silva, Ukuwela & Chathuranga, 2022) and were analysed separately. Using 1,819 observations from 334 locations of the selected 69 species, species distribution models (SDMs) for each species were created. When building these models, 'human population density' (https://open.africa/dataset/sri-lanka-population-density-2015), 'tree cover' (http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.2.html), and 'amphibian endemic regions of Sri Lanka' (adapted from MoMD&E, 2019 were used, in addition to the data used for modelling the high-risk zone (results of SDMs presented in Appendixes S2 and S3).

2.2.2 | Calculation of percentage of *Bd* overlap range ($area_{Bd}$)

The predicted distribution of each of the 69 species was used to create a layer with an occurrence probability of >0.5, which was superimposed on the high-risk zone map to calculate the percentage overlap area ($area_{Bd}$) for each species (Appendix S4). A proxy value of 30% for $area_{Bd}$ was used to select species with the greatest susceptibility to *Bd* infection. For the range-restricted species, their $area_{Bd}$ was considered as 100% if their known localities (such as the type locality) were within the high-risk zone.

TABLE 1 Life-history stage, habitat type, and assigned scores used for the calculation of the biotic index (BI).

Life-history stage	Habitat	Score
Tadpole/ larva	Moist terrestrial	1
Tadpole/ larva	Pond	2
Tadpole/ larva	Stream	3
Adult	Stream (small flowing water habitats)	5
Adult	Stream + pond	4.5
Adult	Ponds (small still water habitats)	4
Adult	Stream associated (boulders and vegetation bordering streams)	3
Adult	Moist terrestrial (paddy fields, marshy areas)	2
Adult	Terrestrial, breeds in streams and ponds	1.5
Adult	Dry terrestrial (dry terrestrial habitats)	1

2.2.3 | Calculation of life-history score for each species

For each species, a life-history score was calculated following a qualitative approach based on the authors' expertise and published literature. Six habitat types used by adult frogs and three habitat types used by their larvae were identified (Table 1). Each habitat type was then assigned a score based on its conduciveness for *Bd* (Johnson & Speare, 2003; Lips, Reeve & Witters, 2003; Lips et al., 2006; Rowley & Alford, 2007; Swei et al., 2011). Adult amphibians have a greater risk of *Bd* infection and subsequent mortality than tadpoles (Rachowicz & Vredenburg, 2004; Garner et al., 2009), and a formula reflecting this fact was used to calculate the life-history score (for details, see Appendix S5):

$$\text{life}-\text{history score of a species} = \text{life}-\text{history score of tadpole} + (\text{life}-\text{history score of adult} \times 2).$$

2.2.4 | Calculation of altitude score for each species

Three different altitude classes for the distribution of Sri Lankan amphibians were identified, congruent with Batuwita et al. (2019): A, 0–800 m a.s.l.; B, >800–1,700 m a.s.l.; C, >1,700–2,500+ m a.s.l. Non-additive values were assigned for each species according to their distribution within these classes. This calculation reflects how higher *Bd* prevalence is associated with higher altitudes (Drew, Allen & Allen, 2006; Whitfield et al., 2012; Sapsford, Alford & Schwarzkopf, 2013) (for details, see Appendix S5).

2.2.5 | Model building and developing the BI for Sri Lankan frogs

Considering susceptibility as the response variable and life-history score and altitude score as predictor variables, a generalized linear model with a binomial error structure was built to predict the susceptibility of frogs to *Bd* infection. Twenty-nine frog species from other countries infected with *Bd* were selected and data from published sources were extracted to calculate their life-history scores and altitude scores (Appendix S5). These species were given a susceptibility value of '1', whereas all local species used in our model were given a value of '0'.

2.3 | Calculating risk factors (RFs) and developing the RI and high-risk species index (HRSI) for Sri Lankan frogs

To calculate the RFs for the Sri Lankan frog species to indicate how susceptible a given species is to *Bd* infection, the RF formula by Rödder et al. (2009) was used:

$$\mathrm{RF} = (\mathrm{BI} \times 100) \times (\mathrm{area}_{Bd}/10{,}000),$$

where, BI is the biotic index or predicted risk derived from the model, and area_{Bd} is the percentage of an amphibian species' distribution that overlaps with the area of the high-risk zone (with *Bd* occurrence probability of >0.5). The BI values were not standardized as they ranged from 0 to 1. A higher RF value indicates a higher risk of *Bd* infection. The highest positions in the RI were assigned to species with the highest RF values.

2.3.1 | Including range-restricted species in the HRSI

The RF value was calculated and the RI position was assigned when the area_{Bd} for the range-restricted species within the high-risk zone ($n = 21$) was 100%, as mentioned above.

3 | RESULTS

3.1 | Most conducive geographical range for *Bd* within Sri Lanka (high-risk zone)

According to the output of the averaged model ($n = 15$), the permutations with highest importance were 'precipitation', 'elevation', and 'precipitation of the wettest month' (Appendix S2). This resulted in a significant proportion of the Central Highlands, the Knuckles Massif, and the Rakwana Hills, which constitute the area >600 m altitude in Sri Lanka, being identified as ideal habitat for *Bd* (Figure 1). The region that is suboptimal for *Bd* prevalence, which constitutes 92.4% of the country (Figure 1), encompasses the entire dry zone and most of the intermediate zone (Diyabalanage et al., 2016; Pethiyagoda & Sudasinghe, 2021).

3.2 | HRSI of Sri Lankan amphibians

Of the 35 species constituting the HRSI (Table 2), 100% are endemic to Sri Lanka. Species in the HRSI comprised eight genera: *Adenomus*, *Ichthyophis*, *Lankanectes*, *Microhyla*, *Minervarya*, *Pseudophilautus*, *Taruga*, and *Uperodon*. The majority of the species ($n = 26$) belong to the genus *Pseudophilautus*. The other nine species include two each from the genera *Microhyla* and *Taruga*, and a single species each from the genera *Adenomus*, *Ichthyophis*, *Lankanectes*, *Minervaya*, and *Uperodon*. The largest RF value and consequent highest position in the HRSI was assigned to *Minervarya greenii* (Figure 2), whereas the 10th greatest RF value and the 10th highest position was assigned to *Adenomus kandianus*. All species in the HRSI are globally Endangered ($n = 20$) or Critically Endangered ($n = 15$) (IUCN, 2022). In addition, *Ichthyophis orthoplicatus*, *Microhyla karunaratnei*, *Microhyla zeylanica*, *Pseudophilautus ocularis*, and *Uperodon palmatus* are considered Evolutionarily Distinct and Globally Endangered (EDGE) species (ZSL, 2015). Of the rest of the 48 species possessing an area_{Bd}, 31 species are threatened with extinction (15 Vulnerable, 13 Endangered, and three Critically Endangered) (IUCN, 2022).

Of the 69 species modelled, only seven had no range overlap with the high-risk zone and all seven species are listed as Least Concern (IUCN, 2022). Of these seven species *Microhyla mihintalei* and *Uperodon rohani* are endemic to Sri Lanka (de Silva, Ukuwela & Chathuranga, 2022). Three other range-restricted species – *Ichthyophis pseudangularis* (Vulnerable), *Polypedates ranwellai* (Endangered), and *Pseudophilautus conniffae* (Endangered) – had no range overlap with the high-risk zone.

4 | DISCUSSION

The results indicate that the region above 600 m a.s.l. of Sri Lanka is highly conducive for the establishment and spread of *Bd* and constitutes the high-risk zone; they also show that at least 89% of Sri Lanka's frogs have at least some range overlap with environments climatically suited to *Bd* (83 out of 93 extant species). Significant overlap between occurrence ranges and areas conducive for *Bd* establishment is evident in species living at high altitudes. The 35 species at highest risk are already globally Critically Endangered ($n = 14$) or Endangered ($n = 21$) (IUCN, 2022). This suggests that research is needed to monitor the prevalence and spread of *Bd*, especially within this geographical region of Sri Lanka and within populations of these species.

The high-risk zone (Figure 1) comprises three out of the five amphibian zones of Sri Lanka (Batuwita et al., 2019; MoMD&E, 2019): the Central Highlands, the Knuckles Massif, and the Rakwana Hills. The importance of these regions as local amphibian hotspots is

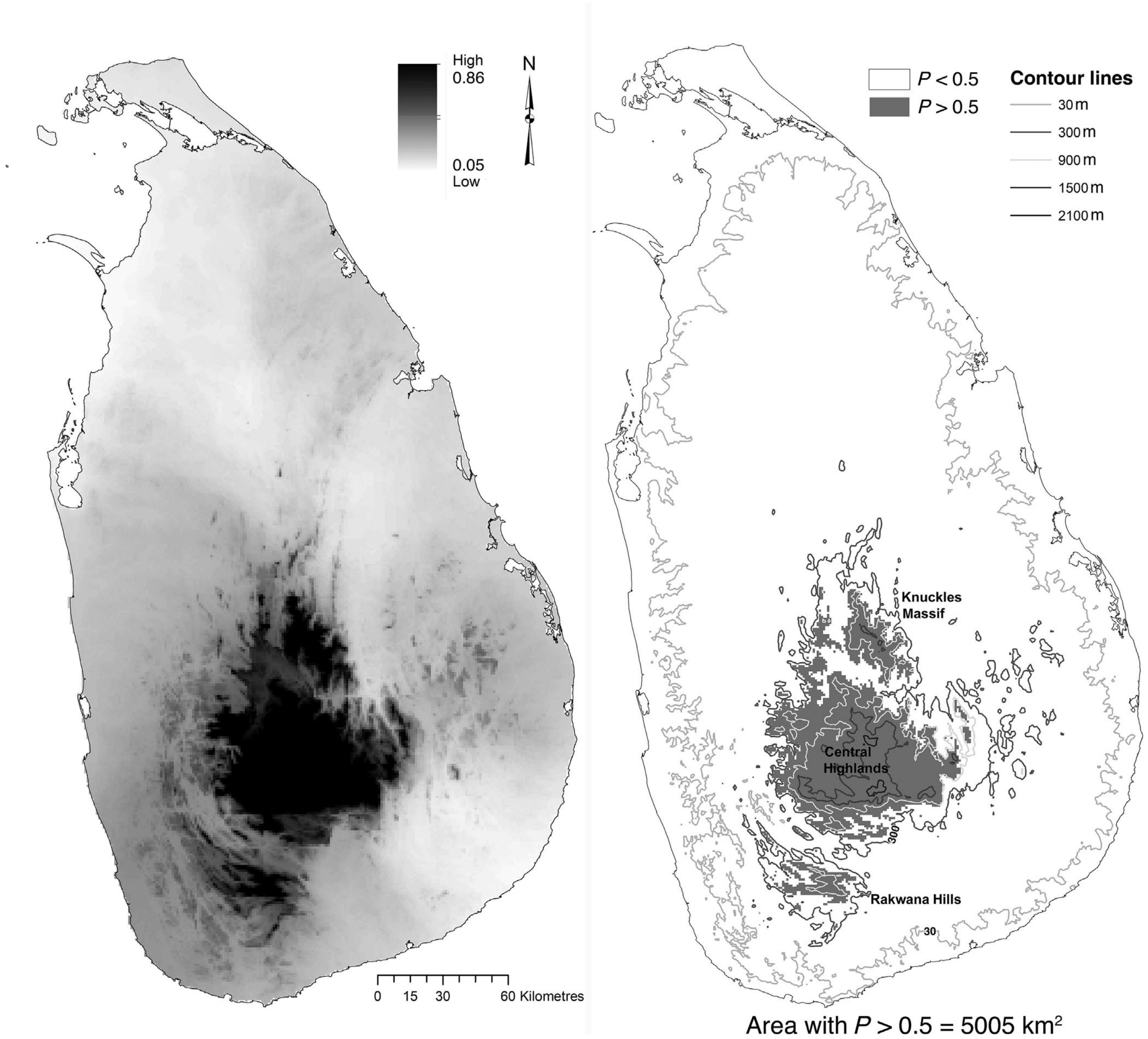

FIGURE 1 Heat map of the probability of *Bd* prevalence within Sri Lanka (left); high-risk zone of Sri Lanka (right).

illustrated by the many new species described from them in the recent past (Manamendra-Arachchi & Pethiyagoda, 2005; Meegaskumbura & Manamendra-Arachchi, 2005; Meegaskumbura & Manamendra-Arachchi, 2011; Wickramasinghe et al., 2013b; Senevirathne et al., 2018), as well as the rediscovery of species (Wickramasinghe et al., 2013a). Thus, the spread of *Bd* in these areas could have devastating consequences for the amphibians of Sri Lanka.

The present scientific consensus is that *Bd* is Korean in origin, and mainland Asian frog populations have a low prevalence and load of *Bd* (O'Hanlon et al., 2018; Sreedharan & Vasudevan, 2021). However, Sri Lanka is an island where the biota speciated in isolation for at least the last 10,000 years, with 86% endemism in frogs (Pethiyagoda & Sudasinghe, 2021). The high endemism suggests that Sri Lankan frogs may not share the same response to *Bd* as mainland Asian frogs, and although it is known that *Bd* occurs in Sri Lanka, its effects on frogs are completely unknown. In addition, although the long-standing co-evolution between endemic *Bd* strains and mainland Asian amphibians has allowed the pathogen to become hypovirulent within the Asian region (Swei et al., 2011; Bataille et al., 2013; James et al., 2015), *Bd* can also hybridize among strains, creating hypervirulent strains (Farrer et al., 2011; Greenspan et al., 2018; Byrne et al., 2019). Therefore, the introduction of a strain such as *Bd*-GPL (global pandemic lineage), responsible for the mass mortality of amphibians (O'Hanlon et al., 2018), or a hypervirulent hybrid strain, on an island with high endemism such as Sri Lanka could prove catastrophic.

The amphibians inhabiting the highlands of Sri Lanka, with a high area$_{Bd}$, face a plethora of additional environmental challenges (IUCN, 2022); indeed, 18 species have recently become extinct. The

TABLE 2 High-risk species index (HRSI) for Sri Lanka.

RI	areaBd	BI	RF	Species
1	100	0.9990	0.9990	*Minervarya greenii*
2	100	0.9977	0.9977	*Pseudophilautus frankenbergi**, *Pseudophilautus jagathgunawardanai**, *Pseudophilautus newtonjayawardanei**, *Pseudophilautus puranappu*, *Pseudophilautus sirilwijesundarai**, *Pseudophilautus stellatus**
3	100	0.9911	0.9911	*Microhyla karunaratnei**, *Taruga fastigo*
4	100	0.9889	0.9889	*Pseudophilautus caeruleus*, *Pseudophilautus decoris**, *Pseudophilautus lunatus**, *Pseudophilautus ocularis*, *Pseudophilautus poppiae*, *Pseudophilautus samarakoo**, *Pseudophilautus simba**, *Pseudophilautus steineri**, *Pseudophilautus stuarti**
5	99.28	0.9929	0.9858	*Pseudophilautus sarasinorum*
6	100	0.9824	0.9824	*Lankanectes pera**
7	100	0.9618	0.9618	*Ichthyophis orthoplicatus**
8	100	0.9574	0.9574	*Microhyla zeylanica*, *Taruga eques*, *Uperodon palmatus*
9	100	0.9471	0.9471	*Pseudophilautus alto*, *Pseudophilautus asankai*, *Pseudophilautus dayawansai**, *Pseudophilautus femoralis*, *Pseudophilautus hankeni**, *Pseudophilautus microtympanum*, *Pseudophilautus mooreorum**, *Pseudophilautus schmarda*, *Pseudophilautus semiruber**, *Pseudophilautus viridis*
10	94.80	0.9725	0.9219	*Adenomus kandianus*

Note: *range-restricted species.
Abbreviations: $area_{Bd}$, overlap of >0.5 of distribution model of species within the high-risk zone (>0.5 occurrence probability of *Bd*) of Sri Lanka; BI, biotic index (the susceptibility of a species calculated using life history and occurrence elevation); RF, risk factor (calculated using $area_{Bd}$ and BI).

precise cause of these extinctions remains unknown but habitat loss in the highlands is suspected (Perera, 1975; Wickramagamage, 2017). The species most at risk from *Bd* infection share certain ecological traits (Appendix S5), such as aquatic life stages and restricted distributions (La Marca & Reinthaler, 1991; Ron et al., 2003; La Marca et al., 2005; Bielby et al., 2008; IUCN, 2020a; IUCN, 2020b). These factors reflect the results of this study, in which the highest ranked frog in the HRSI (*M. greenii*; Table 2), has a pond-dwelling adult life stage and small extent of occurrence, restricted to the highest elevations of the country (Appendix S5). In addition, all species ranked second in the HRSI (*Pseudophilautus frankenbergi*, *Pseudophilautus jagathgunawardanai*, *Pseudophilautus newtonjayawardanei*, *Pseudophilautus puranappu*, *Pseudophilautus sirilwijesundarai*, and *Pseudophilautus stellatus*) have highly restricted ranges within the highest elevation classes (Appendix S5). It is likely that other species are also vulnerable, such as *Lankanectes pera*, which inhabits streams and has a small range of occurrence, yet the distribution of these occurrence localities among a comparatively broad elevational range lowered its ranking. Species with overlap in the climatically suitable zone for *Bd* may still suffer partial declines that can threaten populations. For example, in Australia the partial climatic suitability of frogs in the wet tropics caused drastic range contraction in many species (McKnight et al., 2017).

The fact that the high-risk zone is heavily exploited for agriculture (Wickramagamage, 1998; Weerawardhena & Russell, 2012) may contribute to the persistence of pesticides in these environments. Pesticides have been linked to lowered immunity in amphibian species (Christin et al., 2004; McCoy & Peralta, 2018), which can interact with disease to cause greater impacts. These interactive threats provide even greater risks to the restricted range species.

4.1 | Implementation of pre-emptive conservation strategies

The prescient implementation of pragmatic conservation and management efforts to identify the distribution and curtail the spread of *Bd* at the onset is important. Refuges of disease can provide important safe havens for threatened species (Stockwell et al., 2015; Bower et al., 2017). As *Bd* tends to spread along frequently traversed pathways (Pauza, Driessen & Skerratt, 2010), we propose protocols to disinfect the footwear of all foreign visitors when entering the country. This is economically undemanding and can be readily implemented using disinfectant mats (Amass et al., 2006; Allen et al., 2010). This could also be implemented at locations such as Horton Plains National Park, Adam's Peak, and Knuckles, where visitors traverse on foot. In addition, disease surveillance and long-term amphibian monitoring programmes (Ray et al., 2022) should be established within these high-risk zones, to allow the detection of both *Bd* infections (Seimon et al., 2017) and their related impacts (Russell et al., 2019). Implementation of biosecurity protocols coupled with research to quantify the current status of *Bd* impacts in Sri Lanka could identify the proximate causes of declining species, and shape priorities in conservation.

FIGURE 2 Sri Lankan paddy field frog (*Minervarya greenii*) (photograph by Sanoj Wijayasekara).

4.2 | Global impact

In light of the recent detections of *Bd* in the Asian region (Fu & Waldman, 2019; Rahman et al., 2020; Sreedharan & Vasudevan, 2021), and the already established spread of *Bd* in other parts of the world (Mendelson et al., 2006; Azat et al., 2022), the methods discussed here would enable scientists and policymakers to identify species and regions in need of immediate conservation action. In areas such as the Western Ghats and Taiwan, the existing high diversity of amphibians (Sankararaman et al., 2021; Schmeller et al., 2022) is already facing a myriad of challenges (Sankararaman et al., 2021), including *Bd* (Dahanukar et al., 2013; Thorpe et al., 2018; Schmeller et al., 2022). Therefore, the identification of species at high risk of *Bd* infection in such areas would allow researchers to employ cost-prohibitive tests such as polymerase chain reaction (PCR) (Thomas et al., 2021) more efficiently and in a more focused manner. In tandem with already existing (Rodríguez-Rodríguez et al., 2020) and novel conservation strategies (Button & Borzée, 2021), this could have a significant impact in curtailing future *Bd* outbreaks around the world.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information.

ETHICS STATEMENT

No specimens were collected for this study. All individuals were briefly handled for identification purposes and the collection of photo vouchers was performed following established protocols (Beaupre et al., 2004) and under government research permits (WL/3/2/79/15 and R&E/RES/NFSRCM/2016-02).

ORCID

Ruvinda K. de Mel https://orcid.org/0000-0002-9869-165X
Surendranie Judith Cabral de Mel https://orcid.org/0000-0001-5045-2716

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