Effects of habitat fragmentation on herpetofauna in Southeast Asia

From broad scale responses to fine scale responses in an ever-changing anthropogenic landscape

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Wei Cheng Tan

aus

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1. Gutachter: PD Dr. Dennis Rödder
2. Gutachter: Prof. Dr. Christoph Scherber

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“We don’t own the planet Earth, we belong to it. And we must share it with our wildlife.”

—— Steve Irwin ——

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Contents

Summary 7

CHAPTER 1: General Introduction 9

1.1 Habitat fragmentation: Concept and process 10

1.2 Effects of habitat fragmentation 12

1.2.1 On biophysical aspects of landscape 12

1.2.2 On biodiversity 13

1.3 Southeast Asia as region for conservation study 15

1.4 Herpetofauna as ideal study system for conservation study 17

1.4.1 Freshwater reptiles 18

1.5 Aims and scope 19

1.6 Methodological overview 21

1.6.1 Systematic review 21

1.6.2 Approaches to measure effects of habitat fragmentation 22

CHAPTER 2: A global analysis of habitat fragmentation research in reptiles and amphibians: What have we done so far? 27

2.1 The conundrum of biodiversity decline: a global disparity 28

2.2 Methods and personal contributions 28

2.3 Summary of critical findings and outlook 29

CHAPTER 3: Effectiveness of protected areas for the conservation of critically endangered freshwater reptiles 32

Chapter 3.1: A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia 32

3.1.1 The plight of Asian freshwater turtles 33

3.1.2 Methods and personal contributions 34

3.1.3. Summary of critical findings and outlook 36

Chapter 3.2: Last chance to see? Iran and India as strongholds for the Marsh crocodile (*Crocodylus palustris*) 38

3.2.1 Climate change and habitat fragmentation: Modeling the current and future threats to the Marsh crocodile 39

3.2.2 Methods and personal contributions 39

3.2.3 Summary of critical findings and outlook 41

Chapter 3.3: Disappearing archosaurs– an assessment of established protected areas in the Philippines to save the critically endangered and endemic Philippine crocodile *Crocodylus mindorensis* 44

3.3.1 Habitat modelling and conservation planning for the Philippine Crocodile, an endemic and endangered species 44

3.3.2 Methods and personal contributions 46

3.3.3 Summary of critical findings and outlook 47

CHAPTER 4: High freshwater turtle occupancy in sustainably managed tropical forest in Borneo 49

4.1 Logging as a process of habitat fragmentation in freshwater turtles and the advantages of Reduced Impact Logging 49

4.2 Methods and personal contribution 50

4.3 Summary of critical findings and outlook 52

CHAPTER 5: General discussions and prospects 53

5.1 Current state of research in habitat fragmentation 54

5.2 The benefits and limitations of species distribution models (SDMs) in species conservation 55

5.3 Investigating fine-scale species responses: A case for occupancy models 57

5.4 Personal prospects 59

REFERENCES 61

SUPPLEMENTARY FILES 82

APPENDIX 83

Summary

Habitat loss and fragmentation are undoubtedly significant drivers of biodiversity loss worldwide, with Southeast Asia being a hotspot of biodiversity and facing numerous anthropogenic pressures. However, the impacts of habitat fragmentation on biodiversity are still not fully understood, and further research is required to determine the responses of different taxa to this threat. Reptiles and amphibians (herpetofauna), in particular, are among the most threatened groups globally, with Southeast Asia being home to a high diversity of species and facing imminent threats from habitat loss and fragmentation. By combining bibliographic analyses and macroecological methods, this thesis aims to contribute to the knowledge on the current global state of habitat fragmentation research in herpetofauna and the broad and fine scale responses of Southeast Asian reptiles to various forms of habitat fragmentation.

Chapter 1: This chapter provides a general introduction to the concepts of habitat fragmentation and its effects on biodiversity. It accentuates the importance of Southeast Asia for habitat fragmentation research due to its complex geological history, high species richness, and rapid habitat loss. It also describes the plight of the Southeast Asian herpetofauna, focussing on their vulnerability to habitat loss and fragmentation in freshwater environments. Lastly, the chapter gives a brief overview of the methodologies and approaches used throughout this thesis.

Chapter 2: Recent decades have seen a surge of funding, published papers and citations in the field as threats to biodiversity continue to rise. However, how research directions and agenda are evolving in this field remains poorly understood. This chapter presents a global review of past and current state of research on habitat fragmentation for reptiles and amphibians. Here, I systematically reviewed published literatures on habitat fragmentation effects on reptiles and amphibians from 1990 to 2020, with the aims of identifying geographical and taxonomical trends on the various forms of habitat fragmentation, and the sampling methods and response variables commonly employed to identify them. The study reveals several patterns and biases in research efforts, such as the concentration of studies in wealthy and English-speaking countries, and the under-representation of certain regions (e.g. Africa and Southeast Asia) and taxa (e.g. caecilians, fossorial reptiles). It specifically calls for increased attention to these taxa in Southeast Asia, which have received less scientific scrutiny compared to other regions of the world. Moreover, there is a shift in research agendas towards studies utilising technological advancements including genetic and spatial data analyses. These findings suggest important associations between sampling methods and prevalent response variables but not with the forms of habitat fragmentation. This review suggests the need for more studies on genetic and spatial patterns, with emphasis on underrepresented reptile and amphibian taxa. This chapter sets the context for the subsequent chapters by highlighting the existing gaps in the field.

Chapter 3: This chapter uses species distribution models to investigate the broad-scale responses of threatened semi-aquatic or freshwater reptiles to current and future climatic and anthropogenic conditions. More specifically, it examines the habitat suitability of endangered freshwater crocodiles and turtles and assesses the effectiveness of existing protected areas in conserving these species across Southeast and South Asia (in the Indomalayan realm). Species distribution models are highly successful in predicting potentially suitable habitats of a species based on their environmental niche and presence records. The results suggest that protected areas may be insufficient in the face of current anthropogenic pressures and future climate change. The chapter emphasises the importance of considering both climatic and non-climatic factors in species distribution models. The results of this chapter are essential for conservation planning and management, as they provide insights into important areas and reserves that should be prioritised.

Chapter 4: This chapter zooms in from a broad-scale to fine-scale view of species response to habitat change, focusing on the effect of logging, which affects more than half of the remaining tropical forests in Southeast Asia. Logging has direct and indirect impacts on freshwater turtle habitats, such as altering stream hydrology and increasing sedimentation. In this chapter, I examine the fine-scale responses of two freshwater turtle species to Reduced Impact Logging, a sustainable forestry method, in Deramakot reserve in Sabah, Malaysian Borneo. I use occupancy models to estimate the probability of species detectability and habitat associations across a post-harvest recovery gradient (1 –21 years since logging), using presence and absence data. Results for the non-threatened soft-shelled turtle, *Dogania subplana* are inconclusive. However, the study reveals a significant negative association between monthly rainfall and detection of the threatened hard-shelled turtle, *Notochelys platynota.* The occupancy probability of *N. platynota* is positively associated with greater distance from logging roads. Nevertheless, both species appear to be relatively common throughout the reserve. The chapter suggests that forests managed sustainably, i.e. using Reduced Impact Logging could serve as conservation areas for imperilled freshwater turtle species in the region.

Lastly, **chapter 5** summarises the results of this thesis and its implications and contributions to the field. It also considers the limitations of the approaches and methodologies used. Overall, this thesis emphasises the urgent need for more research on the effects of habitat fragmentation on herpetofauna in in Southeast Asia and the importance of incorporating both broad and fine-scale data. This work is a significant step towards providing easily reproducible studies to be used as baseline to ensure the long-term survival of these vulnerable species in Southeast Asia.

CHAPTER 1

General Introduction

"Rohan Chakravarty, www.greenhumour.com"

1.1 Habitat fragmentation: Concept and process

The concept of habitat fragmentation was highlighted more than 60 years ago by William L. Thomas. Jr. in the book "The Man's Role", (Thomas. Jr, 1956). This book influenced global-scale integrative thinking about the environment. Ecologists began to recognise the negative impacts of habitat destruction and alteration on biodiversity. Since the 1960s, the theory of island biogeography developed by MacArthur and Wilson (1967) laid the groundwork for understanding the role of spatial configuration and connectivity in determining biodiversity patterns. This simple, elegant model aimed to predict the species richness and composition on islands based on their size, distance from the mainland and the rate of colonisation and extinction. The idea was quickly extended to habitat fragments being perceived as "islands" surrounded by a "sea" of unsuitable habitats. This conceptual theory provided a quantitative framework for studying the effects of spatial configuration on our biota and stimulated many studies in which species dynamics were related to fragment size and isolation (Diamond, 1975). However, not until the 1990s did habitat fragmentation-related topics start garnering substantial attention from researchers and conservationists due to its far-reaching ecological implications.

The development of landscape ecology has concurrently revolutionised ways of understanding habitat fragments and landscape processes. The concept of landscape structure, patch dynamics, and spatial pattern analysis within a matrix became an important paradigm (Forman and Godron, 1986). It is important to consider the spatial arrangement and configuration of habitat in fragmented landscapes, because landscapes are not homogeneous entities but rather consist of a mosaic of different habitat types and land uses (Forman, 1995). By highlighting the effects of mosaics on ecological interactions, we can understand how the pattern and structure of the landscape can have profound effects on biodiversity, ecological processes, and human interactions with the environment.

So, what is habitat fragmentation? In a broad sense, habitat fragmentation refers to the division or breaking-up of large, continuous habitats such as grasslands or tropical forests into smaller, isolated patches (Fahrig et al. 2017; see Fig. 1.1.1). This process typically involves several key stages:

(1) A reduction or complete removal of native vegetation due to human activities or natural events. Since this process is more often human-induced than naturally occurring (Forman, 1995; Thomas. Jr, 1956), this thesis will focus mainly on habitat fragmentation caused by anthropogenic pressures.

(2) As habitat is lost, the remaining habitat patches, fragments or remnants become smaller and more isolated from each other, creating fragmented landscapes (Fahrig, 2003).

(3) These habitat patches are then separated by non-habitat or matrix areas, such as agricultural fields, urban areas and roads replacing vegetation that is lost (Haddad et al., 2015).

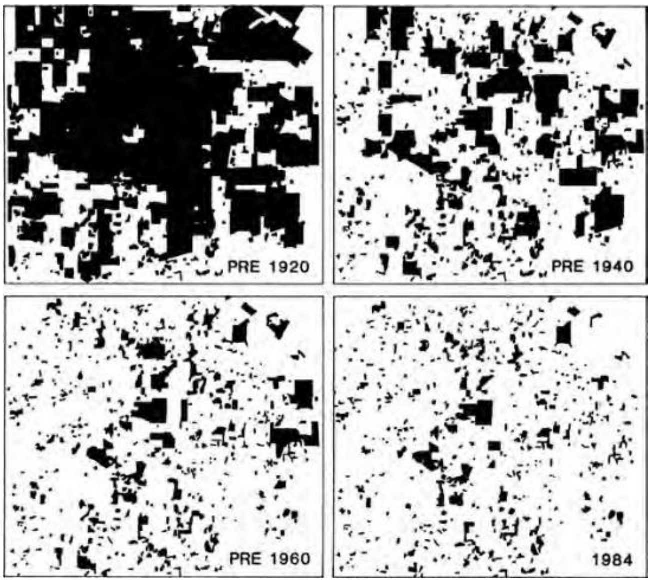

Figure 1.1.1: Changes in the extent and pattern of native vegetation in the Kellerberrin area, Western Australia, from 1920 to 1984, illustrating the process of habitat loss and fragmentation. Reprinted from Saunders et al. (1993) with permission from Elsevier[1]

These three stages are so intertwined that it is often challenging to distinguish the individual impact of each on the species or community of concern. In fact, the loss of habitat (1) and fragmentation *per se* (2), i.e. the breaking of habitat after controlling for habitat loss, should be treated as two separate processes as their effects on biodiversity can vary (see Fig. 1.1.2; Fahrig, 2003). A meta-analysis of landscape scale investigations conducted by Fahrig (2017) has found that 76% of species responses to habitat fragmentation *per se* were positive (but see Fletcher et al. 2018) and recommended that the effects of these two components should be measured independently (Fahrig, 2017). However, many studies failed to differentiate between these components, raising concerns about the ambiguity or lack of meaning associated with the term "habitat fragmentation," given that some researchers have tended to lump the combined consequences of habitat loss and fragmentation under the term without explicitly stating that they have done so (Didham et al., 2012; Lindenmayer and Fischer, 2007, 2006). In this thesis, to provide a holistic view of the effect of modified landscapes, I will employ a working definition of “habitat fragmentation” that encompasses the combined process of any landscape change, habitat loss or/and fragmentation.

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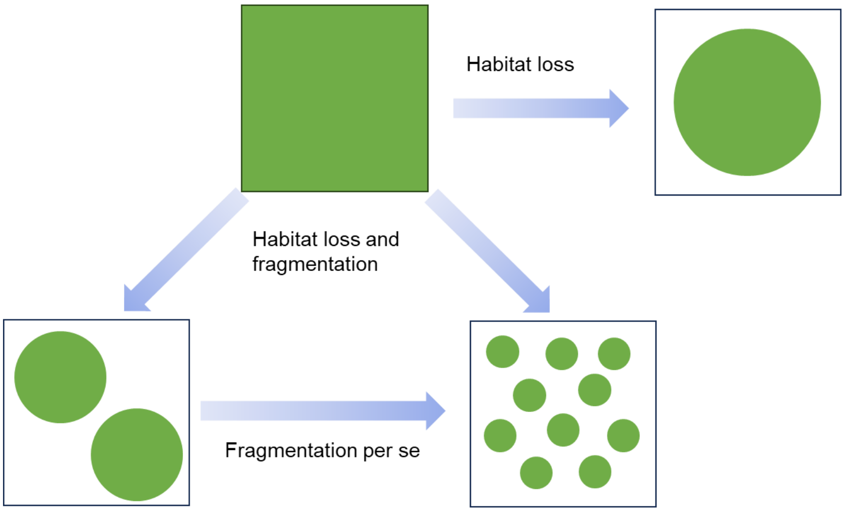


Figure 1.1.2: Habitat loss is a process whereby habitat is reduced over time. In contrast, habitat fragmentation *per se* is a difference in spatial pattern. For a given amount of habitat, a more fragmented pattern has more, smaller patches, with more total edge habitat. Adapted from Fahrig (2017).

1.2 Effects of habitat fragmentation

1.2.1 On biophysical aspects of landscape

There are two key aspects to consider when habitat fragmentation occurs: the changes in landscape patterns and changes in ecosystem processes.

Firstly, the change in landscape pattern is a dynamic process which changes characteristic of the original vegetation through time (Figure 1.1.1). It involves a decline in the total area of fragments, a decrease in fragment size, increased isolation of fragments, and the dominance of straight edges compared to natural features over time (Bennett and Saunders, 2010). These changes result in an increase in the overall proportion of edge habitat, which can largely influence the dynamics of biodiversity (Banks-Leite et al., 2010; Fahrig, 2003; Ries et al., 2004). In addition, it needs to be considered that landscape change is not random everywhere, but rather occurs more in flatter areas, lower elevations and more productive soils, resulting in smaller fragments of original vegetation within agricultural areas (Bennett and Saunders, 2010). As such, remaining fragments represent a biased distribution of the former biota and are often effective predictors of land-use history (Forman and Godron, 1986; Forman, 1995).

Secondly, habitat fragmentation also leads to changes in ecosystem processes (Lindenmayer and Fischer, 2006; Saunders et al., 1993). The removal of native vegetation often result in changes in physical processes such as solar radiation and wind and water fluxes (Chen et al., 1995). The greatest impact on fragments occurs at their boundaries, with patches which are small and irregularly shaped experiencing the strongest “edge effects” (Ries et al., 2004). Edge effects refer to the unique environmental conditions and ecological processes that occur at the boundary between two different habitats. For example, the microclimate at a forest edge adjacent to cleared land differs from that of the forest interior, affecting temperature, humidity, and light availability (Didham and Lawton, 1999; Gehlhausen et al., 2000). These changes in microclimate can affect biological processes such as litter decomposition, nutrient cycling, and vegetation structure and composition, which in turn influence species composition, population dynamics, and ecological interactions (Hofmeister et al., 2019). Depending on the intensity of the edge effects in fragments, it can lead to changes in species composition (Banks-Leite et al., 2010), as some species may be more sensitive to edge effects due to their limited dispersal abilities, resulting in shifts in community structure and dynamics (Cox et al., 2012; Khamcha et al., 2018). In conclusion, changes in ecosystem processes can have cascading effects on the overall functioning and resilience of ecosystems.

1.2.2 On biodiversity

One of the most well-known effects of habitat fragmentation is the reduction of species richness in habitat patches. This is often described by the species-area relationship (Connor and McCoy, 1979), which states that larger areas tend to support more species while smaller and more isolated areas tend to support fewer species, especially those that are rare, specialised or susceptible to disturbance. This relationship has been observed for many groups of organisms, such as birds (Radford et al., 2005), butterflies (Werner and Buszko, 2005), rodents (Bolger et al., 1997), reptiles (Losos and Schluter, 2000) and plants (Connor and McCoy, 1979). However, the species-area relationship does not reveal which particular species will be lost from smaller patches, or how fast this loss will occur. These details would depend on a variety of factors, such as the degree of isolation, habitat quality, disturbance regime, land-use history, and species-specific traits (Banks-Leite et al., 2010; Ewers and Didham, 2006; Lindell et al., 2007; Radford et al., 2005).

Responses to habitat fragmentation differ among species. Some taxa are more vulnerable to habitat fragmentation than others, depending on their ecological requirements, life-history strategies, dispersal abilities, and responses to the type of landscape change (Ewers and Didham, 2006). Generally, species that have specialised habitat needs, large home ranges, low population densities, low reproductive rates, or poor dispersal capacities are more likely to decline or disappear from fragmented habitats than those that are more generalist, adaptable, or mobile (Newbold et al., 2015). Furthermore, some species may even benefit from the positive effects of habitat fragmentation, such as increased abundance or reduced competition or predation in smaller or edge habitats or in human-modified landscapes (Khamcha et al., 2018; Lindell et al., 2007; Ries et al., 2004). For example, hummingbird species are found to be more abundant and diverse at the forest edges compared to the forest interior in Costa Rica (Banks-Leite et al., 2010). These edge-adapted birds may benefit from increased light, food availability or reduced competition. Despite the change in bird community composition at fragmented edges, species and guild richness remain the same (Banks-Leite et al., 2010). Hence, measuring species richness as a single metric can be misleading and should be avoided when evaluating the consequences of habitat fragmentation (Gardner et al., 2007; Palmeirim et al., 2017).

In addition to species responding to habitat fragmentation differently, we should also expect species across varying biomes to response differently to habitat fragmentation (Cordier et al., 2021; Newbold et al., 2020). For example, habitat fragmentation may have stronger negative effects on biodiversity in tropical forests than in temperate grasslands (Lindell et al., 2007), due to the higher sensitivity of tropical species to edge effects, fire, and invasive species (Barlow et al., 2016). For example, in tropical regions where forest cover is high, patch size and isolation may be more important for forest specialists whereas in temperate regions where forest cover is low, patch quality and shape may be more important than patch size for temperate species (Lindell et al., 2007; Radford et al., 2005). Moreover, habitat fragmentation may differentially affect ecological processes in different biomes, such as dispersal, gene flow, species interactions, and ecosystem functions (Wilson et al., 2016). These differences in the effects of habitat fragmentation across biomes can be a result of the variation in the physical and biological characteristics of different biomes, such as climate, topography, vegetation structure, and species composition (Blowes et al., 2019; Keinath et al., 2017; Newbold et al., 2020). Therefore, understanding the effects of habitat fragmentation across biomes is essential for developing effective conservation strategies that account for the diversity and complexity of natural systems.

Another effect of habitat fragmentation is the isolation effect, where there is a reduction of connectivity between habitat patches that impedes the movements and dispersal of species (Diamond, 1975). Connectivity refers to the degree to which landscape facilitates or prevents movement among patches (Crooks and Sanjayan, 2006). The magnitude of connectivity strongly depends on two broad aspects of the landscape (Beninde et al., 2016): (1) structure, which is the spatial arrangement of the landscape elements such as distance between patches and the type and permeability of the matrix; and (2) function, defined as the realised use of the matrix by species, such as frequency and success of movement or gene flow among patches. Connectivity determines the gene flow and genetic diversity among populations, and subsequently the vulnerability to inbreeding and stochastic extinction. Species differ in their sensitivity to connectivity (Kimberley et al., 2021). Structurally well-connected landscapes could be functionally important for some species but not for others (Kimberley et al., 2021). Landscape connectivity can be improved by the presence of corridors, buffers, or stepping stones that facilitate movement and gene flow across the landscape (Bennett, 1999; Forman and Godron, 1986). Ensuring effective connectivity can be essential for maintaining population viability and enhancing resilience in fragmented landscapes (Bennett and Saunders, 2010).

1.3 Southeast Asia as region for conservation study

Because the effect of habitat fragmentation varies greatly depending on the species and biome involved, one must carefully consider the choice of study system. I have selected Southeast Asia as the main geographic focus of my thesis for several reasons. This section provides the background information necessary to understand why this fascinating region deserves special attention.

The high species richness and endemism in Southeast Asia is shaped by its complex geological history, which involves three major events: the assembly of Sundaland from Gondwanan fragments in the Paleozoic, the accretion of various landmasses from Asia and Australia in the Mesozoic, and the subduction and collision at Sundaland margins in the Cenozoic (Hall et al., 2011; Holloway and Hall, 1998; Pubellier and Morley, 2014). These repeated collisions between continental masses and subsequent modifications of interoceanic currents have caused dramatic changes in the climate and contributed to the evolution of distinctive flora and fauna in the area (de Bruyn et al., 2012). Perhaps the most influential events happened during the Quaternary period where the region’s land area varied two-fold as sea levels fluctuated up to ±50 m within each of ~50 Pleistocene glacial cycles, exposing a major portion of the Sunda shelf during the periods of sea level minima, see Fig. 1.3.1 (Woodruff, 2010). There were continuous land bridges between the continent and the islands of Sumatra, Java and Borneo whenever sea levels fell more than 30m below today´s level (Woodruff, 2010). These land bridges facilitated species migrations of Indochinese taxa into the Sundaic regions and vice versa (Sathiamurthy and Voris, 2006; Woodruff, 2010). At 11,000 years before present , the rapid obliteration of land bridges between Indochina and Great Sundas Islands from rising sea levels has left disconnected populations to evolve in isolation on shores of the newly formed South China Sea (Sathiamurthy and Voris, 2006; Sterling et al., 2008). The major river systems (Salween, Malacca, North Sunda, Mekong and Red rivers) and large lakes (only Tonle sap of Cambodia remains) that existed on the exposed Sunda Shelf also played a role in providing opportunities for dispersal and survival of some aquatic and semi-aquatic taxa (Sathiamurthy and Voris, 2006; Woodruff, 2010). Such complex environmental history has had a dramatic effect on the herpetofauna by generating high degrees of endemism in insular and upland systems (Das and van Dijk, 2013). Many of these endemic species are parts of ancient and cosmopolitan lineages that have survived multiple extinction events and colonised other regions of the world (Gower et al., 2012; Procheş et al., 2021).

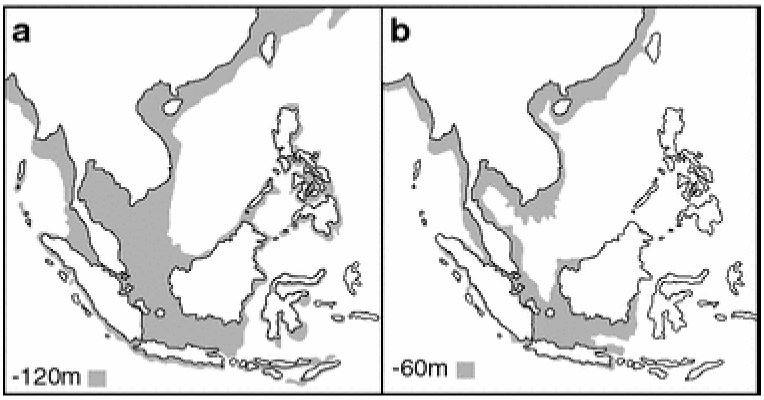


Figure 1.3.1: Outline maps of Southeast Asia depict sea levels at various depths: 120 m and 60 m below today's sea level. The grey area depicts the land extension from present land. Sundaland reached its maximum areal extent approximately 20,000 years ago when sea levels dropped below -120 m. Over the last million years, the average areal extent of Sundaland occurred when sea levels were at -62 m. Image modified from Woodruff (2010)

As one of the global biodiversity hotspots, Southeast Asia harbours the largest mean proportion of country-endemic bird (9%) and mammal species (11%) and the second highest proportion country-endemic vascular plant species compared to other tropical regions (UNEP-WCMC & IUCN, 2020). Concurrently, the region contains the highest proportion of threatened species across all taxonomic groups except amphibians (IUCN, 2023; Sodhi et al., 2010b). Although endemic herpetofaunal elements and threatened amphibians in Southeast Asia are proportionally lower than in the new world (Sodhi et al., 2010b), this is likely a reflectance of the low prevalence of herpetological research in the region due to socioeconomic factors (Guedes et al., 2023), rather than the lack of diversity. New and cryptic species in the region are only discovered recently and many are yet to be described (Moura and Jetz, 2021).

Home to nearly 15% of the world's tropical forest area, the region unfortunately has the highest (and increasing) rate of natural forest loss among all tropical regions (FAO and UNEP, 2020). Between 2001 and 2019, researchers calculated that Southeast Asia had lost 610,000 square kilometres of forest – an area larger than Thailand (Feng et al., 2021). Indonesia alone has been responsible for nearly 14% of global tropical deforestation up to 2019, with a sharp increase in forest loss rate during the last 5 years (Feng et al., 2021). Furthermore, less than 10% of Southeast Asia's forests are under some form of protection (IUCN categories I-VI), which suggests that habitat loss in the region likely will continue (Farhadinia et al., 2022). Moreover, many protected forests are still degraded by illegal logging activities, and secondary forests are also being lost at a high rate (Sodhi et al., 2010b). Deforestation in Southeast Asia is largely fuelled by timber production or logging in the past century and the rapid growth of palm oil production in recent years (Wilcove et al., 2013). Finally, countries in this region also face multiple direct and indirect threats from climate change, invasive species, illegal wildlife trade, corruption, poverty and human population growth (Bickford et al., 2010; Hughes, 2017; Nijman and Shepherd, 2022; Rintelen et al., 2017; Sloan et al., 2019; Sodhi et al., 2004; Tan et al., 2022).

In sum, the region has a long history of landscape change and biotic recolonization following past climatic and anthropogenic disturbances. This history provides an opportunity to examine how species and communities have responded to different degrees and patterns of fragmentation over time, and how they may cope with future changes (Sodhi et al., 2004; Struebig et al., 2015). The region's complex mosaic of land uses and cover types may provide functional connectivity or barriers depending on the species' ecological traits and requirements (Sodhi et al., 2010a). This complexity allows for testing how landscape composition and configuration influence species movements, interactions, and persistence in fragmented landscapes (Lucey et al., 2014; Wilting et al., 2010). Therefore, it is of utmost priority for conservationists to determine whether and how species will shift their ranges in response to habitat fragmentation and global warming or whether they have sufficient genetic variability and ecological plasticity to adapt to the expected changes (Hughes, 2017; Ihlow et al., 2012). Conservation in Southeast Asia requires a diversity of initiatives with country-specific and cooperative actions, such as protection of forests through legislation, reforestation, sustainable agriculture, public education, livelihood support, capacity building, and curbing illegal trade (Sodhi et al., 2010b; Wilcove et al., 2013). These factors combined make Southeast Asia an interesting and important region to study for theoretical and conservation reasons, especially since it has been frequently overlooked in the global discourse on threats to biodiversity (Hughes, 2017).

1.4 Herpetofauna as ideal study system for conservation study

Habitat fragmentation research has long been dominated by birds and mammals (Fardila et al., 2017). Reptiles and amphibians, also known as herpetofauna, are less well studied, making up only a tenth of the studies (Fardila et al., 2017). These groups merit increased attention because they have higher levels of extinction risk globally than birds or mammals. Currently, 40% of amphibian and 21% of reptile species are facing the threat of extinction, whereas only 13% of bird and 26% of mammal species are in the same situation (Cox et al., 2022; Stuart et al., 2004). Amphibians are particularly vulnerable to habitat loss due to their cryptic nature, specific habitat needs, and limited dispersal abilities (Nowakowski et al., 2017; Ofori-Boateng et al., 2013; Sodhi et al., 2008). Reptiles, which are poorly known (with one fifth of the species being data deficient) (Böhm et al., 2013), are exposed to the same threats as amphibians (Cox et al., 2022; Gibbons et al., 2000). A recent meta-analysis showed that habitat fragmentation–especially deforestation–has a negative effect on species richness of reptiles globally (Cordier et al., 2021). Compared to birds, which have higher mobility and dispersal ability, reptiles often have narrow ranges with high endemism (Roll et al., 2017; Weeks et al., 2023). As a result, reptiles are highly sensitive to local extinction due to habitat loss and fragmentation (Meiri et al., 2018).

Human-induced climate change has also been identified as a cause of population decline and local extinction in some species (Bellard et al., 2012; Román-Palacios and Wiens, 2020). Changes in temperature, precipitation patterns, and extreme weather events due to climate change will have a significant impact on the distribution of many species, particularly poikilothermic animals (Bickford et al., 2010; Nowakowski et al., 2017; Sinervo et al., 2010). Due to their intrinsic physiological requirements, they rely on temperature and precipitation levels for their physiological functions and breeding patterns (Nowakowski et al., 2017). Temperature also plays a role in sex determination in many reptile species (Krueger and Janzen, 2022; Mitchell et al., 2013), thus changes in temperature can affect the sex ratio of their offspring (Gómez-Saldarriaga et al., 2016; Hulin et al., 2009). The impacts of climate change are predicted to vary geographically (Bellard et al., 2012; Ihlow et al., 2012; Summers et al., 2012), with Southeast Asia expected to become warmer and drier with high variability in precipitation (Allan and Soden, 2008; Loo et al., 2015). More frequent, prolonged, and severe droughts in some areas can have direct and indirect negative effects on the feeding and breeding behaviour of reptiles and amphibians (Bickford et al., 2010). They generally have conservative thermal niches and limited ability to adapt quickly or disperse (Bodensteiner et al., 2021), so they are more likely to shift their ranges rather than adapt physiologically when faced with new climatic conditions (Bickford et al., 2010; Osland et al., 2021). However, fragmentation of continuous habitat might hinder these range shifts and may result in population extinction (Habel et al., 2019). Modification of habitat and climate during the Anthropocene may occur too quickly for many amphibians and reptiles to adapt (Biber et al., 2023; Habel et al., 2019). As a result, most species will have reached or exceeded their ability to adapt these changes within the next 50 years (Biber et al., 2023; Bickford et al., 2010).

1.4.1 Freshwater reptiles

In this thesis, I will focus on freshwater herpetofauna such as crocodilians and (semi-) aquatic turtles for several reasons. First, there has been relatively little research devoted to the effects of habitat fragmentation on freshwater reptiles in tropical Southeast Asia (Dudgeon, 2022; Gardner et al., 2007). However, the proportion of threatened reptile species is highest in freshwater environments and tropical regions such as Southeast Asia where data deficiency is highest (Böhm et al., 2013; Cox et al., 2022). Second, freshwater systems are particularly susceptible to the changes arising from “the tragedy of the commons” (Dudgeon, 2019). As human populations and water needs expands, so will the threats to freshwater biodiversity. Furthermore, freshwater habitats cover less than 1% of the Earth’s surface, but they contain 10% of all animals and one-third of all vertebrates (Tockner, 2021). As a result, they are scarce, dynamic and highly vulnerable to habitat fragmentation and climate change (Benateau et al., 2019). Such threats leads to a reduction in connectivity (see chapter 1.2.2) among suitable aquatic habitats on which these species largely depend. For example, dam construction can block the movement of crocodilians and turtles between riverine and estuarine habitats, isolating populations and reducing gene flow (Ihlow et al., 2015, 2014). Flow alteration through artificially fluctuating water levels alters breeding and nursery habitats by flooding nesting sites (Dudgeon, 2022; Ihlow et al., 2014). Anthropogenic activities such as agriculture and pollution can alter hydrological regimes, water quality and vegetation structure. Pollution from agricultural runoff can cause eutrophication and algal blooms in wetlands, reducing dissolved oxygen and increasing toxicity for freshwater species (Dudgeon, 2022; Tockner, 2021). Lastly, freshwater reptiles are threatened by overexploitation and poaching for food, medicine or pet trade (CITES, 2010); particularly in Southeast Asia where demand in the market for freshwater turtles has increased drastically in the past years (Stanford et al., 2020). For instance, *B. borneoensis* are prized in the pet trade for their highly attractive colouration during the mating season (Stanford et al., 2018).

1.5 Aims and scope

By combining bibliographic analyses and macroecological methods, this thesis aims to enhance knowledge on the current state of habitat fragmentation in Southeast Asia and the response of Asian herpetofauna to different forms of habitat fragmentation. Due to the COVID-19 restrictions which have impeded the possibility of collecting field data by myself, I have adapted the original research plan by utilising data from open sources and involved collaboration partners in target countries to help with the fieldwork. This thesis would not be possible without them. In short, I first systematically review the state of research and knowledge gaps in habitat fragmentation in chapter 2, then examine the broad scale responses of endangered freshwater reptiles in chapter 3, and finally focus on the fine scale responses of freshwater turtles to logging as effect of habitat fragmentation in chapter 4. Together, these chapters test the following hypotheses:

HYPOTHESIS 1: The published literatures in the last 30 years on habitat fragmentation for reptiles and amphibians vary across geographic regions, taxa and research directions.

The first study (chapter 2) aims to examine the current state of research on habitat fragmentation for reptiles and amphibians by conducting a global-scale review of geographical and taxonomical trends on published literatures. It assesses whether certain sampling methods and response variables are associated to specific forms of habitat fragmentation and how these associations are distributed across geographical space and time. Finally, the study identifies the emerging research agendas and patterns in the published literature on habitat fragmentation for reptiles and amphibians over the last three decades. This study will provide an overview of the state of the art for habitat fragmentation research in herpetofauna and research gaps we should address in the next chapters.

HYPOTHESIS 2: The existing protected areas across Southeast and South Asia are insufficient and ineffective in conserving critically endangered freshwater reptiles from current and future anthropogenic threats.

The objectives of the second, third and fourth studies (chapter 3.1- 3.3) of this thesis are to determine the coarse-scale magnitude of habitat fragmentation for aquatic reptiles exhibiting patchy distributions, and to determine how anthropogenic pressure and climate change affect habitat suitability. Using species distribution models (SDMs) based on bioclimatic variables and remote sensing variables, these studies assess the current and future habitat suitability within and outside designated IUCN protected areas. Lastly, these studies identify suitable conservation areas based on criteria such as climatic suitability, wetland occurrences, water surface areas, and the human footprint index to recommend further surveys and improvements to the current network of existing protected areas.

HYPOTHESIS 3: Habitat fragmentation through logging reduces freshwater turtle occupancy in Bornean tropical forest.

The final study (chapter 4) looks at the fine-scale response of freshwater turtles to one specific type of habitat fragmentation - logging. The aims are to (1) examine the impact of climatological covariates on freshwater turtle detectability, (2) examine the impacts of habitat- and logging-associated covariates on the occupancy of two turtle species, and (3) determine the occupancy probability of the two species within a sustainably logged reserve.

The three thesis chapters (chapter 2-4) consist of several articles that are published or in press for scientific peer-reviewed journals:

Chapter	Citation	Status
2	**Tan, W. C.**, Herrel, A., & Rödder, D. (2023). A global analysis of habitat fragmentation research in reptiles and amphibians: what have we done so far?. Biodiversity and Conservation, 32(2), 439-468. https://doi.org/10.1007/s10531-022-02530-6	Published

3.1	**Tan, W. C.**, Ginal, P., Rhodin, A. G., Iverson, J. B., & Rödder, D. (2022). A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia. Frontiers of Biogeography, 14(1). https://doi.org/10.21425/F5FBG50928	Published
3.2	Mobaraki, A., Erfani, M., Abtin, E., Brito, J., **Tan, W. C.**, Ziegler, T., & Rödder, D. (2023). Last chance to see? Iran and India as strongholds for the Marsh crocodile (*Crocodylus palustris*). Salamandra, 59(4), 327–335.	Published
3.3	Harrer, S., Ginal, P., **Tan, W. C.,** Binaday, J., Diesmos, A., Manalo, R., Ziegler, T., & Rödder, D. (2024). Disappearing archosaurs– an assessment of established protected areas in the Philippines to save the critically endangered and endemic Philippine crocodile *Crocodylus mindorensis*. Salamandra, 60(1), 29-41	Published
4	**Tan, W. C.**, Vitalis, V., Sikui, J., Rödder, D., Rödel, M., & Asad, S. (2024). High freshwater turtle occupancy in sustainably managed tropical forest in Borneo. Journal of Wildlife Management. Advance online publication. https://doi.org/10.1002/jwmg.22633	Published

1.6 Methodological overview

1.6.1 Systematic review

The enormous scope of academic literature presents several challenges (Peričić and Tanveer, 2019). Although reviews can be helpful in summarising existing literatures, they are often incomplete in the coverage of the literature, subjective, biased, and/or unclear in their methodologies (Fraser et al., 2018; Jennions et al., 2013; Whittaker, 2010). To mitigate these threats to credibility, systematic reviews are a powerful tool designed to be comprehensive, objective, transparent, and reproducible in documenting and evaluating and synthesising the current state of knowledge on a specific subject. Systematic reviews have been effective in answering questions relating to both fundamental ecology (Fidai et al., 2020) and applied ecology (Fahrig, 2003). In addition to providing a comprehensive overview of the subject, it is effective in i) identifying research gaps and areas where more studies are needed (Gardner et al., 2007); 2) highlighting methodological issues and limitations in existing studies (Kellner and Swihart, 2014), 3) reconciling inconsistent or contradictory findings (Lindenmayer and Fischer, 2007); and 4) developing new conceptual framework and insights (Ries et al., 2004). Systematic reviews are not easy to conduct, as they require a lot of time, resources, and expertise. However, they are very valuable and useful for advancing knowledge and ultimately offering guidance for future research directions.

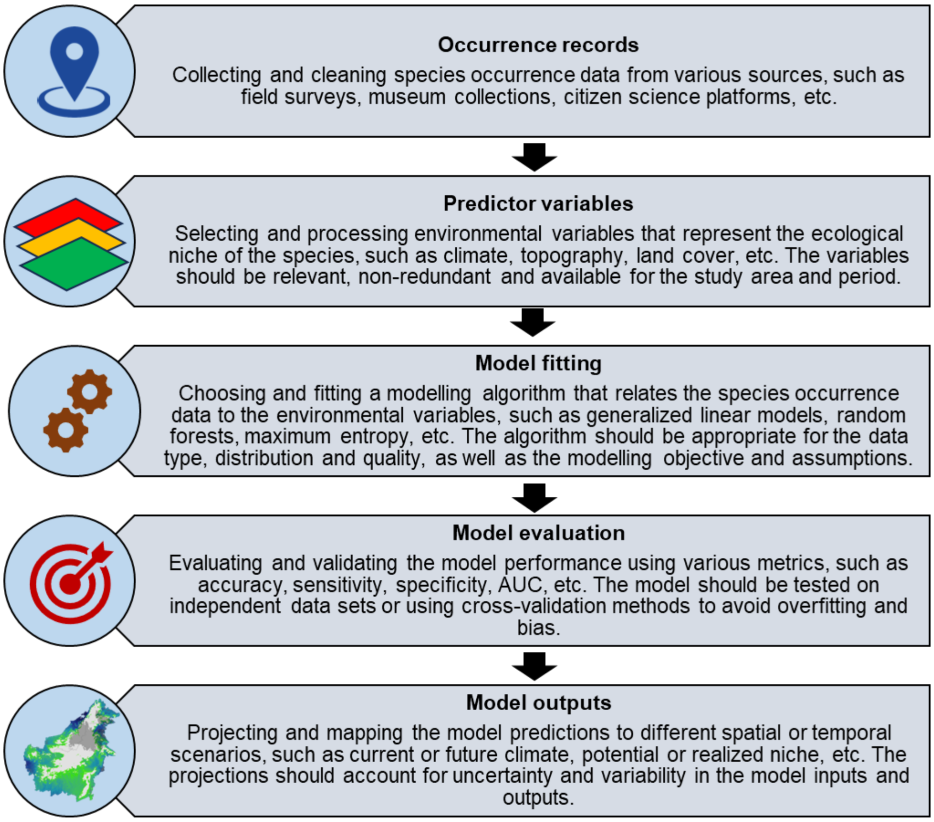
In this thesis, I conducted a systematic review to test hypothesis 1 (chapter 2). I reported the results following a standard structure and format of the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) statement (Moher et al., 2009). I then used the results of the review to guide the research directions and subjects of subsequent chapters, allowing me to address the knowledge gaps and biases identified in the review.

1.6.2 Approaches to measure effects of habitat fragmentation

Fischer & Lindenmayer (2007) categorised approaches used to understand the effects of habitat fragmentation on species and assemblages into two extremes: ‘species-oriented’ and ‘pattern-oriented’. Species-oriented approaches focus on individual species and how they respond to their environment, including habitat loss, degradation, isolation, disruptions to behaviour and biology and species interactions (Fischer and Lindenmayer, 2007). These approaches recognise each species to have unique habitat and ecological requirements facing deterministic and stochastic threats from habitat fragmentation. Pattern-oriented approaches focus on human-perceived landscape patterns and their correlation with measures of species occurrence, such as species richness. These approaches originate from island biogeography (Macarthur and Wilson, 1967) and use conceptual models such as the matrix-corridor model (Forman, 1995) and the variegation model (McIntyre and Hobbs, 1999). These are based on defined landscape patterns and their correlation with aggregate measures of species occurrence such as species richness (Fischer and Lindenmayer, 2007). Unlike the species-oriented approaches, pattern-oriented approaches provide very broad general insights and oversimplify complex casual relationships and subtle differences between individual species, which might not be suitable for testing our second and third hypotheses. Therefore, this thesis focuses on species-oriented approaches, as they fit our objectives related to detecting individualistic species response to their environment based on well-established ecological causalities (Austin and Smith, 1990; Manning et al., 2004). These approaches are also particularly effective in ensuring the continued survival of rare or threatened species (Fischer and B. Lindenmayer, 2006; Fischer and Lindenmayer, 2007). The species-oriented approaches we apply here are species distribution models and occupancy models.

1.6.2.1 Species distribution models (SDMs)

Species distribution models (SDMs), also known as environmental niche models, are powerful tools to predict the potential distribution of a species across geographic space and time (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). Using species occurrence records in combination with biologically meaningful environmental data, these models characterise the environmental niche of a given species, which can then be projected into geographic space (Elith and Leathwick, 2009; Guisan and Thuiller, 2005) (see SDM workflow in Figure 1.6.2.1.1).While early attempts have predominantly used bioclimatic predictors such as temperature, precipitation, and elevation data, recent advances in remote sensing have made classification of land cover types possible (Franklin, 2010; Guisan and Thuiller, 2005). Fine-scale remote sensing data (resolution as fine as 30 meters) from reliable open-source datasets are now available. This allows more accurate predictions of the distribution and potential impacts of environmental changes for species sensitive to fine-scale disturbance, especially when applied in combination with bioclimatic variables (Cord and Rödder, 2011; He et al., 2015; Rödder et al., 2016).



Occurrence records

Collecting and cleaning species occurrence data from various sources, such as field surveys, museum collections, citizen science platforms, etc.

Predictor variables

Selecting and processing environmental variables that represent the ecological niche of the species, such as climate, topography, land cover, etc. The variables should be relevant, non-redundant and available for the study area and period.

Model fitting

Choosing and fitting a modelling algorithm that relates the species occurrence data to the environmental variables, such as generalized linear models, random forests, maximum entropy, etc. The algorithm should be appropriate for the data type, distribution and quality, as well as the modelling objective and assumptions.

Model evaluation

Evaluating and validating the model performance using various metrics, such as accuracy, sensitivity, specificity, AUC, etc. The model should be tested on independent data sets or using cross-validation methods to avoid overfitting and bias.

Model outputs

Projecting and mapping the model predictions to different spatial or temporal scenarios, such as current or future climate, potential or realized niche, etc. The projections should account for uncertainty and variability in the model inputs and outputs.

Figure 1.6.2.1.1: A typical workflow of Species Distribution Modelling.

To date, SDMs have been widely used in conservation biology to inform management decisions (Guisan et al., 2013; Sofaer et al., 2019). They are very successful in identifying suitable habitats in order to fill the gaps in species distribution data, especially for poorly surveyed or inaccessible regions, and help design further field surveys for new populations of cryptic or rare species (Pearson et al., 2007), such as the flat-headed cats (Wilting et al., 2010) and Asian tapir (Clements et al., 2012). They have been further used to investigate the effectiveness of protected areas (Araújo et al., 2004; Ihlow et al., 2014; Tan et al., 2021). Using an approximation of the fundamental niche (potential distribution in the absence of biotic interactions, such as competition or predation) of a given species based on its realised environmental niche (actual distribution of a given species, which can be similar or smaller than its fundamental niche due to biotic or abiotic constraints), one can gain valuable insights on its future and historic geographic ranges (Guisan and Thuiller, 2005; Kearney et al., 2010). For instance, we can project the present-day environmental space occupied by a species or community into future climatic conditions derived from different climatic scenarios to assess climate change impacts (e.g., Araújo et al., 2004; Ihlow et al., 2012; chapter 3 of this thesis). Similarly, predictions from an SDM may be projected onto paleoclimatic reconstructions to infer historical climatic refugia and dispersal corridors (Liz et al., 2021; Rödder et al., 2013). In addition to phylogeography and conservation, SDMs are also useful in many other disciplines, such as community ecology (Guisan and Rahbek, 2011), evolutionary biology (McCormack et al., 2010), and invasion biology (Ginal et al., 2023, 2022, 2021).

In this thesis, I emphasise on the Maxent software which is a machine-learning algorithm following the principle of maximum entropy (Phillips et al., 2017, 2006; Phillips and Dudík, 2008). Among other competing model algorithms, Maxent has been shown to perform well in terms of predictive accuracy, model calibration, and ecological realism (Elith et al., 2006; Phillips et al., 2017). It is known to tolerate complex nonlinear relationships and interactions and avoid overfitting by using regularisation techniques that penalise model complexity and favour simpler models (Merow et al., 2013). More details on the model specifications can be found in the chapter 4. Note that many other complex approaches (e.g., bioclim, Generalised Linear Models (GLM) and neural networks) for making such models exist but do not necessarily improve the utility of a model (Jiménez-Valverde et al., 2008). Species distribution modelling techniques performed by Maxent were applied to quantify present and future habitat suitability to test hypothesis 3 (chapters 3.1-3.3).

Species distribution models can provide valuable insights into the ecology and biogeography of species, as well as useful tools for conservation planning and management. However, they also have some challenges and uncertainties that need to be treated with caution (Merow et al., 2013). Some drawbacks include: study extent for “background” or pseudoabsence data (VanDerWal et al., 2009), model selection (Warren and Seifert, 2011), evaluation for model performance and accuracy (Radosavljevic and Anderson, 2014), and model assumptions (Yackulic et al., 2013). Since a presence-only model does not require absence data, it suffers from sampling bias due to uneven or incomplete survey efforts which can lead to inaccurate predictions (Bean et al., 2012). This is because presence-only models usually use environmental values at occurrences which are typically contrasted with those available in the study region (pseudoabsence samples; Elith et al., 2006). It also shares the assumption of perfect detection, assuming that the focal species is detected everywhere it is present (Yackulic et al., 2013). However, this assumption is not required in occupancy models that use repeat-visit data to estimate detection and occurrence probabilities (MacKenzie et al., 2002; Royle et al., 2005). This point brings us to the next method: occupancy models.

1.6.2.2 Occupancy modelling

Going undetected at given site does not necessarily imply that this species is absent from the site. Instead, it may be simply undetected due to various factors related to observer error, habitat characteristic or species activity level (Kéry, 2011; Kéry et al., 2010). Imperfect detection leads to false absences that can lead to flawed inferences in two ways: 1) an underestimation of actual presence and biased representation of habitat associations that are falsely identified as unfavourable (Gu and Swihart, 2004; Kellner and Swihart, 2014); 2) confusion over the effects of environmental explanatory variables on detection and presence, particularly when detectability is negatively correlated with occupancy or varies independently from it (Lahoz-Monfort et al., 2014). For example, if a species is more likely to be detected near water sources, but its presence is determined by other factors such as temperature or vegetation, then a model that does not account for imperfect detection may wrongly attribute a higher suitability to areas near water sources. False absences can be ultimately interpreted as extinctions, potentially undermining subsequent conservation strategies (MacKenzie et al., 2017; Olea and Mateo-Tomás, 2011).

To this end, statistical models such as occupancy modelling, which account for imperfect detection resulting from covariates, allow accurate estimations of species occurrence (MacKenzie et al., 2002). Data collection is relatively easy and inexpensive, involving multiple visits to same or all the sample sites in a study area to collect species detection data (e.g., through visual, acoustic or camera trap surveys) (MacKenzie et al., 2002). This method provide unbiased estimates of occurrence probability and its associated uncertainty, as well as the factors that influence it by explicitly modelling the detection process and its covariates (Royle and Dorazio, 2008). Hierarchical models such as Bayesian approaches enable the use of prior information and expert knowledge to inform the model parameters and assumptions (Royle and Kéry, 2007). Unlike the classical likelihood-based estimation, Bayesian occupancy models allow for incorporation of random effects to accommodate spatial or temporal variation and structure in model parameters (Royle and Kéry, 2007). This can enhance the inference and prediction of occupancy models and reduce the sample site requirements. Depending on the study design and objectives, the original site-occupancy model can be extended to a dynamic distribution model where demographic rates can be predicted from multiple season detection/nondetection data (MacKenzie et al., 2017; Royle and Kéry, 2007).

Like SDMs, occupancy models have also been widely applied in ecology and conservation biology to address questions on species distribution (Kéry et al., 2010), habitat associations (Asad et al., 2020), community composition (Asad et al., 2021a; Homyack et al., 2016), survey planning (Olea and Mateo-Tomás, 2011), and disease prevalence (Mosher et al., 2018). However, sample surveys must be designed so that population changes to disturbances can be detected reliably. This can be problematic for elusive and cryptic species with highly unpredictable activities, such as freshwater herpetofauna. Detection probability in freshwater herpetofauna have been found to be strongly associated with a range of factors (Armstrong, 2016; Buchanan et al., 2019; Guzy et al., 2019; MacKenzie et al., 2002; Ocock et al., 2018; Ribeiro Jr et al., 2018). In most cases, varying detectability is associated with climatological and temporal factors such as weather conditions, humidity, air and water temperature (Armstrong, 2016; Buchanan et al., 2019; MacKenzie et al., 2002; Ribeiro Jr et al., 2018). In anurans, climatological factors can serve as phenological cues, triggering breeding events (episodic or explosive) (Allentoft and O'Brien, 2010; Asad et al., 2020; Homyack et al., 2016). These breeding events usually encompass highly conspicuous actions such as vocalising, searching for mating partners, and laying eggs, thereby increasing the probability of observation. Meanwhile, freshwater turtle breeding events are less conspicuous, although aggregations of mature adults are common (Asad et al., 2021b). Feeding regimes, predator activity, available shelter or nesting sites of these turtles are also highly determined by climatological factors (Escalona et al., 2019; Geller et al., 2022; Parlin et al., 2018). Understanding these detectability associations will widen our knowledge on the ecology and behaviour of understudied tropical freshwater turtles. Further, reliable estimates of detection and occupancy probability will permit evaluation of freshwater turtle responses to habitat fragmentation such as logging.

In this thesis, occupancy models were applied to quantify the effect of logging to test hypothesis 3 (chapter 4).

CHAPTER 2

A global analysis of habitat fragmentation research in reptiles and amphibians: What have we done so far?

Ouroborus cataphractus from Western Cape, South Africa. Photo by W.C. Tan

This chapter is published in the following article (open access):

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Original article is attached.

2.1 The conundrum of biodiversity decline: a global disparity

Habitat fragmentation is a major threat to biodiversity, especially for reptiles and amphibians, which are among the most endangered vertebrate groups (Cox et al., 2022; Roll et al., 2017). Recent decades have seen a surge of funding, published articles and citations in the field as these threats to biodiversity continue to rise (Battisti et al., 2022). However, the current state of research on habitat fragmentation effects on these taxa is not well understood. Different reviews have largely centred around certain forms of habitat fragmentation, such as land use change (Newbold et al., 2020), logging (Sodhi et al., 2004), fragmentation *per se* (Fahrig, 2017), urbanisation (Hamer and McDonnell, 2008; McDonald et al., 2013), fire (Driscoll et al., 2021), and roads (Rytwinski and Fahrig, 2012). However, few reviews have attempted a global synthesis of all forms of habitat fragmentation and addressed the geographical and taxonomical biases in reptiles and amphibians (Cordier et al., 2021; Gardner et al., 2007). Gardner et al., (2007) analysed 112 articles published between 1945 and 2006 and found substantial biases across geographic regions, biomes, types of data collected as well as sampling design and effort. A more recent review by Cordier et al., (2021) conducted a global meta-analysis based on 94 studies on the responses of reptiles and amphibians to land use changes. However, there has been no comprehensive synthesis of the research patterns and agenda of published literature on habitat fragmentation associated with the recent advances of novel research tools and techniques. This study aimed to review the global patterns and trends of habitat fragmentation research in reptiles and amphibians, focusing on the geographical and taxonomical distribution, the forms of habitat fragmentation, the sampling methods, and the response variables used in the published literature. This may provide new insights on the evolution and biases in the field over the last decades and stimulate further research. Not addressing the knowledge gaps that stem from the biases could hinder the conservation of these threatened taxa.

2.2 Methods and personal contributions

I conceptualised the study together with my direct supervisor, Dennis Rödder, and co-supervisor, Anthony Herrel. We first conducted a comprehensive and systematic search of published articles that reported the consequences of habitat fragmentation on reptiles and amphibians from 1991 to 2019 through Web of Science (https://www.webofknowledge.com/). I then proceeded with the study selection following Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009). The database search returned a total of 1421 unique records after duplicates were removed. Though arduous and exhaustive, I carefully screened all the articles one at a time from the title through the full text to determine whether they met our criteria for inclusion (for more information on the criteria, see Appendix). When an article fit our criteria, I recorded (a) GPS or georeferenced location of the study site; (b) the focal group investigated (amphibian and/or reptile); (c) taxonomic groups (order, family, genus). I also categorised each included article into one or several categories based on the type of data collected. The three main types of data were (1) Forms of habitat fragmentation; (2) Sampling methods and (3) Response variables (See Appendix).

Using the dataset for the 698 included articles, I performed the data analysis in the open source statistical software package R 4.1.0 (R Core Team, 2021) with the guidance of Dennis Rödder. I applied a Multiple Correspondence Analysis (MCA) (Roux and Rouanet, 2004) and Hierarchical Clustering on Principle Components (HCPC) (Ward, 1963) to investigate potential interactions between forms of habitat fragmentation, sampling methods, and response variables. MCA is well-suited for examining datasets with multiple categorical variables and uncovering unbiased relationships among them. I first separated the dataset into articles concerning amphibians and reptiles. I performed MCA using the MCA function from the FactoMineR package (Lê et al., 2008). Then I conducted a cluster analysis on the MCA results using HCPC to identify subgroups (clusters) of similar articles within the dataset. The cluster results were visualised in a factor map and dendrogram using factoextra package for easier interpretation. This allows us to identify categorical variables that have the highest effect within each cluster. I created a bar plot showing the percentage contribution of the categories to the uniqueness of each cluster in amphibians and reptiles using ggplot2 package in R 4.1.0. To have an overview of the geographical representation of the study locations and corresponding clusters of included articles, I projected the locations on the world map using raster and rgdal packages from R. These spatial projections are plotted in figures in the published paper.

We also further analysed our results with VOSviewer, a freeware for constructing and visualizing bibliometric networks (http://www.vosviewer.com/). The program uses clustering techniques to analyse co-authors, co-occurrence of keywords, citations, or co-citations (van Eck and Waltman, 2014). First, I made a geographical network map at country level for co-authorships of included articles. Second, to complement the results from HCPC clusters, I used the co-occurrence of categories associated to each selected paper instead of author's keywords as input to run the software. The clustering of the categories in the co-occurrence network maps confirms what we observed in the HCPC results. The first draft of the manuscript was written by me and all authors critically revised later versions. Figures were created in R and QGIS by me and then modified in Adobe Illustrator with the help of Morris Fleck.

2.3 Summary of critical findings and outlook

Our review revealed several patterns and biases in the habitat fragmentation research on amphibians and reptiles. First, we confirmed the geographical bias that has been previously reported by other studies

(Fardila et al., 2017; Gardner et al., 2007). The research effort was concentrated in wealthy and English-speaking countries, such as the USA, the UK, and Australia, while many regions with high biodiversity and habitat loss, such as Southeast Asia and sub-Saharan Africa, were under-represented. This bias may be due to the lack of funding, infrastructure, and capacity in developing countries, as well as the difficulty of accessing remote field sites (Melles et al., 2019; Meyer et al., 2015). Moreover, this bias may have implications for the conservation of amphibians and reptiles, as many species may be threatened by habitat fragmentation before they are even discovered or studied (Moura and Jetz, 2021). Therefore, we recommend increasing the research investment and collaboration in these regions, as well as improving the dissemination of research findings to decision makers and practitioners (Barber et al., 2014; Kadykalo et al., 2021).

Second, we observed a taxonomic bias in favour of amphibians over reptiles. This may be explained by the fact that amphibians are more sensitive to environmental changes due to their dual aquatic-terrestrial life cycle and permeable skin (Green, 2003; Sodhi et al., 2008). Amphibians have also received more attention due to their global decline caused by chytridiomycosis and other factors (Fisher and Garner, 2020). However, reptiles are also vulnerable to habitat fragmentation due to their high endemism, narrow niche breadth, low dispersal ability, and long generation time (Meiri et al., 2018; Todd et al., 2010). Moreover, some groups of reptiles are difficult to study because of their cryptic behaviour or low detectability (Thompson, 2004). Additionally, our results showed that some families of reptiles and amphibians were neglected or poorly studied, especially those with high endemism and small distribution ranges. Therefore, we suggest increasing the research effort on understudied groups, especially on fossorial reptiles such as worm lizards and blind snakes.

Third, associations among forms of habitat fragmentation, sampling methods and response variables were not random but clustered into three groups. The first cluster represented articles that used simple biodiversity indicators such as species richness, abundance, and presence/absence as response variables. When compared to other clusters, these articles were proportionally higher in regions with high biodiversity but low research capacity, such as Africa, Central and South America. These indicators are easy to measure and do not require advanced technologies or skills (Barber et al., 2014). However, they may not capture the complex effects of habitat fragmentation on population structure, gene flow, dispersal, fitness, or interactions (Palmeirim et al., 2017; Riemann et al., 2015). The second cluster included articles that used experimental methods and fitness measures as sampling methods and response variables, respectively. These articles were mostly found in North America and Australia, where there is more funding and infrastructure for conducting controlled experiments or physiological measurements (Fazey et al., 2005; Holmgren and Schnitzer, 2004). These methods can provide direct causal evidence for the mechanisms underlying the physiological and behavioural responses of amphibians and reptiles to habitat fragmentation (Driscoll et al., 2014). The third cluster comprised articles that applied genetic techniques and population studies. These articles were predominantly located in North America and Europe, where there is more expertise and technology for conducting genetic analyses (Forero et al., 2016). These methods can provide insights into the historical and contemporary effects of habitat fragmentation on genetic diversity, divergence, and connectivity (Allendorf et al., 2010; Manel and Holderegger, 2013; Smith et al., 2016). However, they may also have challenges such as high cost, low sample size, or complex interpretation (Hetu et al., 2019; Holderegger et al., 2019). These clusters were distributed homogeneously across continents but concentrated in certain countries such as the USA, Australia and Europe. This nevertheless shows that sampling methods are shared and used between leading herpetological experts from around the globe and that there are continuing collaborations between them.

In conclusion, our review provided a global synthesis of the habitat fragmentation research on amphibians and reptiles over the last three decades. We found that the research effort was biased towards certain regions and taxa, and that the research methods and outcomes were clustered into three groups based on their associations. We underlined promising research fields and geographic areas and may serve as a guideline or starting point for future habitat fragmentation studies. We suspect similar paradigms of geographic and thematic patterns to occur in other taxonomic groups. Here, we suggested some recommendations for future research directions:

(1) Increasing research efforts in under-represented regions such as Asia and Africa where biodiversity threats are high and data are scarce.
(2) Expanding taxonomical coverage to include more families and species of reptiles and amphibians that are poorly known or endangered.
(3) Measuring response variables that reflect the ecological processes and mechanisms of habitat fragmentation effects such as functional diversity, population dynamics, adaptation and resilience.
(4) Developing international collaborations and integration among researchers from under-represented countries as well as improving the dissemination and application of research findings for conservation. Doing this will help remediate the authorship and taxonomic bias and may have greater conservation consequences to understand global patterns of habitat modification.

CHAPTER 3

Effectiveness of protected areas for the conservation of critically endangered freshwater reptiles

Chapter 3.1

A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia

Batagur affinis edwardmolli, Terrengganu, Malaysia. Photo by E. H. Chan (Rhodin et al., 2021).

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Original article is attached.

3.1.1 The plight of Asian freshwater turtles

Habitat loss due to land use changes is a significant factor leading to the decline of global biodiversity (Foley et al., 2005). South Asia and Southeast Asia have among the fastest rates of deforestation and habitat loss, with over 50% of native forest being depleted over the last two centuries (Sodhi et al., 2004). This, combined with poaching, illegal pet trade, and land degradation, has resulted in habitat fragmentation as well as other negative impacts on the native biodiversity. Of the 356 species of turtles and tortoises recognised globally, about a quarter are found in Asia (Rhodin et al., 2021), making this region one of the species richness hotspots for turtles (Buhlmann et al., 2009; Ihlow et al., 2012; Mittermeier et al., 2015). However, the Asian continent is also a hotbed for turtles facing extinction since it harbors 17 of the 25 (68%) most threatened chelonian species (Stanford et al., 2020, 2018). Vietnam, India, and Indonesia are among the top five countries with the highest number of threatened chelonians. To date, seven species and three subspecies (2.1% of all modern turtle taxa) have already gone extinct (Stanford et al., 2018). In addition, climate change is a major threat to the survival of many turtle species, as it may alter their habitats and force them to move to new areas. According to a study by Ihlow et al., (2012), 86% of all turtle species may lose their current suitable habitats by 2080. Dennis Rödder and I conceptualised this study to evaluate the availability of suitable habitats of three poorly known freshwater turtle species: the painted terrapin (*Batagur borneoensis*), the southern river terrapin (*B. affinis*), and the giant Asian softshell turtle (*Pelochelys cantorii*). The large river turtles of the genus *Batagur* (Gray 1856) are one of the two most critically endangered turtle genera (next to Asian box turtles, *Cuora* [Gray 1856]), accounting for five of the Top 25 threatened species (Rhodin et al., 2021). Populations of these three species have been severely depleted throughout their range and have disappeared from much of their former ranges (Stanford et al., 2018). Human activities including sand mining, the construction of hydropower dams, and urban development have largely contributed to the degradation of nesting and feeding sites for these species (Moll and Moll, 2004; Stanford et al., 2018). Additionally, large-scale agro-based plantations and their associated pollution have damaged the riparian vegetation that these turtles rely on. Furthermore, the trade in Southeast Asian freshwater turtles has increased significantly over the past 30 years, leading to heavy exploitation and exportation of these animals for their eggs and flesh for human consumption (Moll and Moll, 2004; Van Dijk, 2000). Established Protected Areas exist in many parts of southern and southeastern Asia, but there is a lack of assessment of their effectiveness in sustaining viable populations of threatened turtle species. Species distribution modelling (SDM) based on the climatic niche of target species and land cover layers provides a reliable mechanism to assess the suitability and effectiveness of reserve networks (Araújo et al., 2004; Ihlow et al., 2014) . The objectives of this study are to 1) compare the potential suitable habitat to each species' currently known historic range; 2) identify areas of suitable habitat within current reserves 3) assess where the best protected areas are for prioritizing future conservation efforts based on water coverage and; 4) evaluate the impacts of climate change by using climate and socioeconomic projections for the year 2080 to project future changes in habitat suitability and reserve areas. Lastly, I discuss if current Protected Areas are adequate in conserving these critically endangered species.

3.1.2 Methods and personal contributions

I first obtained historic locality records for the study species from museum and literature sources, as well as unpublished data from coauthors Anders Rhodin and John Iverson. Both coauthors represented the Chelonian Research foundation and Turtle Conservancy which consist of many turtle experts from all over the world. As such, species records and presume historic indigenous distribution ranges are verified by species experts. Dennis Rödder and I designed a data analysis workflow. First, I downloaded current climatic conditions from the Worldclim database version 2.1 (www.worldclim.org), derived from climate conditions recorded for 1970-2000 with a spatial resolution of 2.5 arc minutes (Fick and Hijmans, 2017). These set of 19 bioclimatic variables describe annual trends, seasonality and extreme environmental factors. They are suggested to provide biologically meaningful results as they characterise the availability of water and energy throughout the year and thus are suitable predictors in SDM (Busby, 1991). I used a Mantel correlogram from the ecospat package v.31 to determine potential spatial autocorrelation of environmental covariables as a function of distance (Di Cola et al., 2017). I then further removed occurrences too close to each other using species occurrence thinning function from spThin package v0.2.0 to reduce the effects of sampling bias, while retaining sufficient amount of useful information (Aiello-Lammens et al., 2015). I then used the remaining set of records after thinning for subsequent SDM computation. To project future response of species distribution to climate change, I have used four shared socio-economic Pathways (SSPs: 126, 245, 370 and 585), which are emission scenarios driven by different socioeconomic assumptions. I computed the same bioclimatic variables from the average of eight global climate models (GSMs) that simulated different climate scenarios of the period 2081-2100, downloaded from WorldClim at 2.5arc minute resolution to provide a non-biased future climate prediction.

With contributions from Philipp Ginal, I removed variables sequentially by performing a jackknife approach among highly correlated variables based on their percentage contribution to the model and TSS value. This was performed using the *dismo* and *SDMtune* packages for R (Hijmans et al., 2021b; Vignali et al., 2020). This process was repeated until the remaining variables had correlation coefficients less than 0.7. The resulting variables, which contributed less than 5% to initial SDMs, were then removed when performing the models. This approach makes it easier to interpret the model and understand the driving variables when they have low correlation. Next, I used Maxent v3.4.1 (available from http://biodiversityinformatics.amnh.org/open_source/maxent/), to perform SDMs based on the climatic niche of the turtles and the presence-pseudoabsence data. Results obtained from Maxent have been proven effective in predicting habitat suitability in poorly known species (Pearson et al., 2007), with low and bias sample sizes (Elith et al., 2006). Using a bootstrap approach, I made 100 replicates of Maxent runs with standard settings (cloglog output format, 500 iterations, clamping) and used 90% of the records for model training and 10% for testing. I also randomly created 10,000 pseudo-absences within a buffer of 200 km surrounding each species' presumed historic indigenous distribution range. Maxent created potential suitable habitat values ranging from 0 (unsuitable) to 1 (optimal) along with the relative contribution of each bioclimatic variable. I evaluated the model performance using Receiver Operating Characteristic Curves (ROC) based on Area Under the Curve (AUC) (Swets, 1988). The AUC ranges between 0.5 (random prediction) to 1.0 (perfect discrimination between presence and pseudo-absence). I also applied True Skill Statistics (TSS) to evaluate model performance (Shabani et al., 2018). TSS values ranges from -1 to +1, where +1 suggests perfect prediction, whereas values of zero or less suggest equal or lower performance than random. For conservation purposes, I have chosen the minimum training presence threshold to avoid overprediction when assessing suitability (Pearson et al., 2007). I subsequently used the average Maxent prediction across all 100 replicates as consensus map, which was reclassified using the minimum training presence as presence/absence threshold for further analyses. I used multivariate environmental similarity surfaces (MESS) to identify the areas exceeding environmental training conditions under current and future scenarios (Elith et al., 2010).

To assess the coverage of suitable turtle habitats with designated protected areas according to IUCN standard, I downloaded polygons of protected areas from the World Database of Protected Areas (UNEP-WCMC and IUCN, 2020; https://www.protectedplanet.net/). Since freshwater turtles depend largely on riparian habitats including rivers, streams and estuaries, water surface cover is assessed to refine predictions of where the three target species should thrive within protected reserves. I obtained high resolution (30-metre) water maps from Joint Research Centre Global Surface Water Mapping layers [(Pekel et al., 2016); https://global-surface-water.appspot.com]. I reclassified the water surface cover to exclude unsuitable areas lacking permanent water to facilitate interpretation. This water surface cover is then overlaid with Maxent's output map. I conducted all spatial analyses with QGIS ver 3.12.2 (QGIS.org, 2021) and R ver 4.0.2 (R Core Team, 2021). I extracted high resolution information from spatial layers using an automated workflow. Further, I employed the power of parallel processing in computer clusters of Museum Alexander Koenig to reduce computational time. All figures were created in QGIS and R by me and then modified in Adobe Illustrator with the help of Morris Fleck. The first draft of the manuscript was written by me and then reviewed by the turtle experts, Anders Rhodin and John Iverson.

3.1.3. Summary of critical findings and outlook

The results showed that the SDMs had good discrimination ability between suitable and unsuitable habitat for the three species based on AUC values. The environmental variables that contributed most to the models varied between species, with temperature-related variables being important for *B. borneoensis* and *B. affinis*, while precipitation and temperature seasonality were important for *P. cantorii.* This conforms to previously suggested bioclimatic variables crucial for chelonian distributions (Ihlow et al., 2012). The potential climatic suitable habitats predicted were mostly coastal areas for *B. borneoensis* and the wide-ranging species, *P. cantorii*. This corresponds to their habitat preferences and nesting habits. On the contrary, our results showed that the potential habitat for *B. affinis* is further inland, suggesting a rather generalist lifestyle. Further, *B. affinis* has been found foraging up river with the rising tide (Moll et al., 2015). Unfortunately, only a small part of these habitats was covered by protected areas, suggesting high fragmentation among protected populations. This was evident in countries where the species have been severely depleted or extirpated, such as Thailand, Vietnam, and China. Indonesia was identified as the country with the largest extent of protected areas with suitable habitat for all three species, followed by Philippines, Malaysia, Thailand, and Cambodia. However, Indonesia faces many challenges in managing and protecting these habitats, such as lack of funds, law enforcement, public awareness, and coordination among stakeholders.

The study demonstrated the value of incorporating land cover data such as water coverage as a predictor variable to refine the habitat suitability within protected areas of our target species, since they depend on riparian habitats for their survival. Results including water coverage suggested that Thailand was of major importance for *B. borneoensis* and *B. affinis,* while Indonesia was important for *P. cantorii*. We proposed, in our article, several priority conservation areas and reserves for further field surveys and monitoring in the suitable areas to confirm the presence and status of these endangered turtle species. Several important reserves with high water suitability identified in Thailand were: Ao Manow-Khao Tan Yong Reserve for *B. borneoensis* and *B. affinis*, and Ao Phanganga National Park for *P. cantorii*.

The future projections indicated that the potential suitable habitats for the three species would increase in size and shift northwards and inland by 2080 under all emission scenarios. So it seems like these turtles might benefit from climate change in terms of potential range expansion. However, many of these areas had uncertain predictability due to extrapolation beyond the training range of the models. As such, only a few reserves may provide long-term protection for these species under climate change. We also cautioned that climate change may have synergistic effects with other threats such as habitat loss and degradation, poaching, wildlife trades, pollution and detrimental diseases (Fisher and Garner, 2020; Habel et al., 2019; Lazzari et al., 2022).

Even though our Maxent models were based on a relatively small number of occurrence records, they provide a useful guideline for directing further surveys in areas where population may be potentially undiscovered (Pearson et al., 2007). We concluded that current protected areas are insufficient to conserve these critically endangered turtles. We recommended urgent surveys and monitoring to detect and ensure adequate populations in Protected Areas throughout their ranges for their survival. By collecting additional occurrence data from field surveys, we can improve our current predictions. We also highlighted the need for more research, captive breeding programs, community involvement and education and international cooperation to ensure the survival of these poorly known and critically endangered freshwater turtles.

Chapter 3.2

Last chance to see? Iran and India as strongholds for the Marsh crocodile (*Crocodylus palustris*)

Crocodylus palustris from Iran. Photo by A. Mobaraki.

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Original article is attached.

3.2.1 Climate change and habitat fragmentation: Modeling the current and future threats to the Marsh crocodile

One of the major challenges facing biodiversity conservation is the impact of climate change on the distribution and persistence of species. Climate change can affect species directly by altering their physiological and ecological requirements, or indirectly by modifying their habitats, food sources and predators (Segan et al., 2016). Species may respond to climate change in different ways, including changing their behaviour, reproduction, lifestyle and migration pathways (Bellard et al., 2012). Among many species vulnerable to climate change (Newbold et al., 2020), crocodilians are of particular interest because of their role as “keystone species” in freshwater ecosystems, their cultural and economic value, and their evolutionary history. Crocodilians are ectothermic reptiles that depend on external sources of heat to regulate their body temperature. They also have temperature-dependent sex determination, which means that the sex of their offspring is determined by the incubation temperature of the eggs. These traits make crocodilians sensitive and susceptible to increasing temperatures from global warming (Mannion et al., 2015). The Marsh crocodile (*Crocodylus palustris*, also called Mugger) is a freshwater crocodilian species that inhabits the Indian subcontinent and south-eastern Iran (Da Silva and Lenin, 2010). It is classified as Vulnerable by the IUCN Red List, threatened mainly by habitat loss and fragmentation (Mobaraki et al., 2018). The crocodile populations are also suffer from severe periodic droughts, hunting, overharvesting, water pollution and food shortage (Bhatt et al., 2012; Chang et al., 2013; Fellows, 2019). However, there are no existing studies on the current and future habitat suitability of the Marsh crocodile and its coverage by protected areas. Such information is crucial for developing effective conservation strategies and actions for this species in the face of climate change and increasing anthropogenic pressure. Therefore, Asghar Mobaraki, Thomas Ziegler and Dennis Rödder first conceptualised the study to fill this gap by using species distribution models (SDMs). The aim is to identify the environmental factors most related with Marsh crocodile occurrences in the range states and to predict the current and future potential distribution of the Marsh crocodile under different climate scenarios. Finally, priority areas for conservation based on environmental niche stability and potential human conflicts will be identified. Modelling the future distribution of crocodiles will allow us to better propose suitable management actions to rising anthropogenic pressures and temperatures.

3.2.2 Methods and personal contributions

Following a similar workflow as chapter 3.1, Rödder first obtained 636 occurrence records of the Marsh crocodile from GBIF (GBIF.org [accessed on 6 April 2021] GBIF Occurrence Download https://doi.org/10.15468/dl.m2nez8) and added 84 georeferenced records from our own fieldwork from our collaborators, Asghar Mobaraki, Malihe Erfani and Elham Abtin, to increase the coverage of the westernmost part of its range. Rödder then filtered out the records that were too close to each other (less than 10 km apart) to reduce sampling bias and spatial autocorrelation using the thinning function from spThin package (Aiello-Lammens et al., 2015). This results in 380 occurrence records for subsequent model computation. Rödder used 19 bioclimatic variables from Worldclim 2.0 0 (www.worldclim.org), to represent the average climatic conditions from 1970-2000 with a spatial resolution of 2.5 arc minutes. We reduced the multi-colinearity of predictor variables by selecting only the variables that were not highly correlated with each other (spearman rank correlation coefficient less than 0.75). The resulting variables are selected for model computation. To project the future distribution of the Mugger in 2081-2100, Rödder downloaded IPCC6 story lines or future climate scenarios which represent different levels of greenhouse gas emissions and socio-economic development. These scenarios are ssp126, ssp245, ssp370 and ssp585, with ssp126 being the most optimistic and ssp585 being the most pessimistic. The outputs of all eight global circulation models for each scenario were averaged to be used for future ensembles.

Rödder used Maxent ver. 3.4.4. and the R-packages: raster (Hijmans et al., 2021a) dismo (Hijmans et al., 2021b) and ENMeval (Muscarella et al., 2014) for SDM model optimization and processing. Rödder fitted the SDMs with different combinations of regularization multipliers and feature classes, which control the complexity and generalization ability of the model. A total of 25 replicates were computed per combination of regularization multiplier and set of feature classes, wherein the species records were randomly selected each time via bootstrap with 80% used for model training and 20% used for model evaluation. Using Maxent’s raw output, Rödder computed the corrected Akaike Information Criterion [AICc, (Warren and Seifert, 2011)] and the difference between test and training AUC [= Area under the ROC curve (Elith and Graham, 2009; Lobo et al., 2008; Phillips and Dudík, 2008)] for each replicate. Rödder then selected the best model based on a balance between lowest average AICc, the highest AUC (AUC > 0.8), and the smallest difference between training and testing AUC (AUC_{delta}). Using the best fitting model parameters, Rödder then computed 100 replicates of the best model using bootstrap sampling with 80% of the records for training and 20% for testing. Rödder averaged the predictions across the replicates and projected them onto current and future climate data using cloglog output format, which gives occurrence probability values between 0 and 1. Finally, Rödder assessed the uncertainty of our predictions caused by using Multivariate Environmental Similarity Surfaces (MESS), a method that identifies areas of extrapolation outside the training range of the models (Elith et al., 2010).

Rödder obtained information on protected areas within the range of the Mugger from the World Dictionary of Protected Areas (https://www.protectedplanet.net/en), and included only terrestrial reserves with IUCN categories Ia, Ib, II, III, IV, V and VI (UNEP-WCMC & IUCN, 2020). Rödder ranked these reserves according to their conservation value for the Mugger crocodile based on their climatic suitability, availability of suitable microhabitats, and potential anthropogenic pressure under current and future scenarios. As microhabitat surrogates, Rödder used a dataset of tropical wetlands derived from biophysical indices related to water supply, water-logged soils, and geomorphological position where water is supplied and retained (Gumbricht et al., 2017). As river networks were missing from this dataset but may represent valuable habitat for the Mugger crocodile, Rödder added a high resolution water coverage layer (GRDC, 2020) , also see chapter 3.1. As indicators of potential human conflicts, Rödder used future scenarios of human population density based on different storylines (ssp1-3) with a spatial resolution of 0.5° (Murakami and Yamagata, 2019). Rödder downscaled these data to match the resolution of our climate data using a nearest neighbour approach. For each protected area within the currently known range of the Mugger crocodile as suggested by IUCN, Rödder computed the factual area providing suitable microhabitats, the median environmental suitability across the reserve as expected under current and future scenarios and the expected anthropogenic pressure. The final rankings of the reserves were based on the proportion of suitable habitats and climatic stability through all future scenarios. All maps were created in R and QGIS and then modified in Adobe Illustrator with the help of Morris Fleck. I led the writing of the manuscript which are further improved by the Mugger experts, Asghar Mobaraki and Elham Abtin. All authors discussed the results and contributed to the final manuscript.

3.2.3 Summary of critical findings and outlook

Our model showed a good discrimination ability ($AUC_{training}$ = 0.839 and AUC_{test} = 0.827) and identified Temperature Annual Range as the most important variable for the species distribution (contributing 42.9% to the final model). Temperature may reflect the availability of prey such as fish and amphibian species throughout the year. Mean Temperature of Driest Quarter and Annual Precipitation were the next important variables (each contributing 10.7% and 10.5% respectively), which may be crucial in determining vegetation cover but also existence of shallow ponds and burrows, frequent by crocodiles (Abtin, 2012; Da Silva and Lenin, 2010). These microhabitats could be beneficial in the survival of the crocodiles to avoid exposure to extreme temperatures (Whitaker et al., 2007).

The results showed that the current potential suitable habitats of the Mugger crocodile are more fragmented than expected from the native distribution, suggesting that habitat loss and fragmentation have possibly reduced the population size and connectivity of the species. Major suitable habitats are located in Sri Lanka, south-eastern peninsular of India, tropical moist forest along the west coast of India, border between Nepal and India, and south coast of Iran and Pakistan. This fragmented distribution could be explained by the extreme modification of habitat, namely rapid urbanisation (Elmqvist et al., 2016). In India, human population has more than doubled since the 1960s, currently at 1.43 billion (Ritchie et al., 2023). Similarly in Iran, land use modification as well as conflict with local communities and crocodiles are prominent (Hill et al., 2018; Mobaraki et al., 2018).

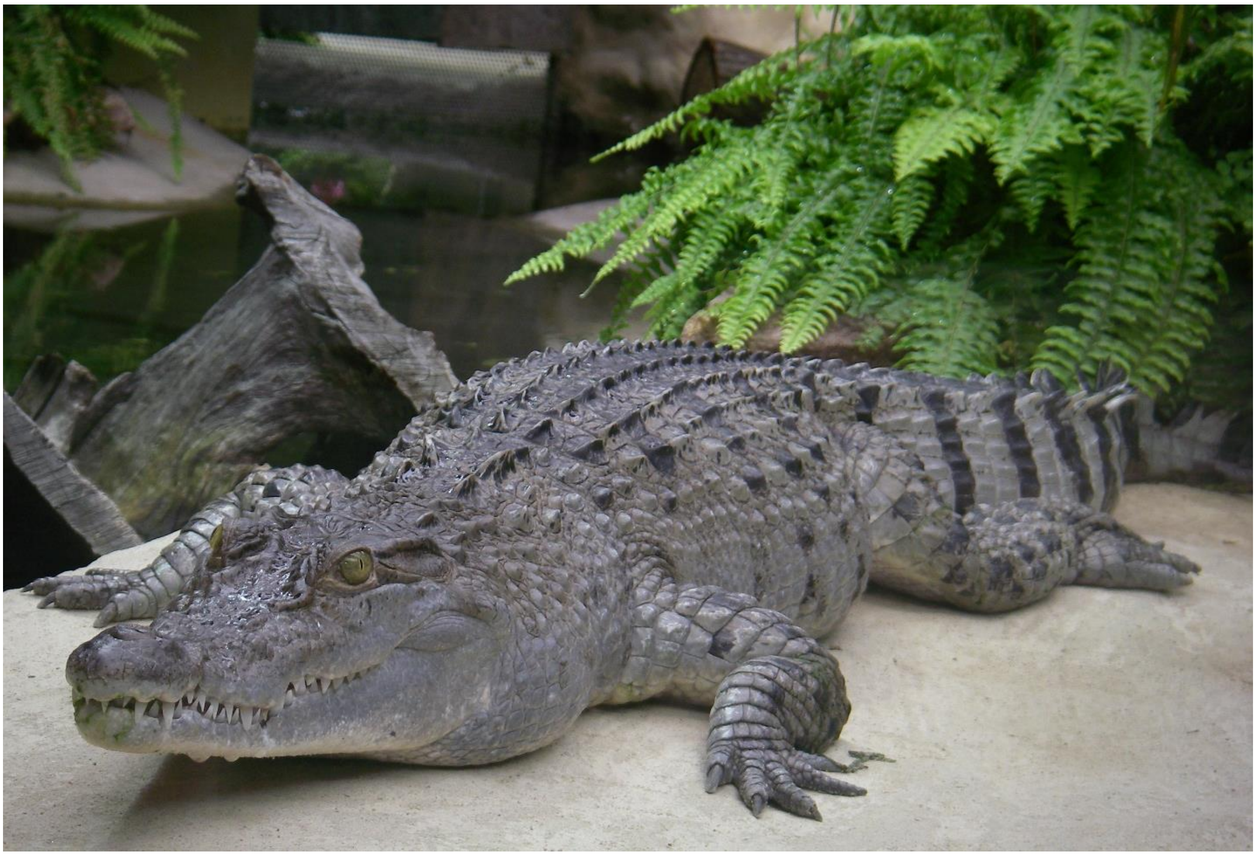
Our projections for all four future climate scenarios suggested that Mugger crocodiles are likely to be affected by climate change by 2081, be it the most optimistic scenario (ssp126) or the worst (ssp585). When areas of uncertain predictability (MESS) were removed, we found a large reduction in potential suitability across the species range, especially in Sri Lanka, southern India and the coastal part of southern Iran. These areas may expect to experience more frequent and severe droughts and high temperatures due to global warming and as such, affect the existence of temporary watercourses and ponds during the rainy season (Pal and Eltahir, 2016). Such temporary rivers and pools are important in seasonally drying habitat for crocodile dispersal (Grigg and Kirshner, 2015).

We also considered climatic stability, habitat availability and anthropogenic pressure within protected areas that overlap with the species range. We found that very few protected areas containing suitable habitats with stable climate through time, when considering all future scenarios. However, many of these reserves are also expected to face increasing human-crocodile conflicts due to population growth and urbanization. Fishing and mining of river materials as well as human garbage and solid waste were ranked as the most sever threat to muggers (Nishan et al., 2023). Whilst accounting for anthropogenic pressure, we proposed to focus future conservation efforts on two protected areas as we believe they represent the best possible refugees for the mugger crocodile under climate change. They are Nanda Devi National Park in northern India and Gando reserve in western Iran. Although close contact between crocodiles and local villages have been recorded in the rivers of Bahu-Kalat and Kaju in the Gando reserve (Mobaraki et al., 2015), these conflicts are predicted to be comparatively stable in the future as human population growth is expected to be rather low in the area. This isolated population in the western extension of its distribution is small, with an estimation of about 500 individuals. Unfortunately, the population is divided into several scattered sub-populations with little population connectivity (Mobaraki et al., 2018, 2015), making them highly susceptible to permanent isolation and extinction due to stochastic effect (Campos et al., 2018). Improving the connectivity of the meta-population network will be of utmost importance in the near future.

The study provided first insights into the habitat suitability derived from climate data of Marsh crocodiles (*C. palustris*) in their native range. The future for this crocodile species appears to be uncertain due to the loss of suitable habitats with stable climate and ever-increasing anthropogenic pressures. We identified potential impacts of climate change on their future distribution, as well as priority areas for conservation actions. However, we acknowledged some limitations of our approach, such as the lack of data on other environmental factors that may affect the species ecology, as well as the uncertainty associated with future climate projections. Therefore, we suggest that further studies are needed to improve our knowledge of the species behaviour and physiology, as well as to monitor their population status and trends. We recommend that conservation actions should include habitat restoration and connectivity, conflict mitigation, ex-situ conservation facilities, and public awareness campaigns to ensure the long-term survival of this vulnerable species.

Chapter 3.3

Disappearing archosaurs– an assessment of established protected areas in the Philippines to save the critically endangered and endemic Philippine crocodile *Crocodylus mindorensis*



Crocodylus mindorensis from Köln Zoo, Germany. Photo by T. Ziegler.

This chapter is in revision with Salamandra:

Sabine Harrer, Philipp Ginal, Wei C. Tan, Jake Binaday, Arvin Diesmos, Ranier Manalo, Thomas Ziegler and Dennis Rödder (2024). Disappearing archosaurs– an assessment of established protected areas in the Philippines to save the critically endangered and endemic Philippine crocodile *Crocodylus mindorensis*. Salamandra, 60(1), 29-4.

Original article is attached.

3.3.1 Habitat modelling and conservation planning for the Philippine Crocodile, an endemic and endangered species

The Philippines is one of the 20 global megadiverse countries, with many endemic and threatened species of plants and animals due to its isolated location and diverse topography (Rintelen et al., 2017). Among them, the Philippine Crocodile (*Crocodylus mindorensis;* Schmidt, 1935) is one of the most endangered. With only about 100 mature individuals left in the wild, it has been classified as 'Critically Endangered' on the IUCN Red List since 1996. Unlike the widely distributed Indo-Pacific Crocodile, *Crocodylus porosus* Schneider, 1801, also known as Saltwater Crocodile, this crocodile is native and endemic to the Philippines. Originally distributed over almost the entire archipelago (Ross and Alcala, 1983), populations are highly fragmented in 'Dalupiri Island', 'Northern Luzon' and 'Ligawasan Marsh' on Mindanao and are estimated to decline (Manalo et al., 2015, 2013; Van Weerd, 2010). The crocodile prefers freshwater wetland habitats such as fast-flowing rivers, marshes, ponds, man-made water reservoirs and mangroves (van de Ven et al., 2009). However, its habitat has been severely degraded and fragmented by human activities including deforestation, fishing and aquatic resource harvesting (Van Weerd et al., 2016). Despite being legally protected since 2001, the Philippine Crocodile has not recovered from the brink of extinction and needs urgent conservation actions to ensure its survival (Van Weerd et al., 2016). One of the key steps for effective conservation planning is to identify and prioritise suitable habitats for the target species. This can be achieved using species distribution models (SDMs), which are powerful tools used to predict potentially environmentally suitable habitat by linking documented presence records of species to environmental variables and spatial characteristics. In this study, we applied SDMs to evaluate the existing protected areas in the Philippines for their suitability to conserve the Philippine Crocodile. Dennis Rödder, Thomas Ziegler, Philipp Ginal and I devised the project, the main conceptual ideas and proof outline as a study for the Bachelor student, Sabine Harrer. In addition to bioclimatic variables used in chapter 3.1 and 3.2, remote sensing variables were included as predictors of our SDMs. Wetland availability and human footprint index were used as additional criteria to assess the habitat quality and anthropogenic pressure in each protected area. The study aimed to answer the following questions: Which protected areas (1) are climatically suitable;(2) provide suitable wetland habitats and (3) have low anthropogenic pressure for the Philippine Crocodile? Based on these questions, the protected areas were ranked according to their suitability for crocodile conservation and identified the important reserves that should be prioritised for future management actions.

3.3.2 Methods and personal contributions

Coauthors from the Phillipines, Jake Wilson Binaday and Rainier Manalo collected species occurrence records from field surveys conducted by between 2003 and 2021. Harrer removed the outliers with QGIS, ver. 3.16.3 with GRASS 7.8.5 (QGIS.org, 2021). Harrer and I used 46 environmental variables (Cord and Rödder, 2011) as predictor variables for the SDMs. These variables included 19 bioclimatic variables from Worldclim database ver 1.4 (www.worldclim.org) with a spatial resolution of 30 arc seconds and 27 remote sensing variables derived from Moderate Resolution Imaging Spectroradiometer (MODIS) sensors of two NASA satellites with spatial resolution of 30 arc seconds and the temporal resolutions are 8-day averages (Mu et al., 2007). Since SDMs are sensitive to multi-collinearity of predictor (Merow et al., 2013), Philipp and Harrer calculated the Variance Inflation Factor (VIF) in R (ver. 403; 'usdm package') and excluded variables with VIF > 10 (Naimi et al., 2014; R Core Team, 2021).

Rödder, Harrer and I performed SDMs using Maxent, as it performs well with small sample sizes and complex environmental data (Elith et al., 2006; Phillips et al., 2006). Harrer and I used the whole Philippines as the background area (Uetz et al., 2021), and reduced the records to one per grid cell to reduce sampling bias (Phillips et al., 2009). Following model fitting and selection described in Ginal et al. (2022), Rödder tested multiple regularisation multipliers (0.5 to 2.5 in steps of 0.1, as well as 5 and 10) and feature classes (LP, LQ, LH, LT, LQP, LQH, LQT, LPH, LPT, LHT, LQPT, LQHT, LPHT, LQPHT; L = Linear, P = Product, Q = Quadratic, H = Hinge, T = Threshold) using bootstrap approach, wherein records were randomly selected each time via bootstrap with 80% used for model training and 20% used for evaluation. Rödder used the raw output format of Maxent for calculation of the averaged AICc [corrected Akaike Information Criterion (Warren and Seifert, 2011)] and AUC [Area Under the Curve (Elith and Graham, 2009; Lobo et al., 2008; Phillips and Dudík, 2008)] of the models across ten replicates. Rödder selected the model with the lowest average AICc and an AUC_{Test} above 0.70 (Phillips and Dudík, 2008; Warren and Seifert, 2011). Finally, Rödder replicated the final model 100 times, again with an 80:20 split for training and testing and evaluated the average of the 100 replicates using a combination of AUC and True Skills Statistics (TSS) (Shabani et al., 2018). Rödder used cloglog format as output for the final model. I applied the 'minimum training presence'-threshold for presence/absence due the limited number of occurrence records.

To assess the effectiveness of suitable habitats in protected reserves, the World Database of Protected Areas (WDPA) polygon shapefiles was first obtained from UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC & IUCN, 2020) to assess the coverage of protected areas in relation to the crocodile habitat suitability. Rödder also downloaded the Global Wetlands Map (https://www2.cifor.org/global-wetlands/) with a resolution of 232 meters. Wetlands were classified into three key biophysical attributes (Gumbricht et al., 2017): 'long-term water supply', 'annually or seasonally water-logged soils' and 'a geomorphological position where water can be supplied and retained'. Harrer and I selected seven categories of wetlands for *C. mindorensis*: 'open water', 'mangrove', 'riverine', 'floodplains', 'marshes', 'swamps' and 'fens'. Because rivers were not included in this dataset but may represent important habitat for the crocodile, Harrer and I imported a high-resolution water layer from the Global Runoff Data Centre to assess the suitability of river networks (GRDC, 2020), similarly to the water surface layer in chapter 3.1. Harrer overlaid the reclassified MaxEnt-output with the wetland shapefile and analysed them together with protected areas using QGIS (QGIS.org, 2021). To assess the effect of anthropogenic pressure on the crocodiles, Rödder obtained the 2018 release of human footprint from SEDAC (NASA Socioeconomic Data and Applications Center). These maps measure the direct and indirect human pressure using eight variables (e.g., population density, crop lands and roads) (Venter et al., 2018). Since the resolutions of the overlaying layers are different, Harrer calculated individual rankings based on the proportions of suitable habitat, wetlands and anthropogenic pressure within each protected area. Lastly, Harrer and Rödder made a final ranking by combining the rankings of these three categories. All analyses were done in QGIS and R by Sabine Harrer with the aid and guidance of Philipp Ginal and Dennis Rödder. Harrer wrote the initial draft of the manuscript with contributions from Wei Cheng Tan and Philipp Ginal. All maps were created in QGIS and then modified in Adobe Illustrator with the help of Morris Fleck. All authors discussed the results and contributed to the final manuscript.

3.3.3 Summary of critical findings and outlook

Our results showed that average daily temperature range, temperature fluctuations during the course of the day and year and seasonality to be most relevant to the occurrence of Philippine crocodile. Ambient temperature can influence the nest temperature which are crucial for the reproduction and long-term maintenance of the species (Akmad and Pomares, 2008). Sporadic climatic events such as floods matter because they cause mortality to juveniles while they are still vulnerable (van de Ven et al., 2009; Van Weerd et al., 2016) while droughts limit the availability of food resources (Mazzotti et al., 2009).

In addition to being in a naturally fragmented island landscape, climatically suitable areas for *C. mindorensis* appear to be mostly fragmented in the Philippines. They were mainly concentrated on the large islands of Luzon and Mindanao, where most of our occurrence records were found. Furthermore, only small fractions (as low as 0.3%) of these suitable areas are wetlands and covered by protected areas. Crocodilians are considered flagship-umbrella species because they are charismatic (Verissimo et al., 2011) and their conservation protects a large number of species that coexist in the same habitat (Fleishman et al., 2000). For example, the Philippine crocodiles have shown to have positive impacts on fish stocks (Bucol et al., 2020; Corvera et al., 2017). Being a top predator, the crocodile has also been suggested to be natural pest control agent for invasive agricultural nuisances such as Golden Apple Snail (*Pomacea canaliculata*), Asian House Rat (*Rattus tanezumi*) (Brown et al., 2021). However, much of the crocodile's habitat has been lost to land expansion for aquaculture and rice or sugar cane cultivation, human settlements, dam construction and lucrative mining (Corvera et al., 2017; Manalo et al., 2018; Van Weerd et al., 2016). As a result, crocodiles are being displaced from their former habitats. They are now found more frequently in rice fields and near settlements, increasing the risk of human-crocodile conflicts (Corvera et al., 2017). As such, Philippine crocodiles face direct threats from poaching, hunting, and persecution by local communities who view it as a pest or a competitor for resources (Van Weerd et al., 2016).

We identified the top five reserves that should be prioritised for future management actions based on the combined ranking of the highest suitable wetlands within a protected area and with low anthropogenic pressures. These are 'Lake Lanao Watershed Reservation', 'Angat Watershed Forest Reserve District (Metro Water District)', 'Northern Sierra Madre Natural Park', 'Talaytay Protected Landscape' and 'Agusan Marsh Wildlife Sanctuary'. These reserves contain a diversity of habitats and ecosystems, such as lakes, rivers, marshes, swamps, mangroves, forests, and mountains, that support a high biodiversity of plants and animals, including many endemic and threatened species such as the Philippine crocodiles (DENR, 2023, 2022). Lake Lanao watershed is even recognised as key biodiversity areas or Ramsar sites, which are of global importance for conservation. However, some of these protected areas are not assigned to any IUCN category nor have been legislated by law, which may limit their legal status and management capacity. Therefore, we recommended these protected areas of high suitability and low human footprint, such as "Angat Watershed Forest Reserve District" and "Lake Lanao Watershed" to be assigned to an IUCN category. We also highlighted that Ligawasan Marsh on Mindanao could harbour a large population of *C. mindorensis* (Manalo et al., 2019) and should thus be further surveyed and potentially declared as a protected area. Moreover, we advised that home ranges of these crocodiles should be taken into account when selecting protected areas and creating appropriate buffer zones (Ven de ven et al., 2017). Suitable home ranges can have a positive impact on genetic diversity and connectivity between populations (Bennett, 1999). Only by implementing effective management plans that address these challenges and threats, as well as involving local communities and stakeholders in decision-making processes can we ensure the long-term survival of this emblematic and imperilled crocodile species in the wild.

CHAPTER 4

High freshwater turtle occupancy in sustainably managed tropical forest in Borneo

Notochelys platynota from Deramakot forest reserve, Sabah, Malaysia. Photo by S. Asad.

This chapter is under revision with the Journal of Wildlife Management:

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Original article is attached.

4.1 Logging as a process of habitat fragmentation in freshwater turtles and the advantages of Reduced Impact Logging

Freshwater turtles and tortoises are among the most endangered vertebrates in the world, especially in Southeast Asia, where they face multiple threats from habitat loss, overexploitation, and trade (Cox et al., 2022; Stanford et al., 2018). However, there is a lack of quantitative data on how these animals respond to different types of anthropogenic disturbances, such as logging, which affects more than half of the remaining tropical forests in the region (Gibson et al., 2011). Logging can have direct and indirect impacts on freshwater turtle habitats, such as altering stream hydrology, increasing sedimentation, facilitating biological invasions, and increasing poaching access (Laurance et al., 2009). Therefore, it is important to assess the effects of logging on freshwater turtle populations and their habitat preferences.

One way to mitigate the negative effects of logging on biodiversity is to implement sustainable forest management methods, such as Reduced Impact Logging (RIL), which follows strict guidelines to reduce damage to forest structure and function (Putz et al., 2008; Zarin et al., 2007). This method, implements harvesting guidelines including reduced harvest rates (< 30m³ timber per hectare) and a series of best practice harvesting techniques including: directional felling, reduced skid trail construction, pre/post-harvest planning, and 30 m riparian buffer zones (Pinard et al., 1995; Putz et al., 2008). These methods result in 50% less damage to remnant forests, thus maintaining watersheds, while reducing sedimentation and riparian habitat disturbance (DFR Forest Management Unit No. 19A, 2015; Pinard et al., 1995). As such, RIL has been shown to maintain higher levels of biodiversity compared to conventional logging methods in various taxa, such as amphibians, mammals, and birds (Asad et al., 2021a; Bicknell et al., 2014; Brozovic et al., 2018). However, the impact of RIL on freshwater turtles has not been studied yet. Given the high conservation value and vulnerability of these animals, it is essential to determine whether RIL can retain suitable habitats for them and support their persistence in logged forests.

4.2 Methods and personal contribution

To address this knowledge gap, Sami Asad, Mark-Oliver Rödel and I conceived the idea to examine the occupancy patterns of two freshwater turtle species within Deramakot, a sustainably managed forest reserve in Sabah, Malaysian Borneo, and assesses the impact of RIL on these species. The two species are a threatened hard-shelled turtle, *Notochelys platynota* (Gray, 1834), and a non-threatened soft-shelled turtle, *Dogania subplana* (Geoffroy Saint-Hilaire, 1809). The study aims to: (1) examine the impact of climatological covariates on freshwater turtle detectability; (2) examine the impacts of habitat and RIL-associated covariates on freshwater turtle occupancy; and (3) determine the occupancy probability of the two species within an active RIL reserve. The study uses single-species occupancy models within a Bayesian framework to account for imperfect detection and incorporate covariate effects on detection and occupancy probabilities (MacKenzie et al., 2018). The study provides the first quantitative data on freshwater turtle responses to RIL and occupancy patterns in Southeast Asia and has important implications for their conservation management.

Coauthors Sami Asad and Victor Vitalis collected data on two freshwater turtle species, *N. platynota* and *D. subplana*, by walking along eight river transects (800-3000 m in length) in a forest reserve managed with Reduced Impact Logging (RIL) techniques. To ensure standardisation of survey effort, they divided each transect into 200 m subplots and surveyed each nested subplots on three occasions between March and July 2019 at night. They recorded all turtles seen in or near the water. They also measured climatic, environmental and logging-related variables that could affect turtle detection and occupancy, such as temperature, humidity, rainfall, lunar phase, forest height, flow accumulation, time since RIL and distance to logging roads. Then Asad scaled these variables and tested them for collinearity before modelling.

Asad and I used single-species occupancy models in a Bayesian framework to estimate the detection and occupancy probabilities of each species as functions of the covariates. To account for the spatial dependence among subplots within the same transect, Asad and I include a random effect in all models. We used default vague priors for all models and ran three parallel Markov chains with 10,000 iterations each, discarding the first 5,000 as burn-in. I checked model convergence using the Rhat statistics. Asad also visually confirmed the linearity of the relationships between covariates and occupancy or detection probabilities. If a nonlinear relationship was observed, Asad used a squared version of the covariate in the model.

Asad and I performed model selection in two steps for each species. First, Asad and I compared single covariate models for detection probability (including a null model) to select the best detection model based on expected log pointwise predictive density (elpd), which measures the predictive accuracy of a model. Second, Asad and I compared single covariate models for occupancy probability (including a null model) in combination with the best detection model to select the best occupancy model based on elpd. I used leave-one-out cross validation to calculate elpd and its standard error for pairwise model comparisons. I considered models with an elpd difference greater than their standard error to be less supported than the top model. Asad and I also calculated the posterior distributions and 95% credible intervals of the covariate effects to assess their significance. Dennis Rödder supervised the project and verified the analytical methods. I wrote the manuscript with the support and guidance from Sami Asad.

4.3 Summary of critical findings and outlook

Our study provides the first quantitative data on the effects of RIL on freshwater turtle occupancy patterns in Southeast Asia. We found that *N. platynota* was negatively affected by logging road proximity, which may indicate increased vulnerability to poaching, predation or habitat degradation. This species also preferred streams with higher flow accumulation, which may reflect its habitat requirements for clear, sandy-bottomed streams with abundant aquatic vegetation (Lim and Das, 1999; Mohd Ibrahim et al., 2019). Results for *D. subplana* were less conclusive but we detected the greatest number of this species in sites subject to RIL 10 – 11 years ago. Previous research identified a preference by this species for heavy siltation deposits (Asad et al., 2021b) and agricultural ponds (Lim and Das, 1999), which suggests higher tolerance to disturbance. However, due to the poor support of this covariate, more data and comprehensive analysis would be required to confirm this observation.

Although our lack of data from undisturbed primary forests undermines our ability to determine the baseline occupancy of these 2 species, our study suggests that freshwater turtles nevertheless exhibited high occupancy throughout the Deramakot forest reserve. As such, sustainably managed forests using RIL methods appear to be suitable landscape-scale habitat for these species. However, our study also highlights the need for further research on the impacts of RIL on other aspects of freshwater turtle ecology, such as population size, survival, reproduction and movement. Moreover, our study was limited by the lack of unlogged control sites and fine scale habitat measurements (stream depth, width, siltation etc). Future studies should include unlogged and conventionally logged sites for comparison and measure more detailed stream characteristics that may affect freshwater turtle occurrence and abundance.

Our study has important implications for the conservation management of freshwater turtles in Southeast Asia. We suggest that RIL can be a viable option for sustainable forest management that can balance timber production and biodiversity conservation. However, we also recommend that RIL should be accompanied by other measures to reduce the negative effects of logging roads on freshwater turtles, such as road closure, buffer zones and anti-poaching patrols. Furthermore, we emphasise the need for incorporating detectability and its associated covariates in further monitoring of turtle populations when attempting to determine anthropogenic impacts. By understanding the factors that influence freshwater turtle occupancy patterns, we can identify priority areas and actions for their conservation.

CHAPTER 5

General discussion and prospects

"Rohan Chakravarty, www.greenhumour.com"

With this thesis, I aimed to provide a multidisciplinary approach to habitat fragmentation and its effects on herpetofauna, with a focus on the unique but neglected region of Southeast Asia. In this final chapter, I contextualise my results, highlighting their implications within the field of conservation biology. Finally, I provide my prospects for potential future studies following the thesis.

5.1 Current state of research in habitat fragmentation

In the last 50 years, habitat loss and fragmentation has become a central theme for conservation biologists as we face the Holocene "sixth mass extinction" event (Finn et al., 2023). Many reviews have shown biases in research efforts across various geographic regions and taxonomic groups (Deikumah et al., 2014; Fardila et al., 2017). For example, studies relating to conservation are often conducted by researchers in wealthy and English-speaking countries (Fazey et al., 2005). The hypothesis that a biased research effort still exists (research hypothesis 1) was fully supported by the results obtained in the first study (chapter 2), which illustrated a high proportion of studies (total of 78%) focused on three continents: North America, Europe and Oceania. On the contrary, there is a lack of studies on other regions (e.g. Africa and Southeast Asia) and taxa (e.g. caecilians, fossorial reptiles), disproportionate to the high biodiversity found in these regions and the threats they are facing. In addition to underscoring the strength and direction of biases in habitat fragmentation research, chapter 2 also revealed that associations of forms of habitat fragmentation with the sampling methods and response variables chosen by researchers are not random but can be clustered into three groups: 1) Measures of direct individual species responses, 2) Physiological and movement ecology, 3) Technology advancement in conservation research. The last group in particular exemplified the role of advances in genetics in habitat fragmentation research. Unlike community-level approaches such as responses in species richness, occupancy, and abundance, genetic structure at population level can offer a higher resolution of species response (Manel and Holderegger, 2013). Advances in techniques for interpreting genetic data coupled with digital technologies such as satellite remote sensing, drones, camera traps, and enhanced computational capacities have revolutionised how we approach questions in conservation. However, in developing regions of the world, particularly in Asia and Africa, studies on population genetics and niche modelling remain scarce (chapter 2). Access to highly specialised expertise in areas such as conservation genetics and other modern techniques may be limited (Hetu et al., 2019). The results of chapter 2 lay the essential groundwork for guiding future research (including my subsequent chapters) in conservation biology of herpetofauna and other taxa as they indicated important trends in where and how research is evolving and where gaps or biases should be targeted in future studies.

5.2 The benefits and limitations of species distribution models (SDMs) in species conservation

In chapter 3, I present three studies applying SDMs in species conservation research. These models supplement the range of available methods and spatial data, allowing the quantification of the threat of landscape fragmentation to species survival. SDMs are suitable tools for studies in conservation research as they do not require high effort field data collection and are solely based on its environmental niche and occurrence records (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). Both survey data and environmental variables have now increased in their availability. Occurrence records can be obtained from natural history collections, field surveys and online databases (e.g. GBIF and iNaturalist) whereas environmental variables linked to climate and land-use parameters can be derived from world climate databases (Fick and Hijmans, 2017) and remote sensing datasets (Mu et al., 2007). One main benefit of SDMs is that they can help identify the most suitable habitats for species of conservation concern, as well as the threats and opportunities that may affect their persistence (Wilting et al., 2010). One such threat could be habitat loss and fragmentation, which was clearly demonstrated in chapter 3.1 – 3.3. We observed a lack of suitable habitat for the critically endangered freshwater turtles and crocodiles in their current environment. SDMs can also help assess the effectiveness of protected areas in potentially sustaining viable populations based on their current or projected distributions (Ihlow et al., 2015; Rödder et al., 2010). As such, we can examine the coverage and connectivity of reserve networks. This information allows us to prioritise areas for protection, restoration or management of the target species or communities. For example, only a handful of protected areas were found to be suitable for the critically endangered freshwater turtles (chapter 3.1) and crocodiles (chapter 3.2 & 3.3), and therefore should be prioritised for conservation.

Another advantage of SDMs is that they can link ecological processes with environmental scenarios, allowing conservationists to explore the potential impacts of climate change, land-use change, or other drivers on biodiversity. The incorporation of land cover data are shown to provide significant insights when used in conjunction to bioclimatic SDMs (Cord and Rödder, 2011). For example, surface water coverage and wetland datasets served as indicators for crucial habitats for our freshwater turtles and crocodiles as they represent river networks and microhabitat surrogates (see chapter 3.1-3.3). Furthermore, to measure the impacts of climate change, we can project our species' current environmental niche to future climatic scenarios (Araújo et al., 2004) (see chapter 3.1). In chapter 3.2, I determined the climate stability for the Marsh crocodile across current and four future climate scenarios (IPCC6 story lines of ssp126, 245, 370 and 585). As a result, I found very few suitable areas (with large protected areas) to be stable for this crocodile species in the future. Finally, to account for impacts from anthropogenic pressures, we assessed current land use changes (NASA Socioeconomic Data and Applications Center) and future human density index (Murakami and Yamagata, 2019), see chapter 3.2 & 3.3. Comprehensive datasets like these can be very important to ensure effective conservation planning for species of special concern.

Despite these contributions, some limitations and uncertainties must be considered and addressed. SDMs often assume that species surveys are representative of the potential range and environmental niche of the species, and that all the essential environmental variables (and species interactions) are captured in the model. Unfortunately, this may not be true for rare or cryptic species, or for species confined to refugia or occupying only a small portion of their suitable habitat. This limitation was observed in the freshwater turtles and Philippine crocodiles in our studies (chapter 3.1 & 3.3) with less than 30 occurrences recorded for each. In these cases, models may underestimate the availability of suitable habitat for the species and may not capture the full complexity of the ecological processes that affect their distribution (De Ornellas et al., 2011; Sinclair et al., 2010). Moreover, SDMs associated to future climate change scenarios are subject to more uncertainty and variability than static SDMs, because they depend on the accuracy and resolution of the climate models, the migration ability and adaptation potential of the species, and the interactions between climate and other anthropogenic stressors. These factors are often poorly known or difficult to quantify, resulting in unrealistic or misleading projections of future distributions (Cayuela et al., 2009; Coreau et al., 2009; Elith and Leathwick, 2009; Franklin, 2010; Sinclair et al., 2010). One way to quantify prediction uncertainty and identify areas where the models are most uninformed is to create a MESS map (see chapter 3.1 & 3.2), which can direct us to the locations where we need to examine our predictions and help us in understanding the model discrepancies.

While correlative SDMs like Maxent assume that species are in equilibrium with their environment and that species responses to habitat change are linear and monotonic, another category of SDM, known as mechanistic SDMs, are worth mentioning. Mechanistic SDMs are process-based models that simulate the physiological or demographic responses of a species to environmental variables, based on independently derived information about a species’ traits and tolerances (Kearney and Porter, 2009). Despite being more complex and data-intensive, mechanistic SDMs can incorporate biotic interactions and population dynamics and are more robust to novel environmental conditions (Kearney et al., 2010). It is even suggested that only mechanistic models based on measured physiological or behavioural parameters of study species can approach an accurate description of the fundamental niche (Kearney and Porter, 2004).

Model limitations should not discourage conservationists from utilising the predictive capabilities of SDMs. Although SDMs should not be seen as definitive forecasts of habitat fragmentation, they provide plausible scenarios that depend on the assumptions and parameters used. The insights from SDMs can serve as a valuable starting point for decision making (Carvalho et al., 2010). To date, SDMs are among the best tools available to inform conservation decisions and policies, especially when based on well-surveyed populations whose responses to changes in critical parameters is well understood. I was able to provide examples of their value in chapter 3.2 and 3.3, where I incorporated survey data and expert knowledge from local specialists on endangered species in the Iran and Philippines. However, applying these models in real world scenarios presents a significant challenge. It is essential that these models are communicated transparently and visualised clearly to decision makers and stakeholders. This communication includes highlighting assumptions, limitations, uncertainties and implications of the models (Driscoll et al., 2012; McIntyre and Strauss, 2013). Furthermore, the information provided by SDMs alone are not sufficient by themselves to achieve effective conservation outcomes. This is because they may convey a false sense of precision or certainty that may mislead or confuse users (Carvalho et al., 2011). Therefore, it is necessary to supplement SDMs with other sources of information, including population viability analysis, expert opinions, scenario planning, adaptive management, monitoring and evaluation (Driscoll et al., 2012).

In summary, the findings of chapter 3 have made a substantial advance in conservation planning for the present and future distribution of key freshwater reptile species in Southeast Asia. I pinpointed priority areas and reserves that are vital for the potential discovery of novel populations. Immediate surveys and monitoring in proposed protected areas will be critical to ensure their survival in the future. Ultimately, these results serve as a roadmap for gathering ecological and genetic data on these lesser-known Southeast Asian reptiles.

5.3 Investigating fine-scale species responses: A case for occupancy models

While SDMs are widely used in predicting potential distributions, identifying suitable habitats, and accessing climate change impacts, they may not be the best fit for understanding fine-scale species responses to specific types/cases of habitat fragmentation. In such cases, occupancy models, which also estimate probability of species occurrence in relation to environmental variables, may be more suitable (Guillera-Arroita et al., 2015). Occupancy models have an advantage over SDMs as they explicitly account for imperfect detection to estimate the true probability of occupancy at a site (MacKenzie et al., 2002). This helps avoid under- or overestimating species occurrence when sampling bias occurs, which can be problematic in SDMs (Bean et al., 2012). Moreover, occupancy models allow the incorporation of habitat covariates that affect occupancy and detection, as well as covariates associated with different forms of habitat fragmentation such as logging and urbanisation (Asad et al., 2021a; Cassel et al., 2019).

They can provide unbiased and precise estimates of habitat relationships even in situations where detection probability is relatively homogenous across sites (Rota et al., 2011). Although requiring added field effort and computational resources than SDMs (Rota et al., 2011), occupancy models are more flexible in terms of the data incorporated. They can incorporate covariates that affect both occupancy and detection, account for spatial and temporal autocorrelation, and allow for multi-species or multi-state extensions (Dormann et al., 2007; Welsh et al., 2013).

To explore the fine-scale responses of Southeast Asian herpetofauna to logging as a form of habitat fragmentation, I employed single season occupancy model in chapter 4. While there is extensive research on how reptiles and amphibians react to habitat fragmentation, using occupancy models to account for the detectability of freshwater turtles in disturbed tropical landscapes is relatively new. To my knowledge, occupancy models have never been applied on Southeast Asian freshwater turtles in conservation biology. This approach (in chapter 4) revealed a negative association between logging road proximity and the occupancy of critically endangered *Notochelys platynota*. This result may indicate a negative indirect impact of logging roads on the soil and hydrology of surrounding habitats (Kleinschroth and Healey, 2017; Laurance et al., 2009). However, both *N. platynota* and *Dogania subplana* had high absolute occupancy probability in the Deramakot reserve regardless of the logging activities. The findings could be attributed to the retention of riparian buffers as part of the regulation of Reduced Impact Logging (RIL) (Pinard et al., 1995; Putz et al., 2008), corroborating the hypothesis that RIL may have limited impacts as a sustainable logging practice on these turtles (research hypothesis 3). Previous research conducted within the same reserve has identified relatively higher species richness in mammals (Bohnett et al., 2022; Burivalova et al., 2014; Sollmann et al., 2017) and in amphibians (Asad et al., 2021a; Burivalova et al., 2014) compared to neighbouring conventional logging sites. However, a major limitation of our study is the lack of control data from conventionally logged or natural intact forests due to data constraints and fieldwork challenges. Nevertheless, our study showed that occupancy modelling can be a promising approach for future studies including further surveys in conventionally-logged forest to confirm the limited impacts of RIL on freshwater turtles.

Occupancy modelling not only offered insights on how species respond to logging while accounting for detectability, but also shed light on the feeding and breeding behaviour of turtles. In chapter 4, I found that the detectability of the two freshwater turtles is influenced by climatological factors, particularly rainfall. Rainfall patterns heavily influence the behaviour and movement of freshwater turtles. Rainfall can mitigate the risk of desiccation and enhance the availability of prey, thereby affecting turtle mobility (Roe and Georges, 2008; Rowe, 2003). Additionally, rainfall can impact turtle nesting behaviour, as it may wash away both physical and olfactory traces of nest deposition, thus reducing the chances of predation (Eisemberg et al., 2015; Geller et al., 2022). The associations of detectability outlined in this study are not only crucial for understanding the activity and breeding behaviour of turtles, but they also provide a foundation for future studies investigating turtle populations in tropical ecosystems.

5.4 Personal prospects

Throughout my thesis, I gained an in-depth understanding of the importance of conducting a systematic review (chapter 2), particularly in relation to the subject of habitat fragmentation. This process not only enlightened me about the past and current methods researchers have been using to decipher species' responses to various forms of habitat fragmentation, but it also exposed me to the geographical and taxonomic research biases that urgently need addressing. The next logical step would be to incorporate grey literature (e.g., unpublished reports) and non-English scientific articles into our current findings. This may potentially alleviate the biased research paradigm we observed in chapter 2 (Angulo et al., 2021; Konno et al., 2020). I would also recommend employing up-to-date standardised methods specific to ecology when conducting systematic reviews or meta-analyses (e.g., PRISMA-EcoEvo v1.0; O'Dea et al., 2021).

I also expanded my knowledge on the advantages of using SDMs to determine habitat suitability of threatened species and further integrate them with remote sensing data. I learned how landscape changes affect the spatial distribution of populations, understood the limitations of data and approaches and discovered ways to address these limitations. A further refinement on SDM predictions would be assessing habitat connectivity using landscape connectivity models where resulting SDMs are used as conductance surfaces in CIRCUITSCAPE to calculate resistances to movement and gene flow among sampling locations (McRae et al., 2008). Following that, it would be enlightening to statistically compare resulting effective distances with estimates of genetic distances to understand the relative importance of the landscape elements. Comparative landscape genetics analysis can be highly effective in predicting impact of landscape parameters and dispersal capabilities of concerned species, hence informing conservation management (Bani et al., 2015; Emel and Storfer, 2012; Pilliod et al., 2015), as highlighted in chapter 2.

Lastly, I delved into the topic of occupancy modelling as an alternative way to examine species fine-scale responses to habitat fragmentation while mitigating some of the limitations posed by SDMs. Although the findings of chapter 4 suggested limited impacts of Reduced Impact Logging on the occupancy of native freshwater turtles, further surveys on the population of the same species on neighbouring conventionally logged or untouched forests are urgently needed to confirm these results. Another intriguing question is whether pre/post logging has impact on local abundance, population gains (reproduction/immigration), and survival probabilities. To determine whether natural habitat features or logging features are better predictors of demographic rates, detection/non-detection data is needed for multiple seasons for a dynamic occupancy model (MacKenzie et al., 2017).

I hope my thesis contributes to the new age of conservation biology and helps address the accompanying research gaps. As emphasised throughout every chapter, baseline ecological information (and biological information more generally) is still largely insufficient for many Southeast Asian taxa. Similarly, biodiversity assessments in the region are far from complete. I stress the importance of a multidisciplinary approach, as presented here, to quantify the current and future state of biodiversity unique to Southeast Asia.

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SUPPLEMENTARY FILES

Chapter 2

Supplementary material for this study can be found under

https://link.springer.com/article/10.1007/s10531-022-02530-6#Sec24 in the online appendices section.

Chapter 3.1

Supplementary material for this study can be found under

https://escholarship.org/uc/item/2m2539gp#supplemental in the Supplemental Material section.

Chapter 3.2

No supplementary material.

Chapter 3.3

Supplementary material for this study can be found under https://www.salamandra-journal.com/index.php/contents/2024-vol-60/2140-harrer,-s-,-p-ginal,-w-c-tan,-j-w-binaday,-a-c-diesmos,-r-manalo,-t-ziegler-d-r%C3%B6dder in the Appendix section.

Chapter 4

Supplementary material for this study can be found under https://wildlife.onlinelibrary.wiley.com/doi/full/10.1002/jwmg.22633

APPENDIX

Wei C. Tan, Anthony Herrel, Dennis Rödder (2023). A global analysis of habitat fragmentation research in reptiles and amphibians: what have we done so far?. Biodiversity and Conservation, 32(2), 439-468. https://doi.org/10.1007/s10531-022-02530-6

Wei C. Tan, Philipp Ginal, Anders G.J. Rhodin., John B. Iverson and Dennis Rödder (2022). A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia. Frontiers of Biogeography, 14(1). https://doi.org/10.21425/F5FBG50928

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REVIEW PAPER

A global analysis of habitat fragmentation research in reptiles and amphibians: what have we done so far?

W. C. Tan[1] · A. Herrel[2,3,4] · D. Rödder[1]

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Abstract
Habitat change and fragmentation are the primary causes of biodiversity loss worldwide. Recent decades have seen a surge of funding, published papers and citations in the field as these threats to biodiversity continue to rise. However, how research directions and agenda are evolving in this field remains poorly understood. In this study, we examined the current state of research on habitat fragmentation (due to agriculture, logging, fragmentation, urbanisation and roads) pertaining to two of the most threatened vertebrate groups, reptiles and amphibians. We did so by conducting a global scale review of geographical and taxonomical trends on the habitat fragmentation types, associated sampling methods and response variables. Our analyses revealed a number of biases with existing research efforts being focused on three continents (e.g., North America, Europe and Australia) and a surplus of studies measuring species richness and abundance. However, we saw a shift in research agenda towards studies utilising technological advancements including genetic and spatial data analyses. Our findings suggest important associations between sampling methods and prevalent response variables but not with the types of habitat fragmentation. These research agendas are found homogeneously distributed across all continents. Increased research investment with appropriate sampling techniques is crucial in biodiversity hotpots such as the tropics where unprecedented threats to herpetofauna exist.

Keywords Habitat change · Herpetofauna · Geographical bias · Taxonomic bias · Research agendas · Systematic review

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W. C. Tan
n.tan@leibniz-lib.de

[1] Herpetology Section, LIB, Museum Koenig, Bonn, Leibniz Institute for the Analysis of Biodiversity Change, Adenauerallee 127, 53113 Bonn, Germany

[2] UMR 7179 C.N.R.S/M.N.H.N., Département Adaptations du Vivant, Bâtiment d'Anatomie Comparée, 55 Rue Buffon, 75005 Paris, France

[3] Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, K.L. Ledeganckstraat 35, 9000 Gent, Belgium

[4] Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerpen, Belgium

Introduction

Habitat loss and fragmentation are the predominant causes underlying widespread biodiversity changes in terrestrial ecosystems (Fahrig 2003; Newbold et al. 2015). These processes may cause population declines by disrupting processes such as dispersal, gene flow, and survival. Over the past 30 years habitat loss and fragmentation have been suggested to have reduced biodiversity by up to 75% in different biomes around the world (Haddad et al. 2015). This is mainly due to the clearing of tropical forests, the expansion of agricultural landscapes, the intensification of farmland production, and the expansion of urban areas (FAO and UNEP 2020). The rate of deforestation and corresponding land conversions of natural habitats are happening rapidly and will continue to increase in the future at an accelerated rate, particularly in biodiversity hotspots (Deikumah et al. 2014; Habel et al. 2019; FAO and UNEP 2020).

For this reason, habitat fragmentation has been a central research focus for ecologists and conservationists over the past two decades (Fardila et al. 2017). However, habitat fragmentation consists of two different processes: loss of habitat and fragmentation of existing habitat (Fahrig 2003). The former simply means the removal of habitat, and latter is the transformation of continuous areas into discontinuous patches of a given habitat. In a radical review, Fahrig (2003) suggested that fragmentation per se, i.e., the breaking up of habitat after controlling for habitat loss, has a weaker or even no effect on biodiversity compared to habitat loss. She further recommended that the effects of these two components should be measured independently (Fahrig 2017). Despite being recognised as two different processes, researchers tend not to distinguish between their effects and commonly lump the combined consequences under a single umbrella term “habitat fragmentation” (Fahrig 2003, 2017; Lindenmayer and Fischer 2007; Riva and Fahrig 2022). Nonetheless, fragmentation has been widely recognised in the literature and describes changes that occur in landscapes, including the loss of habitat (Hadley and Betts 2016). Hence, to avoid imprecise or inconsistent use of terminology and provide a holistic view of the effect of modified landscapes, we suggest the term “habitat fragmentation” to indicate any type of landscape change, both habitat loss and fragmentation throughout the current paper.

One main conundrum is that biodiversity decline does not occur homogeneously everywhere nor among all species (Blowes et al. 2019). Moreover, we should expect a global disparity in biodiversity responses to habitat fragmentation across different biomes (Newbold et al. 2020; Cordier et al. 2021). For example, tropical regions are predicted to have higher negative effects of habitat fragmentation than temperate regions. There are two possible reasons: a) higher intensification of land use change in the tropics (Barlow et al. 2018), and b) forest animals in the tropics are less likely to cross open areas (Lindell et al. 2007). Furthermore, individual species respond to landscape modification differently; some thrive whereas others decline (Fahrig 2003). Habitat specialists with broader habitat tolerance and wide-ranging distributions are most likely to benefit from increase landscape heterogeneity and more open and edge habitat (Hamer and McDonnell 2008; Newbold et al. 2014; Palmeirim et al. 2017). Therefore, appropriate response metrics should be used in measuring the effect of habitat fragmentation on biodiversity depending on the taxa group, biome and scale of study as patterns of richness can sometimes be masked by the abundance of generalist species (Riemann et al. 2015; Palmeirim et al. 2017).

Previous reviews have identified general patterns and responses of reptile and amphibian populations to habitat modification. They have been largely centred around specific types of habitat fragmentation: land use change (Newbold et al. 2020), logging (Sodhi et al. 2004), fragmentation per se (Fahrig 2017), urbanisation (Hamer and McDonnell 2008; McDonald et al. 2013), fire (Driscoll et al. 2021), and roads (Rytwinski and Fahrig 2012). Few reviews have, however, attempted a global synthesis of all types of land use changes and even fewer have addressed biases in geographical regions and taxonomical groups (but see Gardner et al. (2007) and Cordier et al. (2021)). Gardner et al. (2007) synthesised the extant literature and focused on 112 papers on the consequences of habitat fragmentation on reptiles and amphibians published between 1945 and 2006. They found substantial biases across geographic regions, biomes, types of data collected as well as sampling design and effort. However, failure to report basic statistics by many studies prevented them from performing meta-analyses on research conclusions. More recently, a review by Cordier et al. (2021) conducted a meta-analysis based on 94 primary studies on the overall effects of land use changes through time and across the globe. Yet, there has been no comprehensive synthesis on the research patterns and agenda of published literature on habitat fragmentation associated with the recent advances of novel research tools and techniques. Therefore, our review may provide new insights of the evolution and biases in the field over the last decades and provide a basis for future research directions. Knowledge gaps caused by these biases could hamper the development of habitat fragmentation research and the implementation of effective strategies for conservation.

We aim to remedy this by examining research patterns for the two vertebrate classes Amphibia and Reptilia, at a global scale. We chose amphibians and reptiles for several reasons. First, habitat fragmentation research has been dominated by birds and mammals (Fardila et al. 2017). Reptiles and amphibians, on the other hand, are under-represented; together, they constitute only 10% of the studies (Fardila et al. 2017). Second, high proportions of amphibian and reptile species are threatened globally. To date, more than one third of amphibian (40%) and one in five reptile species (21%) are threatened with extinction (Stuart et al. 2004; Cox et al. 2022). Amphibians are known to be susceptible to land transformation as a result of their cryptic nature, habitat requirements, and reduced dispersal ability (Green 2003; Sodhi et al. 2008; Ofori-Boateng et al. 2013; Nowakowski et al. 2017). Although poorly studied (with one in five species classified as data deficient) (Böhm et al. 2013), reptiles face the same threats as those impacting amphibians (Gibbons et al. 2000; Todd et al. 2010; Cox et al. 2022). Reptiles have small distributional ranges with high endemism compared to other vertebrates and as such are likely vulnerable to habitat fragmentation (Todd et al. 2010; Meiri et al. 2018). Third, both these groups are poikilotherms whose physiology makes them highly dependent on temperature and precipitation levels. Hence, they are very sensitive to changing thermal landscapes (Nowakowski et al. 2017).

Here, we first ask how is the published literature distributed across geographic regions and taxa? Is there a bias in the geographic distribution of species studied compared to known species? It is well known that conservation and research efforts are often concentrated in wealthy and English-speaking countries (Fazey et al. 2005), but has this bias improved over the years? Second, how are researchers conducting these studies? We assess whether certain sampling methods and response variables are associated to specific types of habitat fragmentation. Over the past decades new tools and techniques are constantly being discovered or developed. Combinations of methodologies are now shedding new light on biodiversity responses and consequences of habitat fragmentation. In particular, genetic techniques are useful in detecting changes in population structure, identifying isolated genetic clusters, and in estimating dispersal (Smith et al. 2016). Similarly, habitat occupancy and modelling can also provide powerful insights into dispersal (Driscoll et al. 2014). Remote sensing data are now used in analysing effects of area, edge, and isolation (Ray et al. 2002). Finally, how are these associations or research agendas distributed across space? We expect to find geographic structure of emerging agendas across the globe. For instance, we predict genetic studies to be located in North America and Europe but also in East Asian countries such as China and Japan as a result of their advancement in genetics (Forero et al. 2016). On the other hand, simple biodiversity response indicators which do not require extensive capacity building and application of advanced technologies are likely more used in developing regions of the world (Barber et al. 2014). These findings are valuable to evaluate and update the global status of our research on the effects of habitat fragmentation on herpetofauna and to suggest recommendations for conservation plans.

Materials and methods

Data collection

We conducted the review according to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Fig. 1) (Moher et al. 2009). We conducted a comprehensive and exhaustive search using Web of Science to review published studies reporting the consequences of habitat fragmentation on amphibians and reptiles. We consulted the database in November 2019 by using two general search strings: (1) Habitat fragmentation AND (frog* OR amphib* OR salamander* OR tadpole*) (2) Habitat fragmentation AND (reptil* OR snake* OR lizard* OR turtle* OR crocodile*). This returned a total of 869 records from search (1) and 795 from search (2), with 1421 unique records remaining after duplicates were removed. We did not include "habitat loss" in our search term as it would only introduce unrelated articles focusing on biodiversity and conservation management instead of methodology and mechanistic approaches.

Throughout, we use the term papers to refer to individual journal article records. Out of the 1421 papers, we were unfortunately not able to locate seven papers from Acta Oecologica, Zoology: Analysis of Complex Systems, Israel Journal of Ecology and Evolution, Western North American Naturalist, Natural Areas Journal, Ecology, and the Herpetological Journal. We screened all articles from the title through the full text to determine whether they met our criteria for inclusion. To be included, studies needed to fulfil several criteria. First, papers needed to be peer-reviewed journal articles containing data collected on reptiles and/or amphibians at the species level (224 articles rejected because no species-specific data was available). Reviews and metastudies ($n = 102$) were excluded from the data analysis as they may represent duplicates as they are mainly based on data sets from other papers, but these form an integral part of our discussion. Furthermore, papers which do not provide data on contemporary time scales such as long-term (> 10, 000 years ago) changes on the paleo-spatial patterns ($n = 59$) were excluded. Because the effects of fragmentation per se have been measured inconsistently by many authors and have not been differentiated from habitat removal (Fahrig 2003), we consider any recent anthropogenic habitat degradation, and modification at patch or/and landscape scales during the Holocene as an effect of habitat fragmentation. Only papers which examined direct or indirect effects of habitat fragmentation were included in our analysis, regardless of the magnitude and direction. Papers which did not mention specific types of habitat fragmentation as the focus of their study ($n = 338$) were excluded.

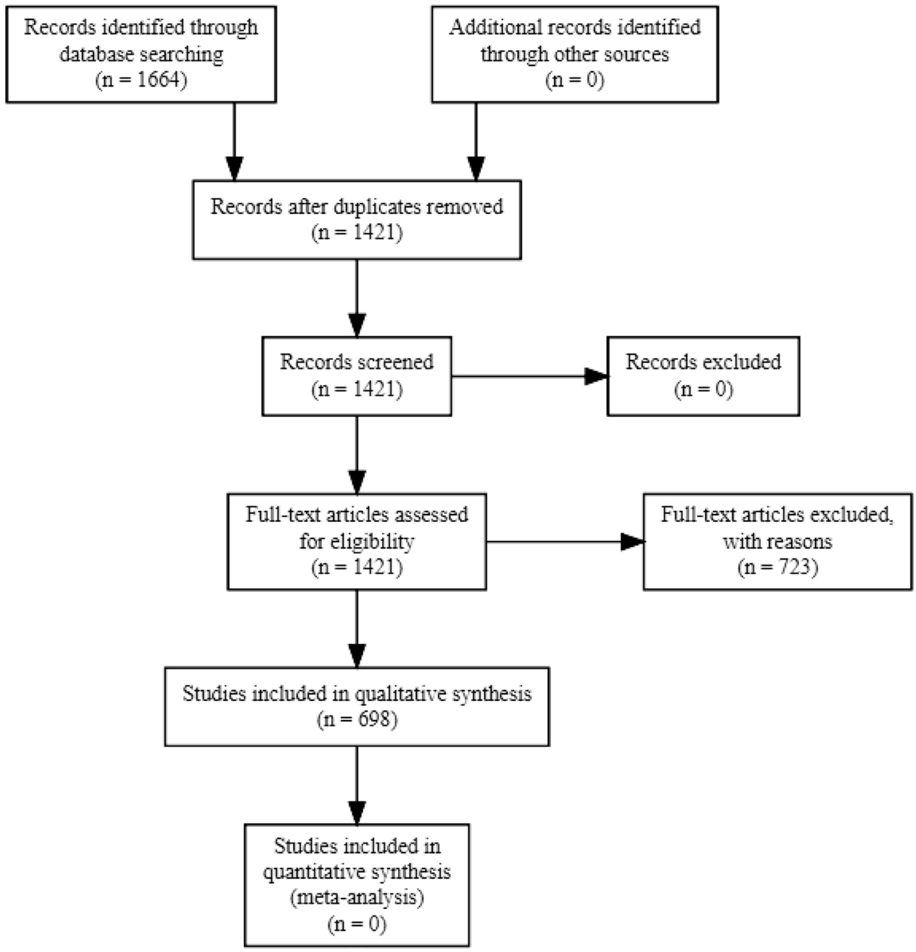

Fig. 1 PRISMA flow-diagram of the study selection process

Geographical and taxonomical distribution

Using the selected papers, we compiled a taxonomic and geographical database for each paper: (a) GPS or georeferenced location of the study site; (b) the focal group investigated (amphibian and/or reptile); (c) taxonomic groups (order, family, genus).

We listed the overall number of species studied covered by selected papers in each continent and compared them to the total number of currently described species. We obtained total described species of both reptiles and amphibians from the following sources: ReptileDatabase (Uetz et al. 2021) and AmphibiaWeb (AmphibiaWeb 2021). Then, we calculated the proportions of species covered by the selected papers compared to total number of described species for each continent. We did not update species nomenclature from selected papers as the mismatches from these potentially outdated taxonomies would be insignificant in our analyses.

Categorisation of papers

Each paper is classified into three main types of data collected: forms of habitat fragmentation, sampling methods, and response variables (Online Appendix 1). A paper can be classified into one or multiple categories in each type of data. The types of data and their following categories were:

Forms of habitat fragmentation

We recorded different types of habitat fragmentation from the selection of studies: (1) “Fragmentation” (includes patch isolation, edge and area effects); (2) “Agriculture” (includes any form of commercial and subsistence farming such as monocultures, plantations, and livestock farming); (3) “Logging” (e.g., agroforestry and silviculture); (4) “Mining” (presence of mining activities); (5) “Urbanisation” (includes presence of cities, towns or villages and parks created for recreational purposes); (6) “Road” (includes any vehicle roadway such as railways and highways) and (7) “Other types of habitat fragmentation” (e.g., fire, river dams, ditches, diseases, desertification etc.). Many studies deal with more than one type of habitat fragmentation. However, we made sure the selection for fragmentation forms is mainly based on the focus and wordings in the methodology section.

Sampling methods

We report trends in the design and sampling methods among the compiled studies over the last three decades. Due to the substantial variability in the level of sample design information reported by different studies, we narrowed them down into six general categories representing common sampling methods. Common methods used in estimating herpetofauna diversity (e.g., visual transect surveys, acoustic monitoring and trapping methods) were not included in the analyses due to their omnipresence in the data. The categories are:

(1) “Genetics” studies documented any use of codominant markers (i.e., allozymes and microsatellites), dominant markers [i.e., DNA sequences, random amplified polymorphic DNA (RAPDs) and amplified fragment length polymorphism (AFLPs)] to analyse genetic variability and gene diversity respectively. (2) “Direct tracking methods” studies measured potential dispersal distances or species movement patterns by means of radio telemetry, mark-recapture methods, or fluorescent powder tracking. (3) “Aerial photographs” studies reported the use of aerial photographs while (4) “GIS/Satellite image” studies described the use of satellite imagery and land cover data (i.e., Landsat) and GIS programs (e.g., QGIS and ArcGIS, etc.) in analysing spatial variables. (5) “Experimental” studies involved predictions tested through empirical studies, regardless if they occur naturally or artificially; in a natural or a captive environment. (6) “Prediction/simulation models” studies made use of techniques such as ecological niche models, habitat suitability (i.e., occurrence and occupancy models) and simulations for probability of survival and population connectivity.

Response variables

To further conceptualise how the effects of habitat fragmentation are measured, we assigned 12 biodiversity or ecological response variables. We recorded the type of data that was used in all selected studies: (1) “Species richness or diversity” which are measures of species richness, evenness or diversity (such as the Shannon–Wiener index) (Colwell 2009); (2) “Functional richness or species guilds” describes diversity indices based on functional traits (such as body size, reproductive modes, microhabitat association or taxonomic groups); (3) “Presence/absence” or species occupancy; (4) “Population” includes an estimation of population size or density (only when measured specifically in the paper). It includes genetic variation and divergence within and between populations; (5) “Abundance” or counts of individuals for comparison between habitat fragmentation type or species; (6) “Dispersal” takes into account any displacement or movement and can include indirect measurements of dispersal using genetic techniques; (7) “Breeding sites” which measures available breeding or reproduction sites; (8) “Fitness measure” are records of any physiological, ecological or behavioural changes; (9) “Interspecific interaction” depicts any interaction between species including competition and predation; (10) “Extinction or colonisation rate” counts the number of population extinctions or colonisations within a time period; (11) “Microhabitat preference” includes any direct observation made on an individual’s surrounding environmental features (substrate type, perch height, vegetation type, distance to cover etc.); (12) “Generalist or specialist comparison” involves any comparison made between generalist and specialist species. Generalists are able to thrive in various environments whereas specialists occupy a much narrower niche; (13) “Other response variables” can include road kill mortality counts, infection rate of diseases, injury, or any effect from introduced animals and a variety of other responses.

Data analysis

All statistical analyses were conducted in the open source statistical software package R 4.1.0 (R Core Team 2021). To gain a broad insight into our understanding of the complexity of habitat fragmentation we applied a Multiple Correspondence Analysis (MCA) (Roux and Rouanet 2004) and Hierarchical Clustering on Principle Components (HCPC) (Ward 1963) to investigate potential interactions between forms of habitat fragmentation, sampling methods and response variables. MCA is ideal for investigation of datasets with multiple categorical variables and exploration of unbiased relationships between these variables.

We first separate the dataset into papers concerning amphibians or reptiles. The MCA was performed using the MCA function from FactoMineR package of R version 3.1 (Lê et al. 2008). To identify subgroups (cluster) of similar papers within our dataset, we performed cluster analysis on our MCA results using HCPC. The cluster results are then visualised in factor map and dendrogram for easier interpretation using factoextra package. This allows us to identify categorical variables which have the highest effect within each cluster. Statistical analyses were considered significant at $\alpha = 0.05$, while a p between 0.10 and 0.05 was considered as a tendency. The p-value is less than 5% when one category is significantly linked to other categories. The V tests show whether the category is over-expressed (positive values) or under-expressed (negative values) in the cluster (Lebart et al. 1995).

Results from the literature review were also analysed with VOSviewer, freeware for constructing and visualising bibliometric networks (http://www.vosviewer.com/). The program uses clustering techniques to analyse co-authors, co-occurrence of keywords, citations, or co-citations (van Eck and Waltman 2014). First, we analyse co-authorships of countries to provide a geographical representation of groups of authors in various countries over the past 30 years. Each circle represents an author's country and the size represents the collaboration frequency with other countries. The lines between the nodes represent the collaboration networks between the countries while the thickness of the lines indicates the collaboration intensities between them. Lastly, to complement the MCA and HCPC, we used VOSviewer to analyse a clustering solution of categories at an aggregate level. Aggregate clustering is a meta-clustering method to improve the robustness of clustering and does not require a priori information about the number of clusters. In this case, instead of author's keywords, we used the co-occurrence of categories associated to each selected paper as input to run the software.

Results

Geographical and taxonomical distribution

We identified a total of 698 papers published between January 1991 and November 2019 reporting consequences of habitat fragmentations corresponding to our selection criteria (Fig. 1). The complete list of studies included (hereafter termed "selected papers") is available in Online Appendix 2. The distribution of these selected papers between focal groups and among continents was non-homogeneous (Fig. 2). Selected papers reviewed were predominantly studies which were conducted in North America 310 (44%) and Europe 131 (19%), but also from Oceania 104 (15%), South America 85 (12%), Asia 37 (5%) and Africa 31 (5%). For co-authorships between countries based on VOSviewer, the minimum document number of a country was set as 5 and a total of 21 and 14 countries met the threshold for amphibians and reptiles respectively (Fig. 3). For amphibians, countries in the American continent such as United States of America or USA (178 articles), Brazil (38 articles) and Canada (35 articles) have the largest research weight (Fig. 3a). Authors from the USA have the largest international cooperation network, followed by Brazil. Australia and other European countries such as Germany, France and England also have high collaboration relationships with other countries. In contrast, reptile studies were mainly concentrated around two countries: the USA (139 articles) and Australia (86 articles) (Fig. 3b). No other country from the rest of the world has more than 20 articles. While both the USA and Australia have the largest collaboration networks, Canada, Spain and Mexico are also highly cooperative with authors from other countries.

Overall, over half of all selected papers included only amphibians (376 papers; 54%), whilst 276 papers (39%) included only reptiles and 46 papers (7%) assessed both reptiles and amphibians. In relation to species richness, we identified 1490 amphibian species and 1199 reptile species across all papers; among which 141 taxa were not identified to species level but were still included in our analyses as taxonomic units analogous to species (Online Appendix 2). Among these species, more than half of the studied amphibians were found in South America (537; 38%) and North America (328; 23%), followed by Africa (297; 21%), Asia (137; 10%), Europe (77; 5%), and Oceania (51; 3%). Half of the reptile species studied were from North America (302; 25%) and Africa (278; 23%), with the other half consisting of species from Oceania (276; 23%), South America (200; 17%), Europe (76; 6%), and Asia (67; 6%).

When compared to the known species richness in the world, large portions of European species are studied while species from other continents were severely under-represented (Fig. 2). The proportions of amphibian species represented in papers were the

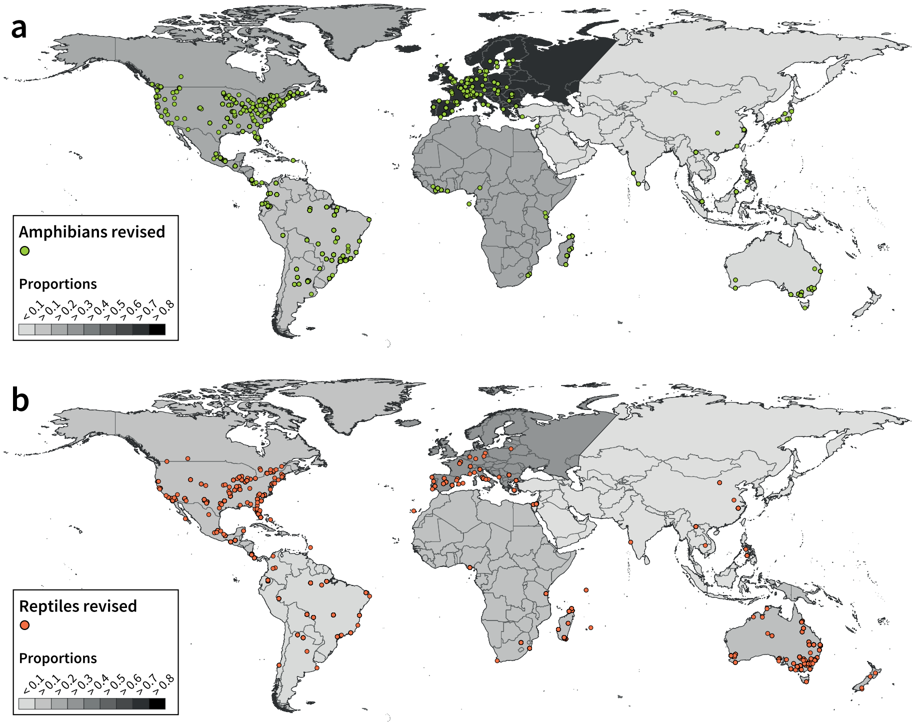

Fig. 2 Map of study locations for **a** amphibians and **b** reptiles with each circle representing the study location of papers included in the review. The colour scale of the continents ranging from 0 – 0.9 indicates the proportions of amphibian and reptile species represented in the reviewed papers when compared to known species in the world (obtained from AmphibiaWeb and ReptileDatabase): **a** Europe (0.73), Africa (0.23), North America (0.23), South America (0.18), Oceania (0.07) and Asia (0.06) and **b** Europe (0.27), Oceania (0.18), Africa (0.12), North America (0.11), South America (0.09) and Asia (0.02)

highest in Europe (73%), while the proportions are much lower for Africa (23%), North America (23%), South America (18%), Oceania (7%) and Asia (6%) (Fig. 2a). Among reptiles, Europe represents again the highest proportion of studied species (27%), followed by Oceania (18%), Africa (12%), North America (11%) and South America (8.9%) (Fig. 2b). In contrast, of all Asian reptile species, only a mere 1.73% were included in the selected papers. The species coverage in our selected papers does not seem optimistic. Amphibians and reptiles each have only six families with more than half of the species covered (including three reptilian families containing one species in total). Meanwhile, 23 and 25 families remain fully neglected for amphibians and reptiles respectively (Figs. 4–5).

Categorisation of papers

Multiple correspondence analysis provided important insights into underlying patterns in our data allowing us to visualise the relationship between forms of habitat fragmentation (Median = 1 [1–4]), sampling methods (Median = 1 [0–5]) and response variables (Median = 2 [1–6]). Percentage of variance (or eigenvalues) from MCA output represents the contribution of each dimension in explaining the observed patterns. The top ten new dimensions identified by MCA explained a total of 61.64% and 61.16% of the total variance

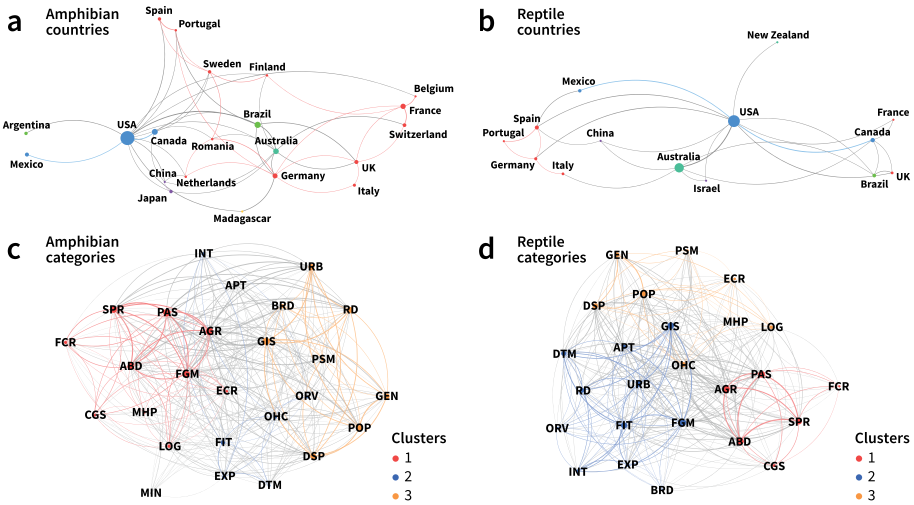

Fig. 3 Co-authorship map of countries involved in habitat fragmentation research in **a** amphibians and **b** reptiles. The colours represent the continents countries belong to. Each circle represents an author's country and the size represents the collaboration frequency with other countries. The lines between the nodes represent the collaboration networks between the countries while the thickness of the lines indicates the collaboration intensities between them. Category co-occurrence network maps for **c** amphibians and **d** reptiles. The colour represents the different cluster groups each category belongs to. Abbreviations for the categories in forms of habitat change: fragmentation (FGM), agriculture (AGR), Logging (LOG), Mining (MIN), Urbanisation (URB), road (RD), other habitat fragmentation (OHC); sampling methods: genetics (GEN), direct tracking method (DTM), aerial photographs (APT), GIS/ Satellite images (GIS), experimental (EXP), prediction/ simulation models (PSM) and response variables: species richness/ diversity (SPR), functional richness/ species guild (FCR), presence/ absence (PAS), population (POP), abundance (ABD), dispersal (DSP), breeding sites (BRD), fitness measure (FIT), interspecific interaction (INT),extinction/ colonisation rate (ECR), microhabitat preference (MHP), comparison between generalist and specialist (CGS), other response varialbes (ORV) (see also Online Appendix 1). Maps are created in VOSviewer

for amphibians and reptiles respectively. The two dimensions with the highest variance percentages explained were found in the first (Dim1, 12.55%) and second (Dim2, 9.13%) dimensions in amphibians (Online Appendix 3–4). Genetics (sampling method; 13.73%) and population (response variable; 12.39%) contributed the most to Dim1, together with species richness (response variable;10.41%) and dispersal (response variable; 9.20%). For Dim2, experimental (sampling method; 14.38%) was the dominant variable, the rest was determined by GIS/Satellite images (sampling method; 9.71%), fitness measure (response variable; 9.12%) and urbanisation (form of fragmentation; 8.94%). For reptiles, the two dimensions explaining the most variation were the first (Dim1, 11.34%) and second (Dim2, 8.28%) dimensions (Online Appendix 3–4). The variables contributing the most to Dim1 were species richness (response variable; 15.51%), abundance (response variable; 10.11%), presence/absence (response variable; 6.97%) and genetics (sampling method; 6.39%). On the other hand, Dim2 was determined by interspecific interaction (response variable; 13.49%), genetics (12.79%), experimental methods (sampling method; 11.21%) and fitness measure (response variable; 10.94%). The contribution of each category to the definition of the dimensions is reported in Online Appendix 3. The categories identified in the MCA dimensions are subsequently used for building the distance matrix in the clustering analysis.

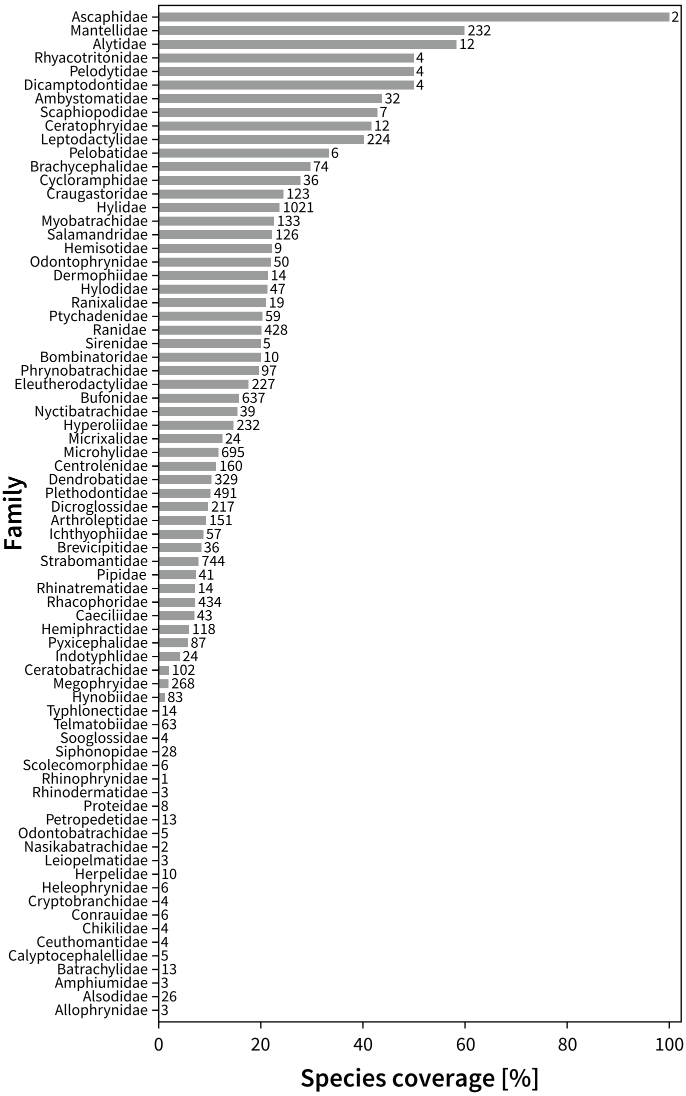

Fig. 4 Species coverage for each taxonomic family in selected papers of amphibians. The numbers on each row indicate the total number of species known in its respective family (obtained from AmphibiaWeb 2021)

The HCPC analysis identified three clusters of variables for amphibians and reptiles (Online Appendix 5–6). The output of the HCPC analysis is reported in Online Appendix 7. V test represent the influence of variables in the cluster composition. In general, three clusters for both amphibians and reptiles appeared to be uniquely similar by definition of categories (Fig. 6). For amphibians, cluster 1 was defined by studies on species richness ($p < 0.05$, V test = 14.30) and presence/absence ($p < 0.05$, V test = 13.42), while cluster 2 was determined by experimental studies ($p < 0.05$, V test = 10.95) and fitness measures ($p < 0.05$, V test = 9.77). Cluster 3 was defined by genetics ($p < 0.05$, V test = 18.44) and

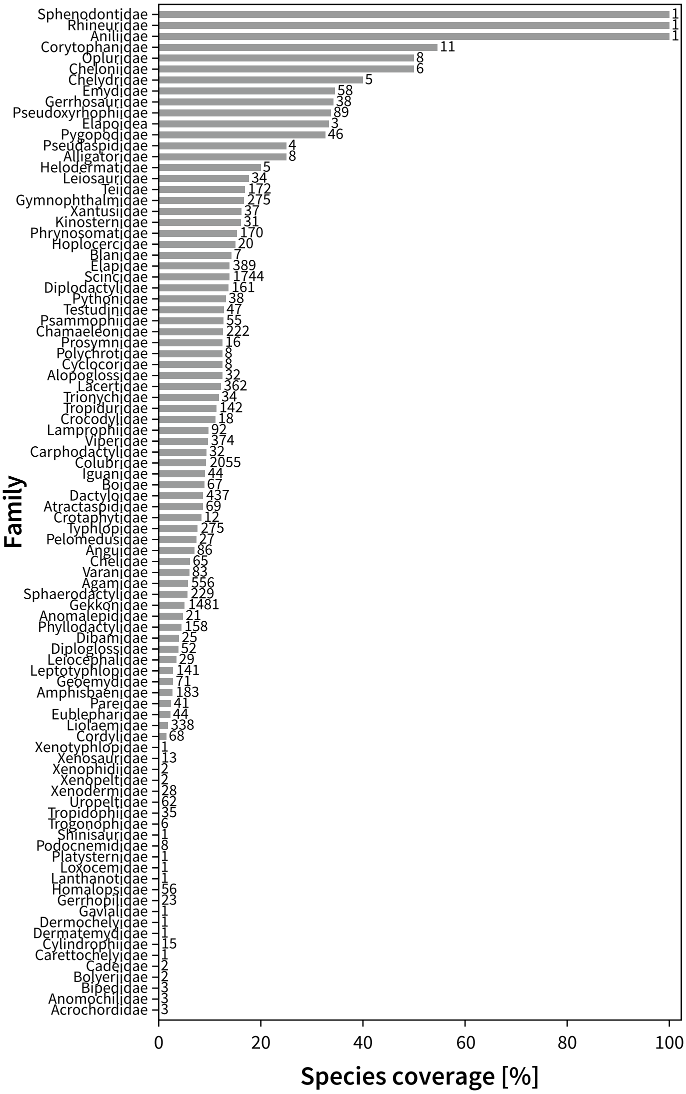

Fig. 5 Species coverage for each taxonomic family in selected papers of reptiles. The numbers on each row indicate the total number of species known in its respective family (obtained from ReptileDatabase)

population studies ($p < 0.05$, V test = 17.73) (Online Appendix 7). Abundance and functional richness were also unique to cluster 1; other response variables and direct tracking methods were important to cluster 2 and dispersal was present in cluster 3 even though these variables are less expressed (Fig. 6a).

For reptiles, cluster 1 was represented by species richness ($p < 0.05$, V test = 14.26), abundance ($p < 0.05$, V test = 11.22) and presence absence ($p < 0.05$, V test = 8.55) papers, whereas cluster 2 was determined by papers on fitness measures ($p < 0.05$, V test = 10.99), direct tracking methods ($p < 0.05$, V test = 8.64) and interspecific interaction ($p < 0.05$, V

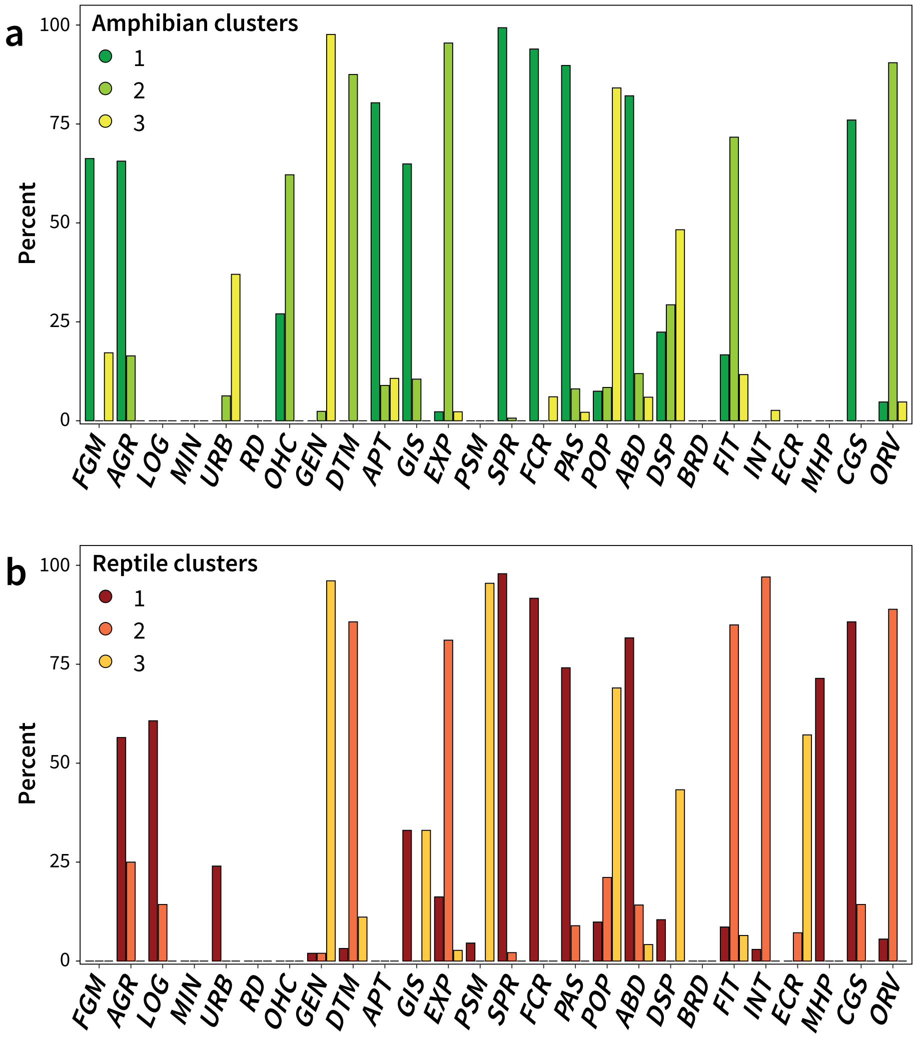

Fig. 6 Percentage contribution of the categories contributing to the uniqueness of each cluster in amphibians (Dark green = 1, Bright green = 2, Bright yellow = 3) and reptiles (Dark red = 1, Orange = 2, Dark yellow = 3) based on the Cla/Mod results of HCPC (see Online Appendix 7). Abbreviations for the categories can be found in Fig. 3 and in Online Appendix 1

test = 7.86), and cluster 3 was defined by genetics ($p < 0.05$, V test = 12.79), population ($p < 0.05$, V test = 9.95) and prediction/simulation models ($p < 0.05$, V test = 7.68) papers (Online Appendix 7). Although slightly less expressed in the clusters, papers using comparisons between generalist and specialist species and papers on functional richness were also unique to cluster 1; experimental methods and other response variables were heavily present in cluster 2, while dispersal studies were distinct to cluster 3 (Fig. 6b).

Results from VOSviewer categories of both amphibians and reptiles appear to be similar to each other (Fig. 3c, d). The clustering of the categories in the co-occurrence network maps confirms what we observed in the HCPC results (Fig. 6). In addition to geographical representation of study locations in (1), the corresponding clusters of selected papers are also mapped in Figs. 7 and 8 to investigate the spatial grouping patterns for the three clusters (see Online Appendix 8–9 for geographical representation for each category). We also plotted the temporal trend in Online Appendix 10 and 11. Overall, the three clusters are distributed homogeneously across the globe, but concentrated in the USA, Europe and south eastern Australia. Cluster 1 papers were found to be the most predominant cluster in amphibians (57% papers) across all continents (see Online Appendix 12; Fig. 7). When

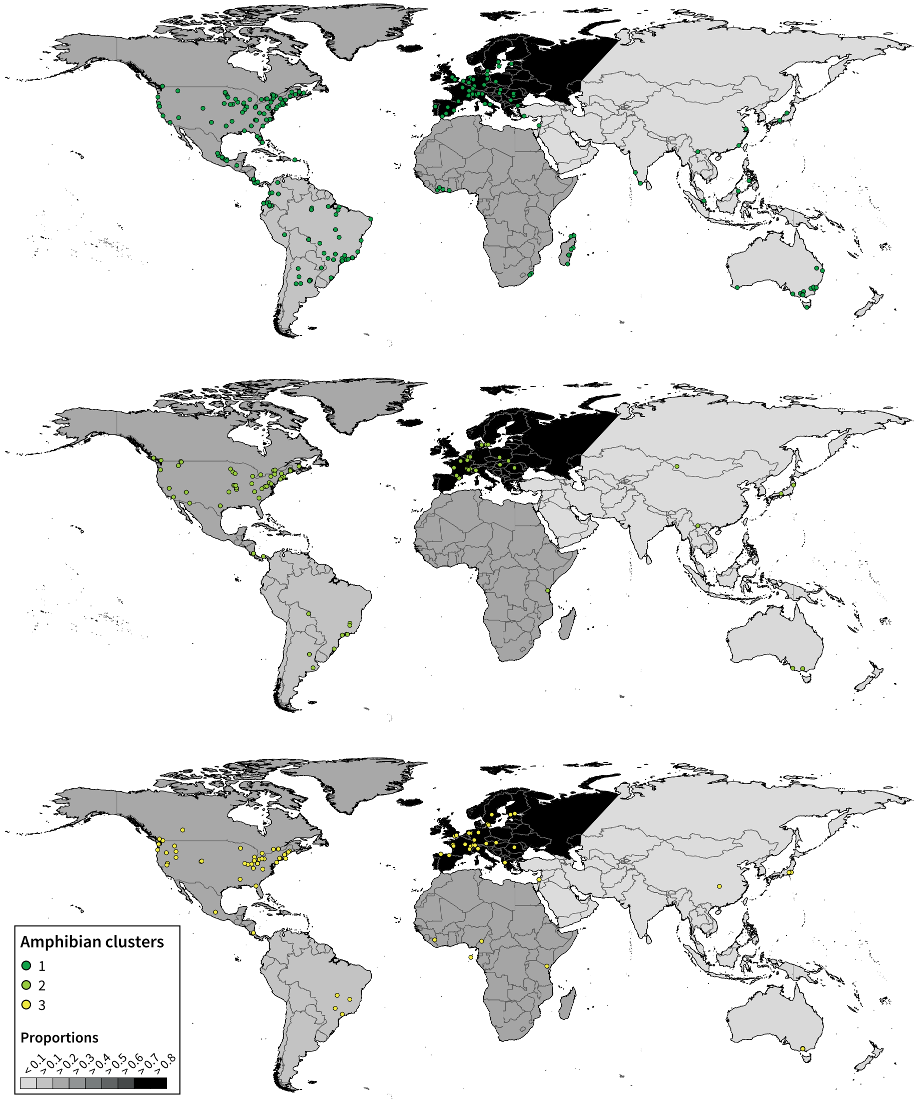

Fig. 7 Map of the individual selected papers belonging to each cluster groups (Dark green = 1, Bright green = 2, Bright yellow = 3) for amphibians, with each circle representing the study location. The colour scale of the continents ranging from 0 to 0.9 indicates the proportions of amphibian species represented in the reviewed papers when compared to known species in the world (obtained from AmphibiaWeb)

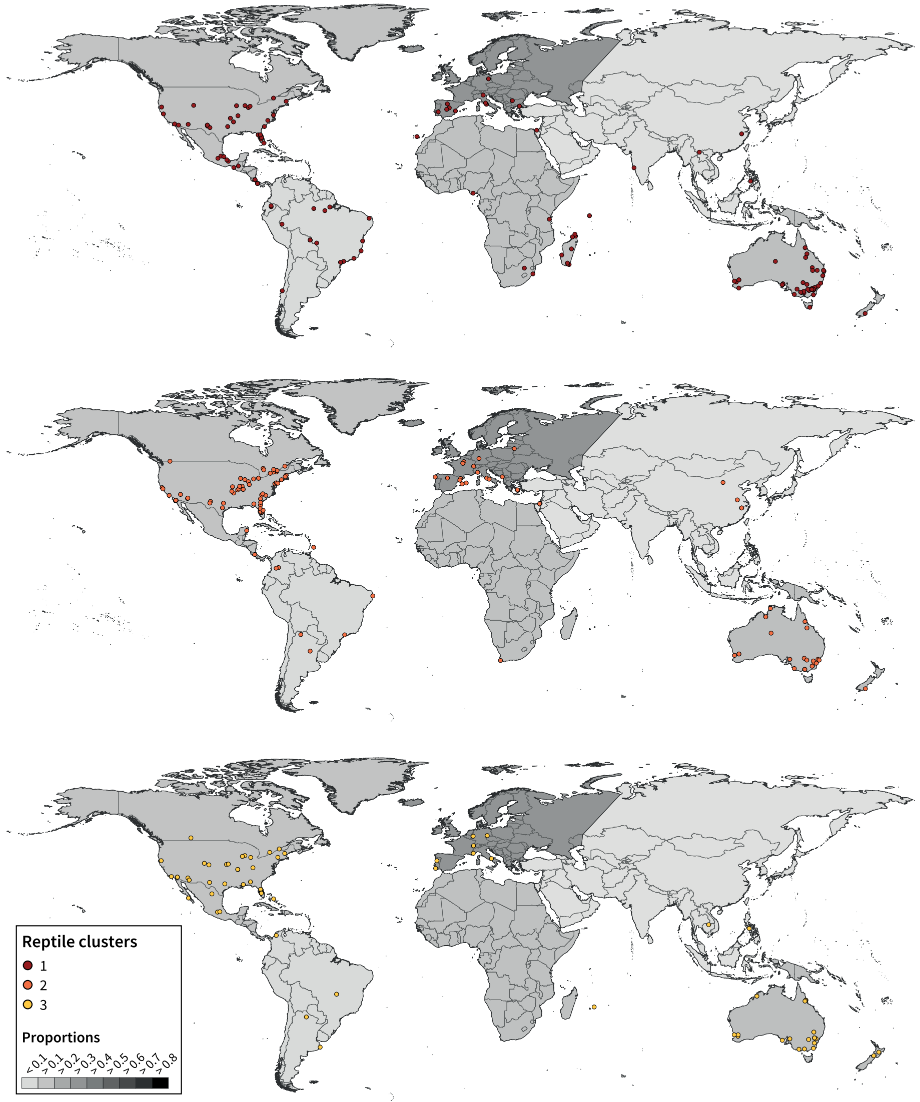

Fig. 8 Map of the individual selected papers belonging to each cluster groups (Dark red=1, Orange=2, Dark yellow=3) for reptiles, with each circle representing the study location. The colour scale of the continents ranging from 0.0 – 0.9 indicates the proportions of reptile species represented in the reviewed papers when compared to known species in the world (obtained from ReptileDatabase).

compared to other clusters, studies from this cluster are often conducted in Afrotropics, particularly Madagascar (100% papers), central (Costa Rica (60% papers) and Mexico (92% papers) and south America (80% papers) (Online Appendix 12, Figs. 7, 8). On the other hand, cluster 2 papers appear to be more prevalent for reptile studies compared to amphibian studies, with a higher number of studies conducted across North America (65 to 51) and Australia (22 to 2) (Figs. 7, 8). Lastly, a vast majority of cluster 3 papers were located in North America and Europe (both contributing to 79% of the papers) for amphibians and North America and Australia (both contributing to 84% of the papers) for reptiles (Online Appendix 12, Figs. 7, 8). Publications from this cluster started to gain popularity from 2005 onwards, following similar increasing trends as cluster 2 (Online Appendix 10–11). Overall, except for cluster 1 in South America, most of the clusters in Asia and Africa appear to experience very little or no increase in publications over the years (Online Appendix 10–11).

Discussion

Our review found no improvement in the geographical and taxonomic bias in habitat fragmentation studies for both reptiles and amphibians compared to earlier studies (Fardila et al. 2017). Yet, our study has made an effective contribution towards identifying major spatial gaps in habitat fragmentation studies over the past three decades (updating reviews such as Cushman 2006; Gardner et al. 2007)). In particular, we found an overall increase in the number of studies measuring species richness and abundance throughout the years while population-level and genetics studies are still lacking in developing countries. Here, we discuss the issues of (1) biogeographical bias, (2) the extent and focus of habitat fragmentation research and (3) the limitations and knowledge gaps in habitat fragmentation research in herpetology and provide recommendations for future research.

Biogeographical bias

Geographic bias in research papers

Given the research effort in relatively wealthy countries (Holmgren and Schnitzer 2004; Fazey et al. 2005) it is not surprising that more than half the papers concern North America and Europe, where there is strong prevalence of herpetological research. This pattern is also evident in other taxonomic groups and biological areas including invasion biology (Pyšek et al. 2008), biodiversity conservation (Trimble and Aarde 2012; Christie et al. 2020), and habitat fragmentation (Fardila et al. 2017). The USA alone contributed more than a third of the publications in terms of both authors and location of study (Fazey et al. 2005; Melles et al. 2019). English speaking countries including the USA, the United Kingdom, and Australia have dominated research output over the last 30 years (Melles et al. 2019). These patterns were reflected in the collaboration network maps generated by VOSviewer (Fig. 3). Similar hotspots found between who does the research (Fig. 3) and the study locations (Fig. 2) suggest that authors tend not to move much and only to study ecosystems near to where they are based (Meyer et al. 2015). One reason for this bias is the distance to field sites accentuated by the costs and time of travelling.

However, the near absence of studies from many parts of the world that are currently under extreme pressures of habitat loss and degradation are of great concern (Habel et al. 2019). We feel that the level of threat associated with habitat fragmentation in these continents is not proportional to the level of research attention required. Naturally biodiverse but less economically developed Southeast Asian and sub-Saharan countries will suffer greatest diversity losses in the next century (Newbold et al. 2015). If this persists at the current rate, biodiverse areas will likely disappear before new discoveries in those hotspots are made (Moura and Jetz 2021). Although conversely our study found that among other developing countries Brazil is currently conducting relatively more in-country amphibian studies and collaboration with other countries. However, how much of this information reaches decision makers and practitioners remains unknown. This is largely due to the lack of intermediary evidence bridges (Kadykalo et al. 2021). These intermediaries identify evidence summaries based on research and priorities and distribute them to practitioners, facilitating exchange of knowledge between and among researchers and practitioners (Holderegger et al. 2019; Kadykalo et al. 2021).

Geographic bias in focal groups

Congruent to results reported in Gardner et al. (2007), studies on amphibians were more abundant than studies on reptiles. Over the past years, there has been a strong focus on amphibian population declines. This was catalysed by the emergence of chytridiomycosis and global decline of amphibians (Fisher and Garner 2020). Amphibians, and predominantly frogs, are the principal focus of herpetological research, with the highest allocation of resources and the highest publication rates (Ferronato 2019). Another reason for this bias may be that amphibians serve as valuable indicators of environmental stress and degradation owing to their aquatic and terrestrial lifestyle and permeable skin (Green 2003). These attributes make them extremely sensitive to changes in temperature and precipitation as well as pollution (Sodhi et al. 2008). Lizards, also susceptible to temperature changes, however, are characterised by a high degree of endemism, restricted geographic ranges, late maturity, a long life-span and are thus very susceptible to population declines (Todd et al. 2010; Meiri et al. 2018). Certain groups of reptiles, such as worm lizards and blind snakes lead cryptic and solitary lives in contrast to the large breeding aggregations and choruses of, for example, frogs. Such characteristics make them difficult for researchers to study as they require large amount of search effort for little data (Thompson 2013).

Taxonomic bias

We found a heightened geographical bias in the taxonomic coverage of studies. Given the sheer number of selected papers investigated, it is not surprising that the continents of North and South America cover more than half of the amphibian species studied whereas North America and Africa cover almost half of the reptile species studied. This trend broadly mirrors the geographic distribution pattern of the global described species in both these taxa (AmphibiaWeb 2021; Uetz et al. 2021). While a large proportion of the known European and North American families such as Alytidae and Ambystomatidae have been investigated (Fig. 4), species from other continents remain severely under-represented. Yet, the European continent represents only 2% of the described species globally. This high research intensity bias in low biodiverse regions of the world has been noted previously (Fazey et al. 2005). In general, reptiles and amphibians have been disproportionately poorly studied in the tropics and in developing areas despite that these areas show among the highest rates of deforestation and a corresponding rise in the number of threatened species (Böhm et al. 2013; Deikumah et al. 2014). These biodiverse areas largely consist of threatened species having restricted home ranges (Meiri et al. 2018). Even though we observed a great fraction of the species investigated in the Afrotropics (Vallan 2002; Hillers et al. 2008; Ofori-Boateng et al. 2013; Riemann et al. 2015; Blumgart et al. 2017), especially Madagascar (see Mantellidae and Opluridae in Fig. 4), it seems insufficient when considering that an estimated 3.94 million hectares of forest area of the continent was cleared yearly over the last century (FAO and UNEP 2020). Further, biodiverse hotspots such as the neotropical regions and Indo-Malayan tropics have the highest chances of new species of amphibians and reptiles being discovered (Moura and Jetz 2021).

Being herpetofauna diversity hotspots, countries in South America and Asia are indeed understudied. Although Brazil has a high number of amphibian studies, less than one percent of known reptile species was studied in both continents (Fig. 2). A number of factors contribute to this lack of representation. First, there is an overwhelming number of new species being discovered every year in these hotspots (Moura et al. 2018; Moura and Jetz 2021). Furthermore, newly discovered species tend to belong to more secretive groups such as burrowing snakes, worm lizards and caecilians (Colli et al. 2016). Yet, these fossorial organisms are clearly neglected in fragmentation studies (see Fig. 4–5) with researchers focusing on well-known taxonomic groups (Böhm et al. 2013). On a positive note, despite having the country (Australia) with the highest reptile diversity (Uetz et al. 2021), Oceania represented a fair coverage of reptile diversity compared to other continents. Since 2001, there has been an increase of fragmentation studies in Australia (e.g., Brown 2001; Mac Nally and Brown 2001; Hazell et al. 2001) and there is a continuing increase in research output (Melles et al. 2019), contributing 85 out of 89 reviewed studies in Oceania over the last 30 years.

Extent and focus of research

Our findings showed important associations between methods and response metrics but not different forms of habitat fragmentation. This either suggests that researchers were not favouring any sampling method and response variable for evaluating the effects of certain habitat fragmentation or this pattern may occur due to a relatively even split of papers dealing with different forms or combinations of habitat fragmentation in the clusters. In general, species richness or diversity appears to explain most of the variation in our data (see Online Appendix 4**).** While species richness remains a popular diversity metric employed in conservation biology (Online Appendix 12; also see Gardner et al. 2007), we also found an increasing trend in the use of genetic techniques for habitat fragmentation studies. More specifically in recent years, molecular genetics have become popular and are often studied together with population connectivity to capture species responses to habitat fragmentation (see Online Appendix 4) (Keyghobadi 2007). The HCPC approach identified three main clusters of research fields which will be referred to as research agendas from here onwards. Contrary to our expectation, we did not find a global spatial pattern of research agendas, but instead a rather homogeneous distribution of papers, possibly due to the lack of selected studies which are found in developing countries outside USA, Europe and Australia (Figs. 7, 8). This nevertheless indicates that different sampling methods are shared and used between leading herpetological experts from different countries and that there are continuing collaborations between countries, particularly in North America and Europe.

Below, we describe the research agendas and their corresponding categories (Fig. 6) that have contributed significantly to the study of habitat fragmentation for the past 30 years: (a) Agenda 1: Measures of direct individual species responses, (b) Agenda 2: Physiological and movement ecology, and (c) Agenda 3: Technology advancement in conservation research.

Agenda 1: Measures of direct individual species responses

We found that the majority of studies around the globe evaluated patterns of assemblage richness, species presence/absence, and abundance (Figs. 7, 8). These simple patterns of richness, diversity and abundance are the most common responses measured because they provide a good indication of species response to habitat fragmentation and are easy to calculate (Colwell 2009). Although species richness does not consider abundance or biomass but treats each species as of equal importance to diversity, species evenness weighs each species by its relative abundance (Hill 1972). Further, composite measures like species diversity indices (e.g., Simpson's 1/D or Shannon's H) combine both richness and evenness in a single measure (Colwell 2009), preventing biases in results. However, directly measuring these species responses might not be ecologically relevant as they fail to account for patterns in species assemblage turnover. In fact, few selected papers (38 out of 697) in our study have attempted to categorise species into meaningful functional groups or guilds, despite that the categorisation of ecological functions such as habitat preference, taxonomic family, reproductive mode, and body size can be easily done (but see Knutson et al. 1999; Peltzer et al. 2006; Moreira and Maltchik 2014). Knutson et al.(1999) was the first in our selected papers to group species with similar life-history characteristics into guilds and to examine their responses to landscape features. They observed negative associations between urban land use and anuran guilds. Analyses of guilds or functional groups can reveal contradictory results (but not always, see Moreira and Maltchik 2014). For example, the species richness of anurans in logged areas of West Africa is found to be as high as in primary habitat (Ernst et al. 2006). Yet, analyses of functional groups indicated significantly higher diversity in primary forest communities (Ernst et al. 2006). Similar differences were also observed for species with varying degrees of niche overlaps, habitat specialists, and for different continents (Ernst et al. 2006; Seshadri 2014). These results underline that species richness alone is a poor indicator of the functional value of species in the ecosystem as the relationships between functional diversity and species richness are inconsistent and can sometimes be redundant (functional diversity remains constant if assemblages are functionally similar; Riemann et al. 2017; Palmeirim et al. 2017; Silva et al. 2022). The results of some species richness studies may consequently provide misleading inferences regarding consequences of habitat fragmentation and conservation management (Gardner et al. 2007).

Although not substantially greater than the agendas 2 and 3, the measure of individual species responses has always been popular across the globe but also increasingly popular in the tropical and subtropical regions (e.g., South America and Africa; Online Appendix 10–11). For example, a research team led by Mark-Oliver Roedel from Germany has conducted numerous studies on Afrotropical amphibian communities (Hillers et al. 2008; Ofori-Boateng et al. 2013; Riemann et al. 2017). Due to the higher biodiversity and species rarity in these regions compared to temperate areas, it is reasonable to expect a greater level of sampling effort in patterns of species richness, abundance, and guild assemblage to obtain comparisons of diversity with sufficient statistical power across different land use changes (Gardner et al. 2007). Access to highly specific expertise and most up to date methods and technology may not be available in these regions, and as such, study designs are limited to multispecies survey addressing simple patterns of diversity and species assemblages (Hetu et al. 2019). Unfortunately at the same time, these forest biomes holding the highest richness and abundance of amphibians and reptiles have showed consistent negative responses to land use changes (Cordier et al. 2021).

Agenda 2: physiological and movement ecology

We did not observe a strong association between occupancy and dispersal in our study. Perhaps this is because only a few papers investigated dispersal via habitat occupancy compared to the overwhelming proportions of papers examining the presence of species in response to habitat fragmentation in research agenda 1. Similarly, few studies measure dispersal with direct tracking methods, with the majority that discussed dispersal being based on indirect inferences, such as genetic divergence (see Fig. 3c, d; Driscoll et al. 2014). Genetic approaches can be effective in situations where more direct approaches are not possible (Lowe and Allendorf 2010). For instance, using microsatellites and mitochondrial DNA, Buckland et al. (2014) found no migration occurring between isolated subpopulations of a forest day gecko (*Phelsuma guimbeaui*) in a fragmented forest and predicted a dramatic decrease in survival and allelic diversity in the next 50 years if no migration occurs (Buckland et al. 2014). In some cases, molecular markers also allow direct dispersal studies by assigning individuals to their parents or population of origin (Manel et al. 2005). However, there are limitations on when these techniques can be applied. Assignment tests require appropriate choices of molecular markers and sampling design to permit quantification of indices of dispersal (Broquet and Petit 2009; Lowe and Allendorf 2010). Parent–offspring analysis is constrained by the uncertainty in assessing whether offspring dispersal is completed at the time of sampling and sample size (Broquet and Petit 2009). Genetic tools may thus be best applied in combination with direct approaches because they contain complementary information (Lowe and Allendorf 2010; Safner et al. 2011; Smith et al. 2016).

Traditional approaches in habitat fragmentation research like radiotracking or capture-mark-recapture of animals can be effective in evaluating dispersal and ecological connectivity between populations. For example, based on mark-recapture data over a nine year period, facultative dispersal rates in an endangered amphibian (*Bombina variegata*) were found to be sex biased and relatively low from resulting patch loss (Cayuela et al. 2018). In our case, direct tracking methods are more commonly and effectively used in examining the impacts of habitat modification on changes in ecology directly relating to fitness (Fig. 6): home ranges (Price-Rees et al. 2013), foraging grounds (MacDonald et al. 2012) and survival rates (Breininger et al. 2012). Yet, such routine movements associated with resource exploitation do not reflect the biological reality and evolutionary consequences of how organisms change as landscape changes (Van Dyck and Baguette 2005). Instead, directed behavioural movements affecting dispersal processes (emigration, displacement or immigration) are crucial in determining the functional connectivity between populations in a fragmented landscape (Bonte et al. 2012). In one study, spotted salamanders *Ambystoma maculatum* tracked with fluorescent powder exhibited strong edge mediated behaviour when dispersing across borders between forest and field habitats and can perceive forest habitats from some distance (Pittman and Semlitsch 2013). Knowing such behaviour rules can improve predictions of the effects of habitat configuration on survival and dispersal. However, ongoing conversion of natural ecosystems to human modified land cover increases the need to consider various cover types that may be permeable to animal movements. As such, experimental approaches can be effective in examining the effect of matrix type on species movements as seen in our results (Fig. 6) (Rothermel and Semlitsch 2002; Mazerolle and Desrochers 2005). For example, researchers conducted experimental releases of post-metamorphic individuals of forest amphibians into different substrates and mapped the movements of paths and performance (Cline and Hunter Jr 2016). They showed that non-forest matrices with lower structural complexity influence the ability of frogs to travel across open cover and to orient themselves towards the forest from distances greater than 40–55 m. Therefore, it is inaccurate to assume matrix permeability to be uniform across all open-matrix types, particularly in amphibians (Cline and Hunter 2014, 2016).

In addition, the ability to move and disperse is highly dependent on the range of external environments and internal physiological limits (Bonte et al. 2012), especially in reptiles and amphibians (Nowakowski et al. 2017). The study of physiological effects on movement was seen throughout our selected studies (Fig. 6). For example, higher temperatures and lower soil moisture in open habitats could increase evaporative water loss in salamanders (Rothermel and Semlitsch 2002). Other tests including interaction effects between landscape configuration and physiological constraints (e.g., dehydration rate Rothermel and Semlitsch 2002; Watling and Braga 2015); body size (Doherty et al. 2019) can be useful to better understand fitness and population persistence. We argue here that multidisciplinary projects examining movement physiology, behaviour and environmental constraints in addition to measuring distance moved are needed to progress this field.

Our results indicate a high bias of agenda 2 papers represented among developed countries, with a strong focus on reptiles compared to amphibians (Price-Rees et al. 2013; Doherty et al. 2019) (Online Appendix 12, Figs. 7, 8). The adoption of direct tracking as well as genetic methods can be cost prohibitive in developing and poorer regions. However, cheaper and simpler methods to track individuals are increasing (Mennill et al. 2012; Cline and Hunter 2014, 2016). Although existing application might not be ideal for reptiles and amphibians, new technologies for tagging and tracking small vertebrates are being developed including acoustic surveys and improved genetic methods (Broquet and Petit 2009; Mennill et al. 2012; Marques et al. 2013). While there are many improvements needed to obtain better quality dispersal data studies on movement ecology, reptiles and amphibians still only account for a mere 2.2% of the studies on dispersal when compared to plants and invertebrates which comprised over half of the studies based on a systematic review (Driscoll et al. 2014). Thus, we urge more studies to be conducted on these lesser-known taxa, especially in biodiverse regions. Given the limited dispersal in amphibians and reptiles, having a deeper understanding on their dispersal can be critical for the effective management and conservation of populations and metapopulations (Smith and Green 2005).

Agenda 3: technology advancement in conservation research

While community level approaches such as responses in species richness, occupancy, and abundance measure biodiversity response to habitat fragmentation, they are limited in inference because they do not reflect patterns of fitness across environmental gradients and landscape patterns. Instead, genetic structure at the population level can offer a higher resolution of species responses (Manel and Holderegger 2013). For instance, genetic erosion heavily affects the rate of species loss in many amphibian species (Allentoft and O'Brien 2010; Rivera-Ortíz et al. 2015). Over the past decades we have seen a rapid increase in studies applying genetic analysis to assess the effects of habitat fragmentation (Keyghobadi 2007), reflecting the strength of these approaches. This growth is mostly evident in North America and Europe (but also Oceania for reptiles) (Online Appendix 10–11). The availability of different genetic markers has been increasing, from microsatellites in the 1990s then shifting towards genotyping by sequencing (NGS) technologies that enable rapid genome-wide development (Allendorf et al. 2010; Monteiro et al. 2019). However, the study of population structure alone can lead to misleading results as environmental changes to species dynamics are not considered. The resistance imposed by landscape features on the dispersal of animals can ultimately shape gene flow and genetic structure (Bani et al. 2015; Pilliod et al. 2015; Monteiro et al. 2019).

To understand this, researchers combine genetic, land cover and climate variables to study the gene flow patterns across heterogeneous and fragmented landscapes (Manel and Holderegger 2013). Spatial analyses can be a powerful tool for monitoring biodiversity by quantifying environmental and landscape parameters. The growing interest in both land-cover data and the rapid development of computer processing power prompted the development of new prediction methods, primarily in spatial models (Ray et al. 2002), ecological niche modelling (Urbina-Cardona and Loyola 2008; Tan et al. 2021), and landscape connectivity (Cushman et al. 2013; Ashrafzadeh et al. 2019). In some cases, niche models are useful in assessing the effectiveness of protected areas for endangered species (Urbina-Cardona and Loyola 2008; Tan et al. 2021).

The integration of genetic data in ecological niche models for recognising possible dispersal movements between populations were observed in our study (Fig. 3c, d), especially in reptiles (Fig. 6b). The hallmark of landscape genetics is the ability to estimate functional connectivity among populations and offer empirical approach of adaptive genetic variation in real landscapes to detect environmental factors driving evolutionary adaptation. The most common approach of landscape genetics is determining whether effective distances as determined by the presence of suitable habitat between populations, better predict genetic distances than do Euclidean distances (assuming spatially homogeneous landscape). However, straight-line geographic distance does not normally reflect true patterns of dispersal as landscape barriers or facilitators in a heterogeneous landscape could strongly affect gene flow (Emel and Storfer 2012; Fenderson et al. 2020). Therefore, in these cases, ecological distances or landscape resistance can often explain a greater deal of genetic variation between fragmented populations (Cushman 2006; Bani et al. 2015). Using a combination of habitat suitability modelling (e.g., Maxent, Phillips et al. 2017), multiple least-cost paths (LCPs) (Adriaensen et al. 2003) and the more recent circuit theory analysis (McRae et al. 2008) to investigate landscape resistance can be highly effective predicting potential pathways along which dispersal may occur, hence informing conservation management (Emel and Storfer 2012; Bani et al. 2015; Pilliod et al. 2015). To date, landscape genetics has been shown to be particularly useful in studying organisms with complex life histories (Emel and Storfer 2012; Shaffer et al. 2015). Yet, the applications of landscape genetics have been limited to contemporary patterns using modern genetic data. Few studies have benefitted from the inclusion of temporal genetic data (Fenderson et al. 2020). For example, historical DNA samples and heterochronous analyses could allow us to explore how anthropogenic impacts have affected past genetic diversity and population dynamics (Pacioni et al. 2015) and identify areas of future suitability of endangered animals in face of climate change (Nogués-Bravo et al. 2016). The possibility to investigate migration through spatiotemporal population connectivity can greatly improve the prediction of species responses under future landscape and climate change scenarios (Fenderson et al. 2020).

Population genetic and niche modelling studies for both taxa are rarely found in developing regions of the world, especially in Asia and Africa (Figs. 7, 8). Even though conservation priorities are concentrated in these biodiverse regions, invaluable highly specific expertise such as conservation genetics and other contemporary methodologies might not be readily available due to lack of funding and infrastructure (Hetu et al. 2019). Thus, we encourage collaborations with the poorer countries initiated by foreign service providers from developed countries. Contrary to expectations, very few studies on conservation genetics were found in China and Japan despite their vast advances in genetic techniques. Fortunately, China has made substantial progress in the last 20 years in understanding human genetic history and interpreting genetic studies of human diseases (Forero et al. 2016) as well as biodiversity conservation (Wang et al. 2020), yet the same cannot be said for conservation genetics on reptiles and amphibians (Figs. 7, 8), but see Fan et al. (2018) and Hu et al. (2021).

Limitations and knowledge gaps

(1) The forms of habitat fragmentation which we categorised may not reflect the ecological impact in the real world as interactions between different habitat fragmentation forms were not accounted for. Although each of these forms of habitat fragmentation possesses serious environmental consequences, their combination could have severe synergistic impacts (Blaustein and Kiesecker 2002). For example, a fragmented landscape is not just reduced and isolated, but subject to other anthropogenic disturbances such as hunting, fire, invasive species, and pollution (Laurance and Useche 2009; Lazzari et al. 2022). Altered climatic conditions and emerging pathogens such as batrachochytrids can also interact with each other, and other threats (Fisher and Garner 2020). The use of habitat suitability models based on climatic scenarios, combined with hydrological and urbanisation models, are effective in detecting best to worst case scenarios and local extinctions, as shown for the spotted marsh frog (*Limnodynastes tasmaniensis*) (Wilson et al. 2013).

(2) We acknowledge the bias of scientific research introduced from the limitation of search term to English-speaking literature on the geographic distribution of the papers we sampled (Konno et al. 2020; Angulo et al. 2021). In Latin American journals for example, we found a number of papers published in Spanish, but unfortunately, they did not fit the criteria of our selection (see Online Appendix 2). Conservation studies written in languages other than English are often published in local journals which do not normally go through international peer review.

(3) The homogeneous distribution of the research agendas across geographical regions in our study may be explained by the lack of studies found in South America, Asia and Africa, preventing us to see a potentially dichotomous spatial pattern among the clusters. However, this reflects the current state of research and the challenges faced in less developed countries.

(4) Our study did not investigate whether habitat fragmentation has led to an improved or decreased biotic response. Predicting species response to habitat modification has been reviewed countless times (Rytwinski and Fahrig 2012; Driscoll et al. 2014; Doherty et al. 2020; Newbold et al. 2020; Cordier et al. 2021). Yet, these reviews often yield little or no general patterns (Doherty et al. 2020; Cordier et al. 2021). Response variables or traits measured are often found to be poor predictors of the impacts of habitat fragmentation. There are two possible explanations for this discrepancy. First, the strength and direction of the responses differs between species, ecophysiological groups (Rothermel and Semlitsch 2002), and phylogenetic or functional groups (Mazerolle and Desrochers 2005; Nowakowski et al. 2017). Second, responses in animals to different types of disturbance may be specific to the ecosystem where they live. Different biogeographic regions or biomes have

different characteristics affecting local species (Lindell et al. 2007; Blowes et al. 2019; Newbold et al. 2020; Cordier et al. 2021).

Conclusions and recommendations

(1) Our results underline promising research fields and geographic areas and may serve as a guideline or starting point for future habitat fragmentation studies. We suspect similar paradigms of geographic and thematic patterns to occur in other taxonomic groups.

(2) Although studies dealing with habitat fragmentation impacts on mammals and birds are already widely recognised (Fardila et al. 2017), research on reptiles and amphibians has been lacking. We argue that amphibians and reptiles need more attention as they are equally or more threatened but highly neglected (Rytwinski and Fahrig 2012; Ferronato 2019; Cox et al. 2022).

(3) Greater investment is required for studies in tropical and subtropical areas (Segovia et al. 2020), especially within the Asian continent. These areas are currently experiencing the highest rates of habitat loss (McDonald et al. 2013). Tropical specialists are further restricted to smaller geographic range sizes according to Rapoport's rule which states that there is a positive latitudinal correlation with range size (Stevens 1989) (at least for amphibians in the Northern hemisphere where there is higher temperature and precipitation seasonality; Whitton et al. 2012). Having a small range size is often associated with negative responses to habitat modification (Doherty et al. 2020). Thus, more effort is needed in developing countries where the crisis is greatest and there is lack of funding and strong language barriers (Fazey et al. 2005). There is an urgent need to better integrate studies published in languages other than English with the broader international literature. Useful integration actions include training of local conservation biologists and promoting partnerships and research visits in these regions may have greater conservation consequences to understand global patterns of habitat modification (Meyer et al. 2015). Doing so will help remediate the sampling bias towards temperate generalists and will shed light on the fate of tropical specialists.

(4) We encourage improved access to intermediary evidence-based conservation data (Kadykalo et al. 2021). Even when well-established genetic and genomic analyses have been proven to be promising area in herpetological conservation (Shaffer et al. 2015), there is a general lack of the transfer of knowledge between scientists and practitioners (Holderegger et al. 2019). As practitioners are generally interested in species monitoring and the evaluation of success of connectivity measures, an establishment of scientist-practitioner community to facilitate a platform for international exchange would help tremendously in future conservation planning and management (Holderegger et al. 2019).

(5) Although different study designs and landscape measures have different strengths and limitations depending on the study objectives, we suggest reporting basic data to describe the effect of habitat fragmentation using standardised sampling methods, indices, and design (Holderegger et al. 2019). The results will allow future meta-analyses to be performed.

(6) Incorporate remote sensing data, whenever possible, in studies involving habitat change and fragmentation. The use of niche modelling techniques combined with high resolution remote sensing has been instrumental in detecting potentially fragmented populations. With advances in landscape genomics, we are now able to examine the correla-

tion between environmental factors and genomic data in natural populations (Manel and Holderegger 2013; Shaffer et al. 2015). Adopting such tools would be valuable in understanding how habitat amounts and configurations affect dispersal, survival, and population dynamics as well as the impacts of anthropogenic changes such as climate change (Shaffer et al. 2015).

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Data availability The datasets generated during the current study are available in Online Appendix 1. Codes used in the analyses are available from corresponding author on request.

Declarations

Competing Interests The authors declare no conflicts of interest.

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A present and future assessment of the effectiveness of existing reserves in preserving three critically endangered freshwater turtles in Southeast Asia and South Asia

Wei C. Tan[1]*, Philipp Ginal[1], Anders G.J. Rhodin[2,3], John B. Iverson[4] and Dennis Rödder[1]

[1] Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D – 53113 Bonn, Germany; [2] Chelonian Research Foundation, Arlington, Vermont 05250, USA; [3] Turtle Conservancy, Ojai, California 93023, USA; [4] Department of Biology, Earlham College, Richmond, Indiana 47374, USA.
*Correspondence: Wei Cheng Tan, N.Tan@leibniz-zfmk.de

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Abstract

Tortoises and freshwater turtles are among the most threatened taxa of vertebrates in the world due to consumption, urban development, agriculture, and land and water pollution. About 50% of the currently recognised chelonian species are considered threatened with extinction according to the IUCN Red List. Asia is an epicentre for the turtle and tortoise extinction crisis, containing the highest diversity of threatened species. In this study, we used species distribution models (SDMs) to assess the effectiveness of existing protected areas across Southeast and South Asia for the conservation of three large critically endangered freshwater turtles (*Batagur borneoensis*, *B. affinis,* and *Pelochelys cantorii*). We derived the models based on selected bioclimatic variables at the sites of known species records. Our SDMs showed that Indonesia is of particular importance in prioritising conservation for these three species, containing the largest areas of suitable habitat within protected areas. However, when considering water surface coverage, Thailand has the highest proportion of suitable areas under protection. Our results suggest that the present cover of protected network reserves seems inadequate in terms of size and should be expanded to sustain populations of the three target species. Therefore, we identified priority areas and reserves critical for further field surveys to guide the potential discovery of novel populations. To investigate the effect of climate change, we also projected potential distributions onto ensembles of four IPCC story lines. As a result, we found larger extralimital areas of suitable environment for all three species, particularly northwards and inland. However, high degrees of uncertainty in climate conditions indicate few reserves may provide long term protection. Lastly, we review the threats and propose recommendations for conservation of these poorly known freshwater turtles.

Highlights

- Species distribution models (SDMs) are useful tools to predict the distribution of rare species.
- We performed SDMs using bioclimatic variables and water surface cover to assess whether existing reserves are effective in the conservation of three critically endangered freshwater turtle species.
- Indonesia and Thailand are countries of major importance in preserving these threatened species, although current established reserves might be insufficient.
- We proposed several priority conservation areas where the species could potentially occur.
- Future projection models suggest an expansion of suitable habitat inland and northward in response to climate change, despite uncertainty due to extrapolation outside the training range of the models.

Keywords: climate change, conservation, endangered species, IUCN, protected areas, species distribution modelling, Testudines, water cover

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Introduction

Habitat loss due to land use changes is a significant factor leading to the decline of global biodiversity (Foley et al. 2005). South Asia and Southeast Asia have among the fastest rates of deforestation and habitat loss, with over 50% of native forest being depleted over the last two centuries (Sodhi et al. 2004). This, combined with poaching, illegal pet trade, and land degradation, has resulted in habitat fragmentation as well as other negative impacts on the native biodiversity.

Of the 356 species of turtles and tortoises recognised globally, about a quarter are found in Asia (Turtle Taxonomy Working Group [TTWG] 2017), making this region one of the species richness hotspots for turtles (Buhlmann et al. 2009, Ihlow et al. 2012, Mittermeier et al. 2015). However, the Asian continent is also a hotbed for turtles facing extinction since it harbours 17 of the 25 (68%) most threatened chelonian species (Turtle Conservation Coalition [TCC] 2018, Rhodin et al. 2018). Vietnam, India, and Indonesia are among the top five countries with the highest number of threatened chelonians. To date, seven species and three subspecies (2.1% of all modern turtle taxa) have already gone extinct (TTWG 2017, TCC 2018).

Predictions for future climate change from the Intergovernmental Panel on Climate Change (IPCC) suggested that 86% of all turtle species will be pushed out of their current realized niche by 2080 (Ihlow et al. 2012). In this study, we evaluated the availability of suitable habitats of three poorly known freshwater turtles. The large river turtles of the genus *Batagur* (Gray 1856) are one of the two most critically endangered turtle genera (next to Asian box turtles, *Cuora* [Gray 1856]), accounting for five of the Top 25 threatened species (TCC 2018).

The Painted Terrapin (*Batagur borneoensis* [Schlegel and Müller 1845]) is a large river turtle that was once widely distributed in the Sundaland region, occurring from southernmost Thailand southward through Peninsular Malaysia to the islands of Sumatra and Borneo (TTWG 2017). Once common, only three rivers in Peninsular Malaysia are believed to have more than 100 remaining nesting females, while a few other populations have less than 50. The species inhabits estuaries of medium to large rivers and mangrove swamps. Females tend to move from freshwater to oceanside beaches to nest (Dunson and Moll 1980).

The Southern River Terrapin (*Batagur affinis* [Cantor 1847]) was considered to be part of the species *Batagur baska* in South Asia until DNA sequence analysis demonstrated that the latter comprised at least these two genetically distinct species (Praschag et al. 2008). This recently described species is also a large river turtle found along the coasts of Peninsular Malaysia, eastern Sumatra, southernmost Thailand, and Cambodia, where a relic population persists (Platt et al. 2003, Moll et al. 2015). It has been suggested that *B. affinis* was historically distributed in all major rivers draining into the South China Sea (Moll et al. 2015). The species inhabits tidal regions of large rivers in coastal waters and estuaries, but unlike *B. borneoensis*, females prefer to migrate upriver to nest on sandbanks exposed after the monsoon season (Moll et al. 2015).

The Asian Giant Softshell Turtle (*Pelochelys cantorii* [Gray 1864]) has recently been provisionally assessed as critically endangered by the Tortoise and Freshwater Turtle Specialist Group (Rhodin et al. 2018). This species is a very large freshwater turtle with arguably the widest distribution of all non-marine turtles (Das 2008). It is remarkably widespread, occurring from southwestern Peninsular India to Southeast Asia and China and the western Indonesian and Philippine archipelagos. It was suggested by Taylor (1970) that its distribution might have been shaped by past human introductions as food during transportation, but this appears highly unlikely (Das 2008). Its widespread distribution along coastlines and across island archipelagos appears to be due to its tolerance of salt water. The species occurs in a variety of habitats, including lakes, rivers and seacoasts. Females are known to nest on sandbars alongside deep pools or ocean beaches (Das 2008).

Populations of these three turtle species have been severely depleted throughout their range and have disappeared from much of their former ranges (TCC 2018). *Batagur affinis* is considered to be extinct in the wild in Thailand, Vietnam and Singapore (Moll et al. 2015) while populations of *P. cantorii* appear to be locally extinct in China and Vietnam (Das 2008). Habitat destruction and alteration such as sand mining, hydropower dams, and urban construction have greatly affected nesting and feeding sites (Moll and Moll 2000, TCC 2018). Large scale agro-based plantations and the associated pollution have degraded the riparian vegetation on which these species rely. On top of that, trade in southeast Asian freshwater turtles has increased drastically in the past 30 years. They have been heavily exploited and exported for eggs and flesh for human consumption (Moll and Moll 2000, van Dijk 2000, CITES 2010). Wild *B. borneoensis* are also prized in the pet trade for their highly attractive colouration during the mating season (TCC 2018).

Established Protected Areas exist in many parts of southern and southeastern Asia. However, there is a lack of assessment of their effectiveness in sustaining viable populations of threatened turtle species. Species distribution modelling (SDM) based on the climatic niche of target species and land cover layers provides a reliable mechanism to assess the suitability and effectiveness of reserve networks (Araújo et al. 2004, 2007, Hannah et al. 2007, Ihlow et al. 2014). The survival of freshwater turtles largely depends on riparian habitats, including rivers, streams and estuaries (Moll and Moll 2004). We therefore assess the water surface cover to refine our predictions of where the three target species should thrive within protected reserves. Here, we sought to 1) compare the potential suitable habitat to each species' currently known historic range; 2) identify the areas of suitable habitat within current reserves; 3) based on water coverage, assess where the best areas are for prioritising future conservation efforts; and 4) assess the impact of climate change by using climate and socioeconomic projections for the year 2080 to project future changes in habitat suitability and in reserve areas from (3). We conclude by discussing whether current Protected Areas are sufficient to protect these critically endangered species.

Materials and Methods

Species records and climate data

Coauthors AGJR and JBI provided historic locality records for *Batagur borneoensis* (25), *B. affinis* (18), and *Pelochelys cantorii* (28), based on museum and literature records and unpublished data as well as their presumed historic indigenous distribution ranges (TTWG 2017, in press). We obtained information on current climate conditions from the Worldclim database, version 2.1, derived from climate conditions recorded for 1970-2000 with a spatial resolution of 2.5 arc minutes (Fick and Hijmans 2017, www.worldclim.org). We then computed a set of 19 bioclimatic variables derived from the monthly temperature and precipitation patterns. These variables, describing annual trends, seasonality and extreme environmental factors, are suggested to yield biologically meaningful results as they characterise the availability of water and energy throughout the year and thus are suitable predictors in SDMs (Busby 1991). We used a Mantel correlogram from the *ecospat* package v3.1 for R to determine potential spatial autocorrelation of environmental covariables within a set of occurrences as a function of distance (Broennimann et al. 2020). We further removed occurrences too close to each other using species occurrence thinning function from *spThin* package v0.2.0 for R (Aiello-Lammens et al. 2015). This is a robust function to reduce spatial biases and unevenness. We then used the remaining set of records (*B. borneoensis* [19], *B. affinis* [12], and *Pelochelys cantorii* [26]) after thinning for subsequent SDM computation.

To project future changes in distributions with respect to climate change, we used four shared socioeconomic pathways (SSPs: 126, 245, 370 and 585), which are emission scenarios driven by different socioeconomic assumptions. We chose the future period of 2081–2100, comprising an average of monthly values for the 19 bioclimatic variables. Due to uncertainty in forecasting future climate, we computed the average of eight global climate models (GCMs) that simulated the impact of climate scenarios: BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0, downloaded from WorldClim at 2.5arc minute resolution to provide a non-biased future climate prediction.

Species distribution models

In interpreting a model, deciphering the driving variables is much simpler when variables have low correlation (Heikkinen et al. 2006). Therefore, using the *dismo* and *SDMtune* packages for R (Hijmans et al. 2017, Vignali et al. 2020), we assessed highly correlated variables and sequentially removed variables by performing a jackknife approach among correlated variables (based on Spearman rank correlations $|rs|\geq 0.7$) based on their percentage contribution to the model and TSS value. We repeated the process until the remaining variables had correlation coefficients less than 0.7. We then removed these resulting variables, which contributed less than 5% to initial SDMs when performing the models.

We used Maxent v3.4.1 (Phillips et al. 2006, 2017; available from http://biodiversityinformatics.amnh.org/open_source/maxent/) for SDM computation to assess the potential suitable habitats of the turtles. This program applies a machine-learning technique, which follows the principle of maximum entropy for modelling with presence-pseudoabsence data. It has been suggested that Maxent outperforms other established modelling methods such as generalised additive models and BIOCLIM, especially for low and biased sample sizes (Elith et al. 2006, Wisz et al. 2008, but see Peterson et al. 2007 on GARP). Results obtained from Maxent have been proven effective in predicting habitat suitability in poorly known species (Pearson et al. 2007), and reptiles and amphibians (Raxworthy et al. 2008, Ihlow et al. 2014).

Applying a bootstrap approach, we performed 100 replicates of Maxent runs with the standard settings (cloglog output format, 500 iterations, clamping) using the selected subset of climate variables. We used 90% of the records for model training and 10% for testing. To build models, we randomly created 10,000 pseudo-absences within a buffer of 200 km surrounding each species' presumed historic indigenous distribution range. These distributional areas were projected ranges based on GIS-defined hydrologic unit compartments (HUCs) with verified localities, and combined with HUCs that connected known point localities in the same watershed that had similar habitats and elevations as the verified HUCs (TTWG 2017, in press). They therefore provide suitable distribution backgrounds for these freshwater turtle species. The cloglog format creates potential suitable habitat values ranging from 0 (unsuitable) to 1 (optimal) along with the relative contribution of each bioclimatic variable as Maxent outputs.

To evaluate our models, we used Receiver Operating Characteristics (ROC) curves based on Area Under the Curve (AUC, Swets 1988). Values of AUC can range from 0.5 (when model predicts no better than random) to 1.0 (when model has perfect prediction). We also applied True Skill Statistics (TSS) to evaluate model performance (Shabani et al. 2018). TSS values ranges from -1 to +1, where +1 suggests perfect prediction, whereas values of zero or less suggest equal or lower performance than random. The minimum training presence threshold assumes that the lowest predicted suitability is the least suitable habitat in which the species may occur. Hence, for conservation purposes, we have chosen the minimum training presence threshold to assess suitability to avoid overprediction (Pearson et al. 2007). We subsequently used the average Maxent prediction across all 100 replicates as consensus map, which was reclassified using the minimum training presence as presence/absence threshold for further analyses.

The average model was projected on four different future scenarios, which were rescaled using the same threshold value. We performed multivariate environmental similarity surfaces (MESS; Elith et al. 2010) to identify the areas exceeding environmental training conditions under current and future scenarios within the projection layers.

Protected area network and water surface cover data

To assess the coverage of suitable turtle habitats with designated protected areas according to IUCN standard (criteria I, II, IV, V, VI), we downloaded polygons of protected areas from the World Database of Protected Areas (UNEP-WCMC and IUCN, 2020; https://www.protectedplanet.net/). These Protected Areas are clearly defined geographical areas, recognised, dedicated and managed to achieve long term conservation objectives and classified under the different objectives recognised by international bodies such as the United Nations as well as many national governments (Dudley 2008, IUCN 2020). We selected the following assigned categories: (Ia) Strict Nature Reserve, (Ib) Wilderness Area, (II) National Park, (III) National Feature, (IV) Habitat/ Species Management Area, (V) Protected Landscape/Seascape, (VI) Protected area with sustainable use of natural resources (more information available on https://www.iucn.org/). This assessment will help to identify future conservation areas and facilitate recommendations for improvements in existing reserve networks.

The incorporation of land cover data has been shown to perform better than using bioclimatic predictors alone (Cord and Rödder 2011). Freshwater turtles (especially our three target species) are strongly associated with water. We obtained high resolution (30-meter) water maps from Joint Research Centre Global Surface Water Mapping layers (Pekel et al. 2016; https://global-surface-water.appspot.com). The maps document the surface water present on the Earth's surface over 32 years using three million Landsat satellite images (Pekel et al. 2016). This presence of surface water (occurrence hereafter) gives the frequency of occurrence of water on land surface recorded in monthly time steps.

We then reclassified the original water occurrence to facilitate interpretation. We included only 100% occurrence (all monthly observations classified as water) and excluded other occurrences which were periodically under water or have never been under water. Since these turtles thrive in large meandering freshwater systems, we restricted our study to areas with only freshwater and land mass by cropping the coastline and using an inward buffer to exclude any uncertain seawater border strip of 90 m. Although *P. cantorii* appears to be tolerant of saltwater (Das 2008), a high-resolution salinity map was not available.

Using Maxent's output map as a base layer, we overlaid the water surface cover to exclude unsuitable areas lacking permanent water. Finally, we removed overlapping polygons of suitable areas in Protected Areas from the analysis to prevent computational redundancy. We conducted all spatial analyses with QGIS ver 3.12.2 (QGIS Development Team 2020) and R ver 4.0.2 (R Core Team 2020).

Results

We removed all auto-correlated occurrence records using spatial thinning in the radius of 20 km for both *Batagur borneoensis* and *B. affinis* and 50 km for *Pelochelys cantorii* based on the Mantel correlogram. The bootstrap of 100 Maxent models of the spatial extent gained good average AUC values for the three species (*B. borneoensis*: AUC_{test} = 0.9298, TSS = 0.6850; *B. affinis*: AUC_{test} = 0.7782, TSS = 0.3681; *P. cantorii*: AUC_{test} = 0.7305, TSS = 0.2606) (Table 1). AUC values suggest a high discrimination ability between suitable and unsuitable habitat. The minimum training presence threshold values in the training records of *B. borneoensis, B. affinis* and *P. cantorii* were 0.1473, 0.3541 and 0.2525, respectively (Table 1).

The variable contributions are presented in Table 1. In *B. borneoensis*, the environmental variable which contributed the most to the model (76%) was the "mean temperature of the driest quarter". The same pattern was also evident in *B. affinis* for the "minimum temperature of coldest month" (71.1%), followed by "annual mean temperature" (20.7%). In contrast, the "precipitation of driest quarter" (21.5%) and "temperature seasonality" (25.7%) contributed almost equally to the final model of *P. cantorii*, followed by "annual mean temperature" (16.2%), "mean temperature of warmest quarter"(12.5%), "mean diurnal range"(11.2%) and "precipitation of warmest quarter"(9.7%). We also provided Maxent lambda files for more details on the assessment of the variables used in the models (see Appendix S1).

Potential suitable habitats of *B. borneoensis* predicted by climate are mostly coastal areas comprising the estimated distribution by TTWG (2017) in Malaysia (Peninsular and Sarawak), Indonesia (Sumatra and Kalimantan) and a small area of southern Thailand. Other highly suitable habitats outside of the estimated distribution were identified in Sabah Malaysia and southern Sumatra, western Java, and the Philippines (Fig. 1b). However, only a small part of these potentially suitable habitats occurs within designated Protected Areas. The country with highest proportion of suitable surface area being protected is Indonesia (76%), followed by Malaysia (8%) and Thailand (7%) while the coverage is low (<5%) in other countries (Fig. 1c, Table 2). A ranking by water coverage in these suitable areas within reserves reveals that Thailand (65%) and Indonesia (26%) are of major importance compared to the other countries which contain less than 5% coverage (Table 3). Combining the estimated distribution of *B. borneoensis* and the water coverage of suitable habitat, highly important conservation areas applying IUCN standards were identified (Fig. 1d). These reserves include Selirong, Berakas Forest Reserves (both recreational and conservation) and Pulau Siarau Nature Reserve in

Table 1. Results of the relative variable contribution in 100 Maxent models and the evaluation metric (AUC and TSS) values computed for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*. Environmental variables had a spatial resolution of 2.5 arc minutes. Study regions had an extent from 93°E to 120°E and from -8°N to 15°N for *Batagur* spp. and from 72°E to 129°E and from -8°N to 32°N for *Pelochelys cantorii*.

Variable contribution (%)	*B. borneoensis*		*B. affinis*		*P. cantorii*	
	Mean	SD	Mean	SD	Mean	SD
Precipitation Seasonality (Coefficient of Variation)	12.18	8.51	8.22	15.50		
Precipitation of Warmest Quarter	11.51	4.82			9.36	7.33
Mean Temperature of Driest Quarter	76.32	10.40				
Annual Mean Temperature			20.65	24.29	16.18	13.75
Min Temperature of Coldest Month			71.13	32.46		
Mean Temperature of Warmest Quarter					15.50	12.49
Precipitation of Driest Quarter					21.54	9.65
Mean Diurnal Range (Mean of monthly (max temp - min temp))					11.73	11.22
Temperature Seasonality (standard deviation ×100)					25.68	12.86
Minimum training presence cloglog threshold	0.15	0.09	0.35	0.12	0.25	0.11
AUC training	0.95	0.02	0.80	0.06	0.85	0.03
AUC test	0.93	0.09	0.78	0.21	0.73	0.18
TSS	0.69	0.28	0.37	0.30	0.26	0.26

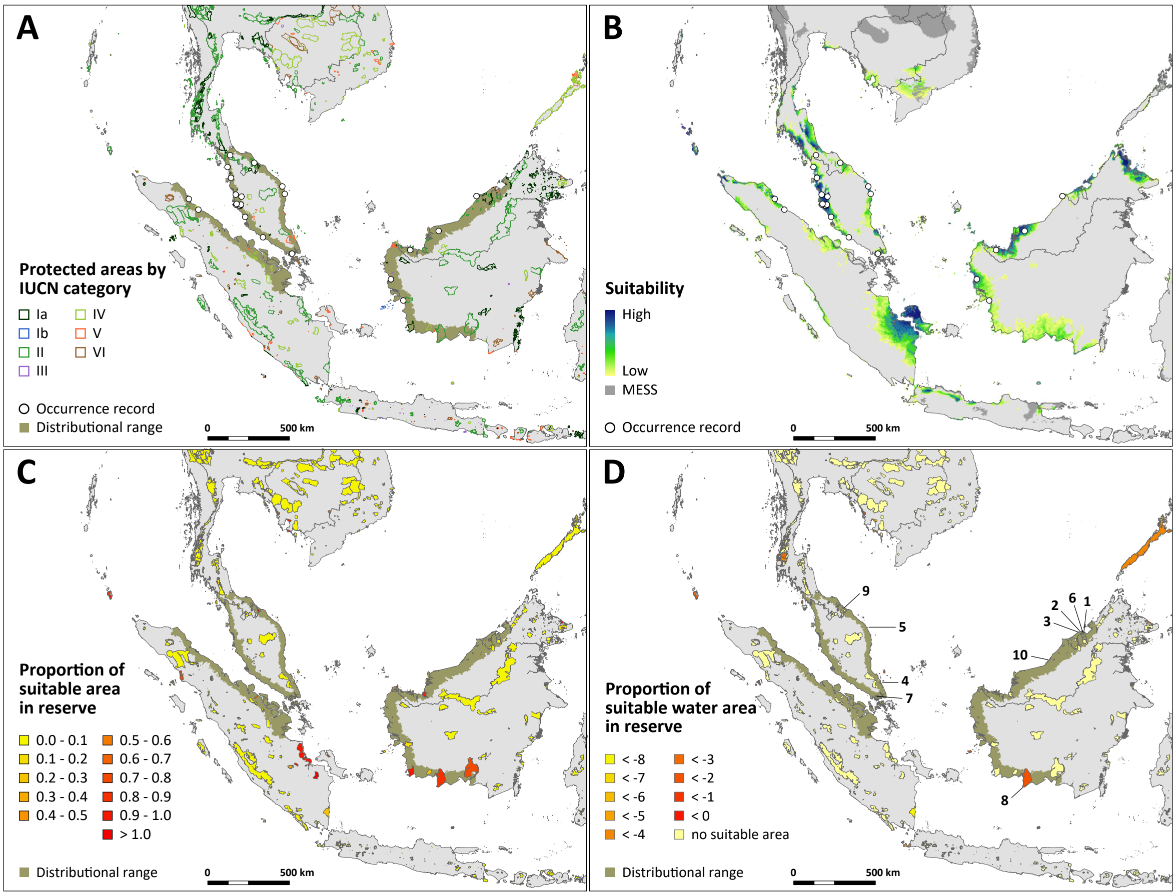

Figure 1. (A) The distribution of *Batagur borneoensis* estimated by TTWG (2017, in press) and the Protected Areas or reserves according to IUCN standards. **(B)** Potential distribution derived from the Maxent model ranging from high (blue) to low (yellow). **(C)** Potential suitable habitat within the reserves, ranging from high (red) to low (yellow). **(D)** Potential suitable water cover within the reserves ranging from high (red) to low (yellow). Proportions displayed are results of $\log_{10}$ computation. We labelled the reserves of top conservation priority based on the potential suitable water cover within the reserves found in the species estimated distribution. Information on these reserves can be found in Table 4.

Table 2. Proportions of suitable habitat within designated protected areas per country for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*.

Species	Country	Current (%)	Future scenarios (%)			
			ssp126	*ssp245*	*ssp370*	*ssp585*
Batagur borneoensis	IDN	76.37	44.78	41.26	38.66	37.73
	MYS	7.53	8.87	10.85	10.50	9.87
	THA	6.76	16.91	15.58	16.35	18.41
	PHL	2.85	5.53	9.86	8.18	7.29
	KHM	2.73	17.13	15.80	19.90	20.38
	IND	2.17	0.24	0.48	0.37	0.32
	BRN	1.07	0.55	0.88	0.81	0.71
	VNM	0.52	3.29	2.11	1.92	2.04
	SGP	0.01	0.01	0.03	0.02	0.02
	LAO	0.00	1.88	2.24	2.27	2.15
	MMR	0.00	0.81	0.90	1.01	1.07
Batagur affinis	IDN	61.65	42.86	38.56	38.29	38.37
	PHL	22.65	10.54	8.34	7.31	6.76
	MYS	8.14	11.29	10.69	10.04	9.63
	THA	2.73	12.86	15.61	17.87	19.12
	BRN	1.72	1.01	0.83	0.72	0.67
	KHM	1.36	16.97	20.63	20.26	19.69
	VNM	0.87	1.30	2.24	2.33	2.46
	IND	0.84	0.51	0.38	0.32	0.29
	SGP	0.05	0.03	0.02	0.02	0.02
	LAO	0.00	2.40	2.43	2.23	2.11
	MMR	0.00	0.22	0.28	0.62	0.87
Pelochelys cantorii	IDN	24.00	22.60	20.35	18.95	18.96
	PHL	18.45	9.05	11.07	11.54	11.51
	THA	12.60	2.70	7.15	9.73	11.81
	KHM	9.65	2.61	5.89	6.84	6.89
	LKA	8.85	7.73	6.47	5.34	4.86
	IND	8.24	23.88	19.05	17.38	15.85
	MYS	6.52	1.65	4.17	4.81	4.89
	VNM	3.40	5.06	4.29	3.97	3.85
	LAO	2.61	1.96	4.74	7.28	8.04
	MMR	1.96	13.32	9.98	8.59	8.07
	BGD	1.16	1.83	1.23	0.91	0.80
	TWN	0.93	1.17	0.90	0.79	0.78
	NPL	0.85	4.66	3.12	2.36	2.16
	JPN	0.33	0.53	0.35	0.26	0.31
	BRN	0.25	0.07	0.32	0.37	0.38
	CHN	0.15	0.61	0.44	0.37	0.33
	BTN	0.02	0.52	0.47	0.48	0.49
	SGP	0.02	0.03	0.02	0.01	0.01
	GBR	0.01	0.01	0.01	0.00	0.00
	MDV	0.00	0.00	0.00	0.00	0.00

Table 3. Proportions of suitable habitat containing water area cover existing within Protected Areas per country for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*.

Species	Country	Current (%)	Future scenarios (%)			
			ssp126	***ssp245***	***ssp370***	***ssp585***
Batagur borneoensis	THA	65.22	65.64	66.22	66.25	65.97
	IDN	25.84	14.25	14.15	14.15	14.09
	MYS	2.37	3.07	3.10	3.10	3.09
	KHM	2.06	0.82	0.82	0.82	0.82
	IND	1.76	0.70	0.71	0.70	0.70
	PHL	1.45	5.41	5.47	5.46	5.44
	BRN	1.31	0.52	0.52	0.52	0.52
	SGP	0.01	0.00	0.00	0.00	0.00
	MMR	0.00	5.43	5.49	5.48	5.46
	VNM	0.00	4.17	3.51	3.50	3.91
	LAO	0.00	0.00	0.00	0.00	0.00
Batagur affinis	THA	51.98	65.26	65.91	65.91	65.91
	IDN	27.85	14.56	14.08	14.08	14.08
	PHL	9.24	5.63	5.44	5.44	5.43
	MYS	5.99	3.19	3.08	3.08	3.08
	KHM	1.42	0.85	0.82	0.82	0.82
	VNM	1.41	3.61	4.00	4.00	4.00
	IND	1.21	0.73	0.70	0.70	0.70
	BRN	0.90	0.54	0.52	0.52	0.52
	SGP	0.00	0.00	0.00	0.00	0.00
	MMR	0.00	5.64	5.45	5.45	5.45
	LAO	0.00	0.00	0.00	0.00	0.00
Pelochelys cantorii	IDN	53.82	24.33	50.85	54.83	56.01
	IND	25.14	17.05	5.34	4.60	4.70
	PHL	10.65	27.14	31.07	29.41	28.42
	THA	6.26	19.82	8.09	7.17	7.03
	LKA	0.85	2.74	1.02	0.85	0.82
	JPN	0.74	2.76	0.86	0.74	0.71
	MMR	0.67	1.76	0.93	0.80	0.77
	VNM	0.59	1.00	0.37	0.34	0.33
	MYS	0.51	0.61	0.53	0.45	0.43
	GBR	0.35	1.45	0.45	0.39	0.37
	BGD	0.23	0.80	0.25	0.21	0.21
	KHM	0.11	0.45	0.14	0.12	0.12
	BRN	0.07	0.03	0.09	0.08	0.07
	MDV	0.01	0.05	0.02	0.01	0.01
	TWN	0.00	0.00	0.00	0.00	0.00
	SGP	0.00	0.00	0.00	0.00	0.00
	NPL	0.00	0.00	0.00	0.00	0.00
	BTN	0.00	0.00	0.00	0.00	0.00
	CHN	0.00	0.00	0.00	0.00	0.00
	LAO	0.00	0.00	0.00	0.00	0.00

Table 4. Ranking of national and planned reserves of top conservation priority for *Batagur borneoensis, B. affinis* and *Pelochelys cantorii*. Reserves which are also found potentially important under climate change and outside their respective MESS ranges are listed under future scenarios (SSPs: 126, 245, 370, 585; NA: Not Available). More information on the IUCN categories can be found at https://www.iucn.org/.

Rank	Reserves	IUCN	Country	Status	Designation	Future scenarios (SSP)
Batagur borneoensis						
1	Selirong (Productive Production)	V	BRN	Designated	Forest Reserve	NA
2	Berakas (Recreation)	V	BRN	Designated	Forest Reserve	NA
3	Berakas (Conservation)	Ia	BRN	Designated	Forest Reserve	NA
4	Four Islands	IV	MYS	Designated	Wildlife Reserve	NA
5	Pulau Kapas	II	MYS	Designated	Marine Park	NA
6	Pulau Siarau Nature Reserve	Ia	BRN	Designated	Forest Reserve	NA
7	Sungei Buloh Wetland Reserve	Ib	SGP	Designated	Nature Reserve	NA
8	Tanjung Puting National Park	II	IDN	Designated	Ramsar Site, Wetland of International Importance	NA
9	Ao Manow-Khao Tan Yong	II	THA	Proposed	National Park	NA
10	Similajau	II	MYS	Designated	National Park	NA
B. affinis						
1	Thanh Phu	IV	VNM	Designated	Nature Reserve	126
2	Pulau Kapas	II	MYS	Designated	Marine Park	126
3	Sungei Buloh Wetland Reserve	Ib	SGP	Designated	Nature Reserve	126
4	Ao Manow-Khao Tan Yong	II	THA	Proposed	National Park	126
5	Dong Peng	VI	KHM	Designated	Multiple Use Management Area	126
6	Way Kambas	II	IDN	Designated	National Park	126, 245
Pelochelys cantorii						
1	Initao-Libertad	V	PHL	Designated	Protected Landscape and Seascape	NA
2	Sto. Niño-Basiawan	VI	PHL	Designated	Fish Sanctuary	NA
3	Naujan Lake	IV	PHL	Designated	National Park	NA
4	Sibuti	IV	MYS	Designated	Wildlife Sanctuary	NA
5	Turtle Islands Park	II	MYS	Designated	State Park	NA
6	Ao Phanganga	II	THA	Designated	Marine National Park	NA
7	Mu Ko Lanta	II	THA	Designated	Marine National Park	NA
8	Padada (Malalag)	VI	PHL	Designated	Fish Sanctuary	NA
9	Haliday Island	IV	IND	Designated	Sanctuary	126, 245
10	Had Vanakorn	II	THA	Designated	Marine National Park	126

Brunei; Four Islands, Pulau Kapas, and Similajau in Malaysia; Sungai Buloh Wetland Reserve in Singapore; Tanjung Puting National Park in Indonesia, and Ao Manow-Khao Tan Yong Reserve in Thailand (Table 4).

Most of the distribution estimated by TTWG (2017) for *B. affinis* overlaps the potentially suitable habitats predicted by the model. In contrast to *B. borneoensis*, the potential distribution of the species inferred from climate data includes extensive inland areas, especially on Sumatra and Borneo (Fig. 2b). Other suitable habitats include Java in Indonesia, Palawan in the Philippines, eastern Thailand, and southern Vietnam and Cambodia. Note that although the species has not been reported there, the climate on Borneo and in the Philippines is predicted to be suitable for the species. Unfortunately, only a small part of the potentially suitable distribution is covered by Protected Areas. As for *B. borneoensis*, Indonesia has the highest proportion (62%) of potential distribution of *B. affinis* within protected reserves, followed by Philippines (23%), Malaysia (8%) and other countries (<5%) (Fig. 2c, Table 2). Figure 2d shows the reserves of major importance in terms of suitable areas with water surface cover, with the highest proportion in Thailand (52%), followed by Indonesia (28%), Philippines (9%) and Malaysia (6%), while coverage is low in other countries (<5%) (see also Table 3). Within the estimated distribution of *B. affinis*, several reserves with conservation priority were identified (Fig. 2d): Thanh Phu and Dong Peng (Cambodia), Pulau Kapas (Malaysia), Sungei Buloh Wetland Reserve (Singapore), Ao Manow-Khao Tan Yong (Thailand), and Way Kambas (Indonesia) (Table 4).

For the wide-ranging *P. cantorii*, the potential distribution predicted by climate covers a large part of the distribution estimated by TTWG (2017), which spans from peninsular India to Southeast Asia and China (Fig. 3b). Other suitable habitats were predicted in Sri Lanka, southern Myanmar, southern Cambodia, Java and Sulawesi in Indonesia, and the central Philippines. Ranking suitability of Protected Areas by country in Fig. 3c suggests that Indonesia

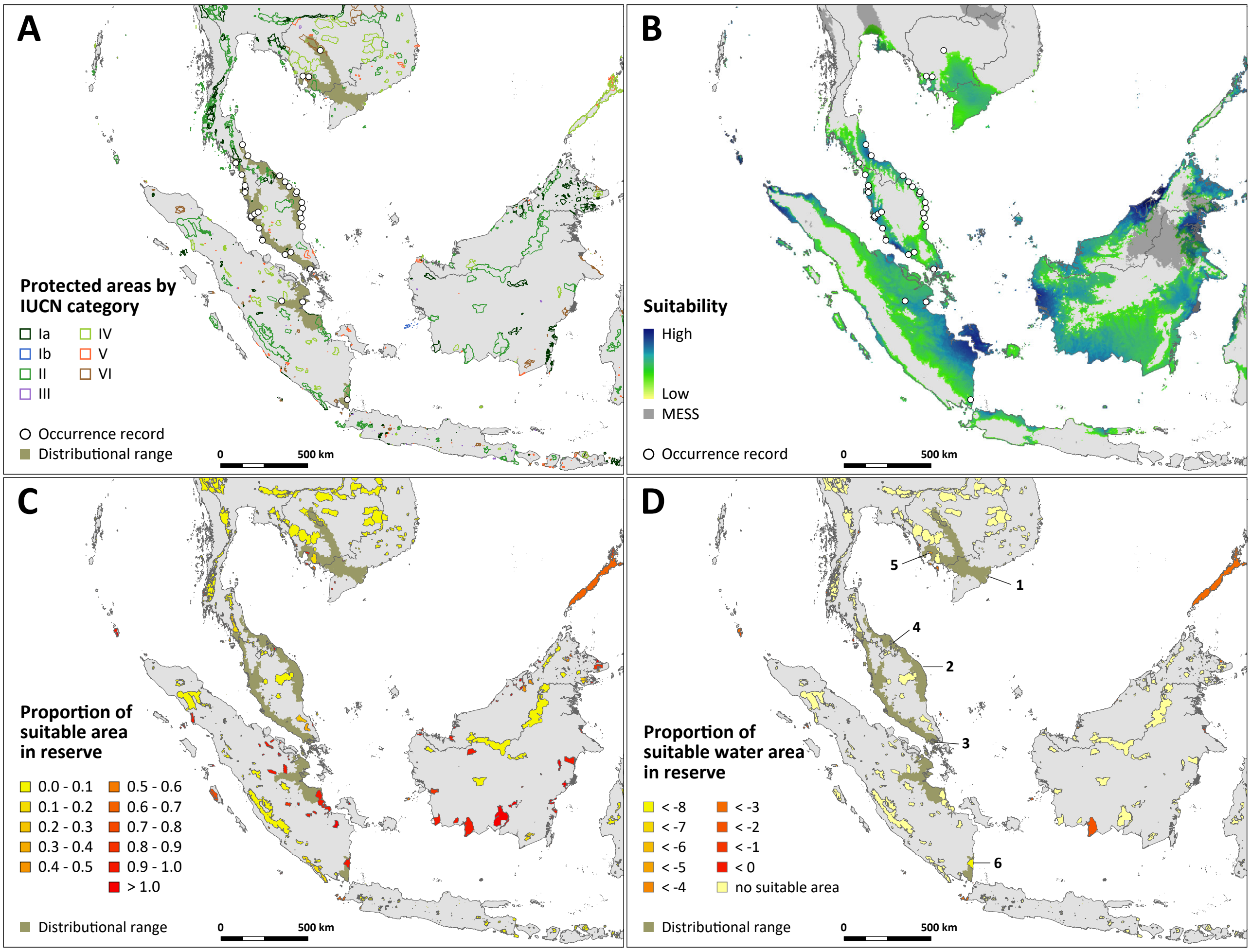

Figure 2. **(A)** The distribution of *Batagur affinis* estimated by TTWG (2017, in press) and the Protected Areas or reserves according to IUCN standards. **(B)** Potential distribution derived from the Maxent model ranging from high (blue) to low (yellow). **(C)** Potential suitable habitat within the reserves, ranging from high (red) to low (yellow). **(D)** Potential suitable water cover within the reserves ranging from high (red) to low (yellow). Proportions displayed are results of $\log_{10}$ computation. We labelled the reserves of top conservation priority based on the potential suitable water cover within the reserves found in the species estimated distribution. Information on these reserves can be found in Table 4.

(24%) and Philippines (18%) are of major importance, while coverage is low in Thailand (13%), Cambodia (10%), Sri Lanka (9%), India (8%), Malaysia (6%), and other countries (<5%) (Table 2). The inclusion of water occurrence indicates that Indonesia (54%) represents the highest coverage of suitability, followed by India (25%), Philippines (11%) and Thailand (6%), whereas the coverage is less than 5% in other countries (Fig. 3d, Table 3). Several important Protected Areas providing major suitable water coverage for *P. cantorii* within the estimated distribution were identified: Initao-Libertad, Sto. Niño-Basiawan, Naujan Lake and Padada (Malalag) in Philippines; Sibuti and Turtle Islands Park in Malaysia; Ao Phanganga, Mu Ko Lanta and Had Vanakorn in Thailand, and Haliday Island in Indonesia (Table 4).

Future projections and potential distribution

Our models predicted future potential increases in the size of the geographic range for the three turtle species in all emission scenarios. Potential suitable habitats for *B. borneoensis* and *B. affinis* are predicted to move further north and inland as compared to current predictions (Fig. S1-S3). Large parts of Southeast Asia, including new areas, such as Myanmar and Laos are predicted to become suitable for both *Batagur* species (Fig. S1-S2). However, climate in mountainous regions seem to remain unsuitable. Surprisingly for *P. cantorii*, climate in coastal areas of Southeast Asia, peninsular India and Sri Lanka which are currently suitable are predicted to become less suitable than the current prediction (Fig. S3). The bioclimatic range of *P.cantorii* is predicted to increase northwards, especially into India, Myanmar, Vietnam, and China.

The four scenarios show that Indonesia still remains the country of the largest extent of designated Protected Areas with suitable habitat for all three species. The following countries of major importance in suitable Protected Areas are Cambodia, Thailand, Philippines, and Malaysia for all species, while Myanmar,

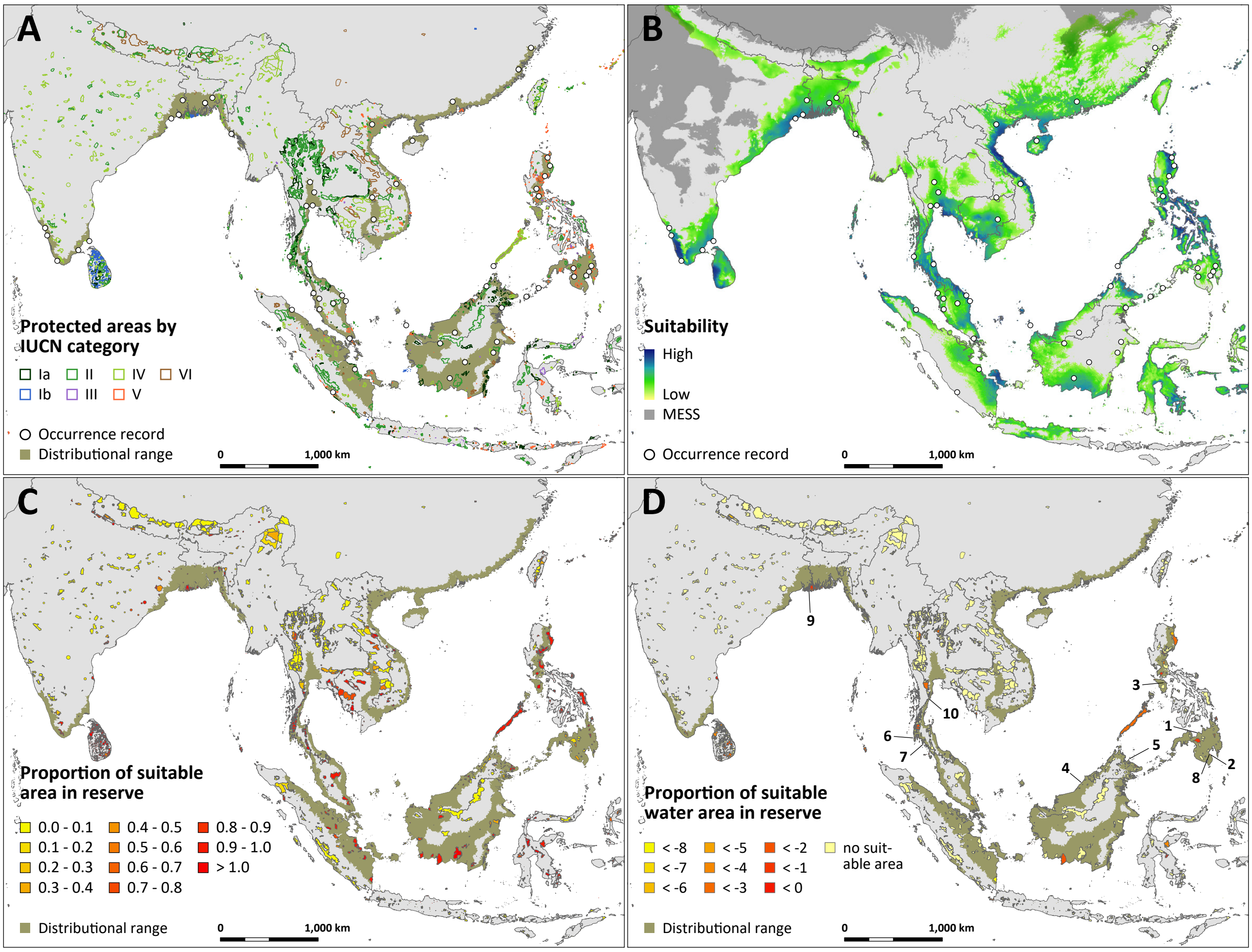

Figure 3. (A) The distribution of *Pelochelys cantorii* estimated by TTWG (2017, in press) and the Protected Areas or reserves according to IUCN standards. **(B)** Potential distribution derived from the Maxent model ranging from high (blue) to low (yellow). **(C)** Potential suitable habitat within the reserves, ranging from high (red) to low (yellow). **(D)** Potential suitable water cover within the reserves ranging from high (red) to low (yellow). Proportions displayed are results of $\log_{10}$ computation. We labelled the reserves of top conservation priority based on the potential suitable water cover within the reserves found in the species estimated distribution. Information on these reserves can be found in Table 4.

Sri Lanka, and India are also important for *P. cantorii* (Table 2). Interestingly, Cambodia has the highest gain of potentially suitable habitat in Protected Areas in the future, up to 17% for *B. borneoensis* and 19% for *B. affinis*, while a similar pattern was also evident in Thailand (Table 2). Results of water coverage within reserves show that Thailand and Indonesia are predicted to remain highly suitable in all future scenarios of these two species (Table 3). For *P. cantorii*, the four scenarios show that water coverage located in reserves in the Philippines is predicted to increase by up to about 21%. Under the SSP126 scenario, this species is predicted to lose 20% of suitable water coverage in Indonesia while gaining 14% in Thailand. For all three species, we listed the future emission scenarios, containing the same predicted protected reserves found outside MESS area with the highest important water coverage as the current prediction, in Table 4.

Discussion

Our models may have a tendency for over-fitting. However, this should mean that they avoid over-prediction, which would be more problematic in the context of our study. As our goal is providing guidance for conservation, we prefer to have a robust assessment of those areas which are most suitable, avoiding predicting marginal habitats. The wide spatial extent of potentially suitable habitat for the three freshwater turtles detected by our models, compared to the distributions previously estimated by TTWG (2017), indicates that a number of potential undiscovered populations and/or anthropogenic exploitation of these populations may exist. The variables of highest contribution to the model (except for annual mean temperature and temperature seasonality) in this study correspond to those previously suggested to be of general importance to chelonian distributions (Ihlow et al. 2012). Although the incorporation of additional predictors of the three study species' habitat requirements and physiological data would improve the accuracy and performance of the models, current knowledge on their ecology is very limited. Our results suggest that based on Protected Areas designated under the IUCN standards, Indonesia appears to be of major importance for conservation priorities in all three species for current and future scenarios. However, Thailand has the highest ranked conservation areas with suitable water coverage for *Batagur borneoensis* and *B. affinis*. Even though no species records have been found on the small islands off the coast of the mainland, we did not exclude the possibility that these islands might harbour viable native or introduced populations.

Batagur borneoensis

Most of the potential distribution of *B. borneoensis* predicted by our model is restricted to coastal areas (see Fig. 1b). This corresponds to the species' habitat and nesting preferences. The species' presence is usually influenced by salinity level and availability of mangrove apples (*Sonneratia* spp.) in the mangrove forest biome, reflecting conditions which occur in the lower course of rivers (Hernawan et al. 2019). Also, females migrate as a group up to 20 km from the river mouth to find sandy areas as nesting sites (Dunson and Moll 1980). However, this species has been reported to have experienced a marked decline in the global population within the last century (Hernawan et al. 2019). On the east coast of Peninsular Malaysia, the largest known breeding populations are in the Paka and Setiu river systems, where two decades ago more than 100 breeding females possibly occurred (Sharma and Tisen 2000), but populations have since apparently continued to decline. Unfortunately, too few of these coastal areas are designated Protected Areas under the IUCN categories.

Because this species lives in close proximity to humans, its populations have been threatened by construction of beach front property and harvesting of adults and eggs for food (TCC 2018). Therefore, we strongly recommend the designation of additional reserves, applying IUCN standards, along the suitable coasts of Malaysia (e.g., Setiu Wetlands). In Indonesia, however, numerous designated and proposed reserves cover large parts of potential suitable habitat of *B. borneoensis*. Although highly suitable protected reserves with the highest proportion of water suitability are also found in Thailand and Brunei Darussalam (Table 4, Fig. 1d), limited evidence of sightings of *B. borneoensis* in these countries have been reported (TCC 2018). Further monitoring in these conservation priority areas is urgently needed to identify if they harbour viable populations of this endangered turtle species.

Batagur affinis

Once widespread in all major rivers draining into South China Sea, *B. affinis* is also a critically endangered species listed on the IUCN Red List, and its populations are declining or extirpated over most of its former range (Moll et al. 2015). The potential distribution of this species from our analysis showed that it might possibly be found further inland as compared to *B. borneoensis* (Fig. 2b), suggesting that *B. affinis* could be more of a generalist species. The inland preference could also be associated with movements of *B. affinis* up river with the rising tide in order to forage (Dunson and Moll 1980). Furthermore, this species migrates as much as 80 km upstream to riverine sand banks to nest during the dry season (Holloway 2003). Estuaries and tidal regions in large rivers (e.g., Perak and Setiu in Malaysia) are dominant habitats for this species where they feed on plant materials in water with salinities of not more than 20 ppt (Davenport et al. 1992). However, sand mining and dam construction have decimated suitable nesting areas in many areas. One example is the upstream dam construction on the Kedah River, which was built directly on the nesting beaches (Moll and Moll 2000, 2004). At the same time, this species has been locally exploited for its eggs and internationally for its meat from the vast demand for turtle consumption in China (Moll et al. 2015).

Again, we propose the same recommendations as for *B. borneoensis,* to add additional designated reserves on the coasts of Malaysia, particularly in the states of Negeri Sembilan, Perak and Terengganu to prevent further habitat destruction and poaching. In the Sre Ambel River in Cambodia, a small population was rediscovered in 2001 (Platt et al. 2003) and currently is under the protection of the Dong Peng management area (Fig. 2d). Future conservation efforts should be focused in the river systems in southern Cambodia and the Mekong delta of Vietnam, where isolated populations represent important genetic variation within the species (Çilingir et al. 2019). A survey from a report by Mistar et al. (2012) [unpublished] to find wild *B. affinis* in Sumatra was futile (Moll et al. 2015, TCC 2018). However, a remnant population was found by local fishermen in the Indragiri River and mangrove swamps around Mumpa (Mistar et al. 2012 unpublished). Hence, we recommend further surveys for *B. affinis* populations in eastern and southeastern Sumatra (Fig. 2b) where a large part of the suitable area remains unprotected (Fig. 2c).

Pelochelys cantorii

Although it has a wide distribution, *P. cantorii* has disappeared from most of its former range, with only scattered individuals reported recently (TCC 2018). Our analysis confirmed the widespread habitat suitability of this species, with potential habitat matching closely with that estimated by TTWG (2017) (see Fig. 3a and 3b). This suggests that *P. cantorii* might be a generalist with a sparse geographical occurrence but with a wide range of habitat preferences (Das et al. 2008). Nesting habits on ocean beaches (Das et al. 2008) and tolerance of seawater are probably responsible for its occurrence along the coast. Therefore, despite having suitable climate, the potential inland occurrence along the Ganges and Brahmaputra basins shown in Fig. 3b is not possible due to the overwhelming distance from and lack of suitable connection to the sea.

Within recent decades, this species has often been caught for human consumption (Das 2008). Habitat destruction has also depleted and fragmented populations. For example, though protected as a national priority aquatic species, *P. cantorii* once occurred in large numbers in China, but is now presumed to essentially be extirpated there as a result of overcollection for food, urbanisation, water pollution, and overfishing (Lau and Shi 2000, Xiaoyou et al. 2019). Despite being a small country, Sri Lanka appears to have many suitable Protected Areas, although no sightings of *P. cantorii* have been observed there (Fig. 3c). In India, many individuals have been encountered in the suitable areas predicted in the peninsula and northern parts of the east coast (Rashid and Khan 2000), but there is a lack of designated or proposed reserves (Fig. 3c). A similar situation can be found in Bangladesh. In peninsular Malaysia, *P. cantorii* has been found in fair numbers (Sharma and Tisen 2000), with many suitable reserves far inland, even with an individual found in Taman Negara (TTWG 2017). However, the situation seems bleak in Thailand and Vietnam, where most populations are believed to be extirpated, leaving only one apparent viable population in the lower Mekong River in Cambodia (Touch et al. 2000). Indonesia currently holds the largest area suitable for conservation of *P. cantorii,* but breeding populations may be rare (TCC 2018). However, a fishery survey detected some collected specimens for trading in southern Sumatra (Oktaviani and Samedi 2017). The Philippines and Borneo seem to be the last strongholds, with suitable protected reserves which may support viable breeding populations. In Kalimantan Borneo, an individual was found as far as 200 km from the nearest coast (Fig. 3a). We thus urge further research and conservation efforts in these areas, particularly in the reserves with high suitability (Table 4).

Impact of climate change

Our initial results show that all three turtle species might benefit from climate change by 2080 in terms of potential increases in their suitable ranges. Not surprisingly, their ranges are predicted to expand northwards in mainland Asia and inland in southeast Asia due to more favourable climate conditions at higher elevations and latitudes. These patterns are consistent with the shift in species richness and in *Kinosternon* species predicted by Ihlow et al. (2012) and Butler et al. (2016), respectively.

However, many of these future potentially suitable areas of expanding range have uncertain predictabilities due to extrapolation (see MESS maps Fig. S1-S3). The MESS results suggest that climatic conditions in many areas, especially on the coasts, which are predicted to be suitable for these species, represent extrapolations beyond the training range of the models and hence might not be reliable. One stable suitable area for the future survivability of *P. cantorii* could exist in northern Vietnam and China under different scenarios (Fig. 3). Assuming the current water bodies and protected reserves remain, only *B. affinis* would be classifiable as 'least threatened' in scenario SSP 126, while in most other future scenarios, the long-term situation for the conservation of each of the three species appears bleak (Table 4). It is important to recognise that variance in future model prediction increases when only a small number of presence points are considered over large areas (Bean et al. 2012, Rej and Joyner 2018).

Loss of large suitable areas was also predicted by a similar climatic model for *B. borneoensis* in 2080 (Ihlow et al. 2012). Moreover, only up to a quarter of these areas were outside the extrapolation area (i.e., beyond training ranges) (MESS). However, the wide-ranging species *P. cantorii* was found to be least potentially impacted by climate change (Ihlow et al. 2012). The answer to the question of whether these turtle species can adjust to new climatic conditions generated by climate change, is still unclear. However, with the unavailability of stable suitable Protected Areas suggested by our models and assuming highly conservative climatic niches and low potential for rapid evolutionary adaptations in turtles (Stephens and Wiens 2009, Berriozabal-Islas et al. 2020), we would expect a severe decline in their populations in the future. In addition, synergistic effects from continued exploitation, habitat loss and degradation, economic development, agricultural pressures, and endemic plant species loss predicted by the year 2050 increase the uncertainty of long-term persistence of these turtles (Habel et al. 2019).

Conclusions

Although our Maxent models are derived from climate data and comparatively small numbers of occurrence records, they nevertheless provide a useful guideline to direct further surveys in areas of potentially unknown populations (Pearson et al. 2007). Urgent surveys and monitoring to detect and ensure adequate populations in Protected Areas throughout their ranges will be critical to the survival of these critically endangered turtles. As a result, having additional occurrence data from field surveys can be used to improve our current predictions. Continuing to collect ecological and physiological data and studying the genetic diversity, population structure and microhabitat preferences of these species will in turn help evaluate their future status. As our study area is currently a turtle diversity hotspot (Ihlow et al. 2012, Mittermeier et al. 2015), we might expect to find many other species in the Protected Areas included within the bounds of our study.

Our findings demonstrate that although these three endangered freshwater turtles are protected by several IUCN designated and proposed reserves, their populations are vulnerable as a result of extensive habitat loss and fragmentation in the present and expected to increase in the future (Sodhi et al. 2004, Habel et al. 2019). Despite being protected under national laws, many of these species are still relentlessly poached for eggs and meat and exported due to the lack of law enforcement (van Dijk et al. 2000, TCC 2018). Proposing new reserves may seem to be an easy direct approach to conserving these threatened species but insufficient funds in park management and monitoring remain a problem. Perhaps small-scale conservation efforts are more effective in preserving remaining specimens rather than allocation of new reserves in areas which are intensively degraded. In Peninsular Malaysia, captive breeding programs are currently operating in Terengganu and Melaka for *B. borneoensis* by the Fisheries Malaysia and WWF Malaysia, while similar hatcheries have long been established for *B. affinis* in the states of Perak and Kedah by the Department of Wildlife and National Parks (Duli 2009 unpublished). Several captive breeding centres in Guangdong and Yunnan China are starting to achieve some success in breeding and reintroducing *P. cantorii* (Xiaoyou et al. 2019). Van Dijk (2000) further recommended coordinating breeding programs between engaged countries. Successful conservation programs in the future will require cooperation from multiple countries in exchanging information and scientific knowledge. Lastly, awareness programs with community involvement and education are necessary in promoting the conservation of these turtles (Moll et al. 2015, TCC 2018).

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Author Contributions

WCT and DR conceived the ideas, designed methodology and analysed the data. PG helped with data analyses and giving guidance in the models. WCT led the writing of the manuscript. AGJR and JBI provided locality and range data and added their expertise on the topic. All authors contributed to the drafts.

Data Accessibility

All locality data will be published in TTWG (in press) and are available from AGJR.

WorldClim: www.worldclim.org

World Database of Protected Areas: https://www.protectedplanet.net/

Water cover data: https://global-surface-water.appspot.com

Supplementary Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Figure S1. Future potential distribution of Batagur borneoensis by the year 2080 derived from the Maxent model.
Figure S2. Future potential distribution of Batagur affinis by the year 2080 derived from the Maxent model.
Figure S3. Future potential distribution of Pelochelys cantorii by the year 2080 derived from the Maxent model.
Appendix S1. Lambda files from Maxent models.

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Last chance to see?
Iran and India as strongholds for the Mugger Crocodile (*Crocodylus palustris*)

Asghar Mobaraki[1], Malihe Erfani[2], Elham Abtin[3], José Carlos Brito[4,5,6], Wei Cheng Tan[7], Thomas Ziegler[8] & Dennis Rödder[7,9]

[1] Natural Environment Deputy, Wildlife Conservation and Management Bureau, Department of Environment, Tehran, Iran
[2] Department of Environmental Sciences, Faculty of Natural Resources, University of Zabol, Iran
[3] Natural Environment Division, Department of Environment Office in Sistsan and Baluchistan Province, Zahedan, Iran
[4] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, Portugal
[5] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Portugal
[6] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Vairão, Portugal
[7] Leibniz Institute for the Analysis of Biodiversity Change (LIB) – Museum Koenig, Adenauerallee 127, 53113 Bonn, Germany
[8] AG Zoologischer Garten Köln, Riehler Str. 173, 50735 Köln, Germany
[9] Postgraduate Program in Zoology, State University of Santa Cruz – UESC, Ilhéus, Brazil

Corresponding author: Dennis Rödder, ORCID: https://orcid.org/0000-0002-6108-1639, e-mail: d.roedder@leibniz-lib.de

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Abstract. Justified predictions of future changes in species distributions are necessary for defining adequate conservation plans over space and time. The Marsh or Mugger Crocodile (*Crocodylus palustris*) is native to freshwater habitats of the Indian subcontinent and in southeastern Iran. Habitat loss is currently the most important threat to crocodile dispersal and persistence, and climate change will likely exert increasing pressure on populations. This study used ecological niche modelling (maximum entropy) to predict the current distribution of this species and project it to future climatic conditions. For this purpose, 380 occurrence records were used for model computation and environmental data were obtained from Worldclim 2.0. Averages of eight global circulation model outputs, assuming four IPCC6 per story lines in 2081–2100, were used as future ensembles. Furthermore, future possible anthropogenic pressure was quantified using economic growth models. Temperature Annual Range was the climatic variable with the highest contribution to the modelling. Presently, most potential suitable habitats are located in Sri Lanka, in the southeastern peninsular of India, the tropical moist forest along the west coast of India, the border region between Nepal and India, and the south coasts of Iran and Pakistan. In the future, these suitable habitats are predicted to be further fragmented and to shift farther inland. Additional threats may arise from increased human/crocodile conflicts due to human population growth. Conservation should therefore focus on those areas that remain climatically comparatively stable with a low potential of human/crocodile conflicts. Key areas are located in the northern parts of India and at the westernmost range limits of this species in Iran.

Key words. Crocodylidae, biodiversity, global warming, habitat suitability, spatial conservation planning, species distribution modelling.

Introduction

Justified concerns about the vulnerability of wildlife to the effects of climate change are increasing globally, and the potential response of species to such changes have been discussed widely (Segan et al. 2016, Newbold et al. 2020). Likely impacts of climate change have been predicted for different species and their related ecosystems and well documented in different studies conducted on a variety of species (Newbold et al. 2020). Species may face direct and indirect impacts from climate change, which pushes them further to the brink of extinction (Segan et al. 2016). As such, predicting climate change effects on species has important impacts on conservation plans, as the magnitude of the threats that species and their habitat can be facing becomes clearer and alerts decision- and policy-makers (Carvalho et al. 2010, Butt et al. 2016). It follows that predicting the response of species to climate change is critical, as species may respond in different ways, including changes in their behaviour, reproduction, lifecycle and migration (Bellard et al. 2012). Dispersal may occur and species may actually expand their presently occupied habitats, or, on the contrary, experience significant range contractions. Ecological models can predict the responses of extant species distributions to rising temperatures (Summers et al. 2012). In this context, species distribution models (SDMs) have the potential to predict current species distributions and their responses to climate change (El-Gabbas & Dormann 2018). SDMs have been widely used for different aims, including conservation and ecological research, and, since recently, predicting the effects of climate change on the future distribution patterns of species (Elith et al. 2006, Kafash et al. 2015).

Freshwater ecosystems provide essential services and functions, even though they cover less than one percent of the planet. Due to a variety of threats, including climate change effects, they are classified as one of the most threatened ecosystems worldwide. Furthermore, the freshwater species living in these ecosystems, which account for almost 10% of globally described species, are inevitably faced with severe climate change effects (Benateau et al. 2019).

As "Key Stone Species", crocodilians are an important biodiversity component in their habitats, playing various ecological, commercial, cultural and livelihood roles. Most of the crocodilian species are globally threatened due to habitat destruction, overharvesting and climate change effects (Grigg 2015). Due to their Temperature Dependent Sex Determination (TSD) reproduction strategy, crocodiles are highly vulnerable to increasing temperatures from global warming (Mannion et al. 2015). The Marsh or Mugger Crocodile (*Crocodylus palustris*) is native to freshwater habitats of the Indian subcontinent, with its westernmost population occurring in southeastern Iran (Da Silva & Lenin 2010). As a globally threatened species, the Mugger Crocodile is categorized as Vulnerable in the IUCN Red List and mostly threatened by habitat loss. The total adult population of Mugger Crocodiles exceeds 2500 individuals across its entire range (Da Silva & Lenin 2010). These populations are threatened by severe periodic droughts and floodings, which may be interpreted as consequences of climate change. Habitat destruction and modification exert pressures on crocodiles (Mobaraki et al. 2015). Hunting, water pollution, sedimentation, food shortage, egg collection, seasonal fluctuation of water levels, and death from accidental capture in fishing nets are other threats for crocodiles (Bhatt et al. 2012, Chang et al. 2013, Fellows 2019). Predictions of climate change for southwestern Asia identifies this region as one of the world's most vulnerable places to warming (Pal & Eltahir 2016). A study using Habitat Evaluation Procedure (HEP) to identify the best and most suitable habitats for crocodiles along the Sarbaz River, Iran, indicated that they prefer habitats with 2–4 m water depth, a mean vegetation cover of 35%, a mean slope of 25–35%, and a high density of fish and amphibians (Abtin 2012). Another study revealed that the main variables determining habitat suitability are climatic fluctuations and the amount of accessible water (Mobaraki et al. 2018).

To date, there exists no study assessing the climatic suitability throughout the range of the Mugger Crocodile and the subsequent potential effects of climate change (see Mobaraki et al. 2021). In this work we aim to: 1) identify the environmental factors most closely related with Mugger Crocodile occurrences in the range states; 2) model the potential distribution of the species; 3) predict the changes in future distribution of the species according to potential climate changes; and 4) identify priority areas for conservation given environmental niche stability and potential future human/crocodile conflicts. Modelling the potential effects of climate change on crocodiles allows us to predict their future distribution, which may in turn aid in proposing suitable conservation management actions.

Material and methods

Data preparation

To assess the potential distribution of the Mugger Crocodile, we obtained unique 636 occurrence records from GBIF covering the native range of the taxon based on preserved specimens and observations. Further, we georeferenced 84 occurrence records from our own fieldwork to increase the number of records in the westernmost parts of its range. We corrected the set of species records for potential sampling bias and spatial autocorrelation by a 10-km distance filtering using the thinning function in the spThin package for R (Aiello-Lammens et al. 2015, R Core Team 2019). Finally, a set of 380 occurrence records was used for model computation.

Environmental data were obtained from Worldclim 2.0 (www.worldclim.org). Based on monthly data, these 19 bioclimatic variables characterize average climatic conditions from 1970–2000 with a spatial resolution of 2.5 arc minutes (Fick & Hijmans 2017). Multi-co-linearity of predicting variables was reduced by computing pairwise Spearman rank correlations and selecting only one variable in cases where R^2 exceeded 0.75. The final variables selected for model computation comprised BIO1 = Annual Mean Temperature, BIO7 = Temperature Annual Range, BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO13 = Precipitation of Wettest Month, BIO14 = Precipitation of Driest Month, BIO16 = Precipitation of Wettest Quarter, BIO17 = Precipitation of Driest Quarter, BIO18 = Precipitation of Warmest Quarter, and BIO19 = Precipitation of Coldest Quarter.

To evaluate potential impacts of future climate change as can be expected in 2081–2100, we downloaded global circulation model (GCM) outputs assuming the IPCC6 story lines of ssp126, 245, 370 and 585 from Worldclim.org (BCC-CSM2-MR, CanESM5, CNRM-CM6-1, CNRM-ESM2-1, IPSL-CM6A-LR, MIROC6, MIROC-ES2L, MRI-ESM2-0). Averages across all GCM simulations per story line were used as future ensembles.

Species distribution modelling

To perform SDMs, we used Maxent ver. 3.4.4 and the R-packages: raster (Hijmans et al. 2021a), dismo (Hijmans et al. 2021b), and ENMeval (Muscarella et al. 2014) were used for model optimization and processing. The available climate space was defined by a polygon provided by the IUCN Red List, representing a distribution range estimate based on expert opinion (Fig. 1). For model fitting, we tested several regularization multipliers (from 0.5 to 2.5 in steps of 0.25, plus 5 and 10) and feature classes (L, LP, LQ, LH, LT, LQP, LQH, LQT, LPH, LPT, LHT, LQPT, LQHT, LPHT, LQPHT; L = Linear, P = Product, Q = Quadratic, H = Hinge, T = Threshold). A total of 25 replicates were computed per combination of regularization multiplier and set of feature classes, wherein the species records were randomly selected each time via bootstrap with 80% used for model training and 20% used for model evaluation.

Based on the Maxent's raw output, we computed for each replicate the corrected Akaike Information Criterion [AICc, (Warren & Seifert 2011)] and the difference between test and training AUC [= Area under the ROC curve (Lobo et al. 2008, Phillips & Dudík 2008, Elith & Graham 2009)]. The best combination of settings was selected by balancing the average predictive ability of the model (AUC > 0.8), the smallest difference between $AUC_{training}$ and AUC_{test} (AUC_{delta}), as well as the lowest average AICc.

Using the best fitting model parameters (LPT, regularization parameter = 1, AICc = 2430.2, $AUC_{Training}$ = 0.833, AUC_{Test} = 0.813, AUC_{delta} = 0.019), we finally computed 100 replicates , again using a bootstrap approach with an 80:20 split for model training and testing. The average predictions across the 100 replicates were projected onto current and future climatic conditions using the cloglog output format. Multivariate Environmental Similarity Surfaces (MESS [Elith et al. 2010]) maps were used to assess potential uncertainties caused by extrapolation beyond the training range of the models. As the presence-absence threshold we selected the 10% training omission threshold, assuming that 10% of the species records may represent sink populations or georeferencing artefacts.

Coverage with protected areas, habitat availability and anthropogenic pressure

Information on the distribution of protected areas within the range of the Mugger was obtained from the World Dic-

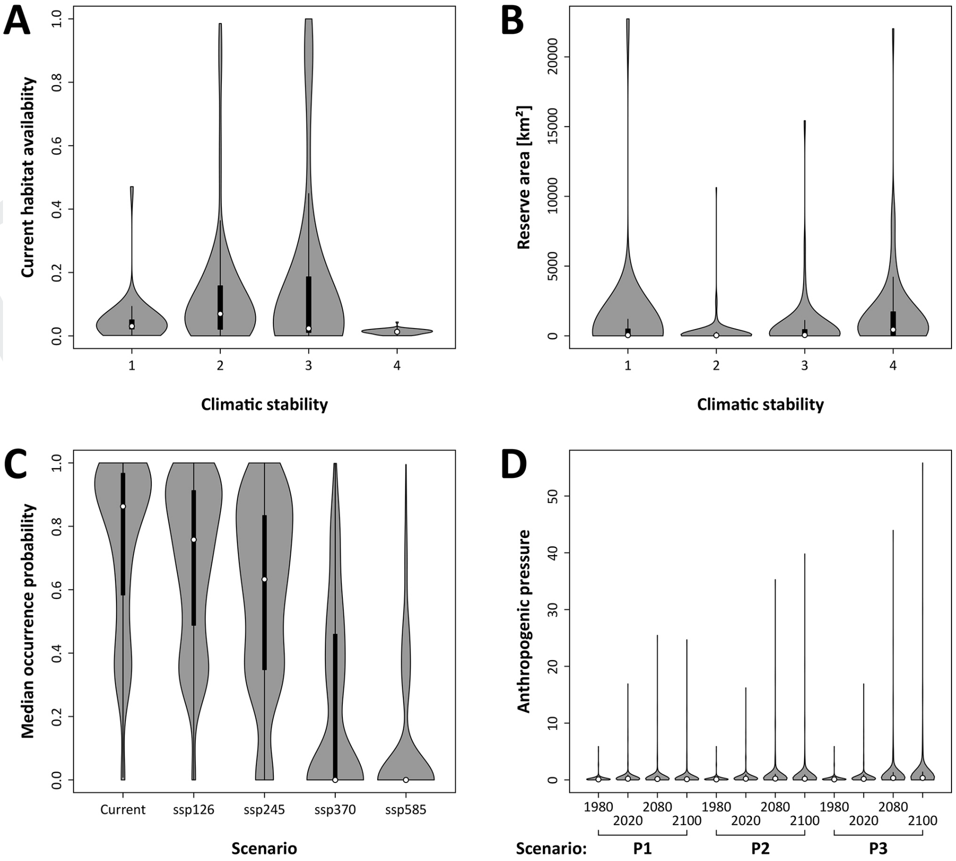

Figure 1. (A) Proportion of suitable habitat for, and (B) area of protected reserves holding the Mugger Crocodile at different degrees of climatic stability in future scenarios (1–4: stable climate in 1 to 4 of all scenarios). (C) Occurrence probability of the crocodile in current and future scenarios. (D) Anthropogenic pressures in time slices 1980, 2020, 2080 and 2100 across 3 storylines.

tionary of Protected Areas (https://www.protectedplanet.net/en), wherein only terrestrial, IUCN-categorized reserves of the categories Ia, Ib, II, III, IV, V and VI are included. To rank protected areas according to their conservation value for the Mugger, we assessed for each site their climatic suitability based on the SDMs, the availability of suitable microhabitats, and the potential anthropogenic pressure in current and future scenarios.

As microhabitat surrogates we used the recent assessment of tropical wetlands by Gumbricht et al. (2017). This data set has a spatial resolution of 232 m and is derived from biophysical indices related to wetland, i.e., a long-term water supply that exceeds atmospheric water demand; annually or seasonally water-logged soils; and a geomorphological position in which water is supplied and retained (Gumbricht et al. 2017). As river networks are missing from this data set but may represent valuable habitat for the Mugger, we added a high-resolution water layer as an additional category (GRDC 2020).

Expecting increasing potential conflicts between Muggers and local human communities with increasing population densities of the latter, we obtained potential future scenarios of the ssp1-3 storylines with a spatial resolution of 0.5° from Murakami & Yamagata (2019). The data set was downscaled to the resolution of our climate data with a nearest neighbour approach in R, and the time slices 1980, 2020, 2080 and 2100 were used for further processing.

For each protected area within the currently known range of the Mugger as suggested by the IUCN, we computed the factual area providing suitable microhabitats, the median environmental suitability across each reserve as expected in current and future scenarios, and the expected anthropogenic pressure. Our ranking of reserves was finally based on the proportion of suitable habitats and climatic stability throughout all future scenarios.

Results

Across the 100 replicates we obtained good AUC values ($AUC_{training}$ = 0.839 and AUC_{test} = 0.827), which indicates a good discrimination ability of our model and absence of overfitting. Temperature Annual Range (Bio7) made the highest contribution (42.9%), followed by Mean Temperature of Driest Quarter (BIO9, 10.7%), Annual Precipitation (BIO12, 10.5%), and Annual Mean Temperature (BIO1, 9.2%), Mean Temperature of Wettest Quarter (BIO8, 6.6%) and the other variables contributed less than 5% to the final model (BIO13 (4.8%), BIO18 (4.7%), BIO14 (3.6%), BIO16 (2.9%), BIO19 (2.6%) and BIO17 (1.4%)).

Potential suitable habitats of the Mugger Crocodile seem to be more fragmented than expected from the native distribution at present (Fig. 1B). Major suitable habitats are situated in Sri Lanka, in the southeastern peninsular of India, tropical moist forests along the west coast of India, the border region between Nepal and India, and lastly on the south coasts of Iran and Pakistan. In Iran, suitability decreases the farther the distance is from the coast, indicating a potential preference for coastal areas for the Iranian population. For the future, our models predicted a general reduction in potential suitability (except for the western parts of the distribution) in all story lines. When the MESS area is included, storylines ssp126 and ssp245 predict similar and only slightly smaller suitable habitats than is the case currently. More loss of suitable habitats was found in the other two storylines (ssp 370 and 585) (Figs 1C, 2E–F). However, when the MESS area is omitted, storylines ssp360 and ssp585 appear to contain 'highly unsuitable' in currently suitable areas, namely in Sri Lanka, southern India, and the coastal part of southern Iran. Potentially suitable habitats are predicted to shift farther inland (Fig. 3). Furthermore, we found that areas that are currently highly suitable do not appear to have a stable climate over time (see Figs 2B and 4A). In fact, there is little suitable habitat to be found in protected reserves with higher climatic stability, especially when the climate is stable in all four fu-

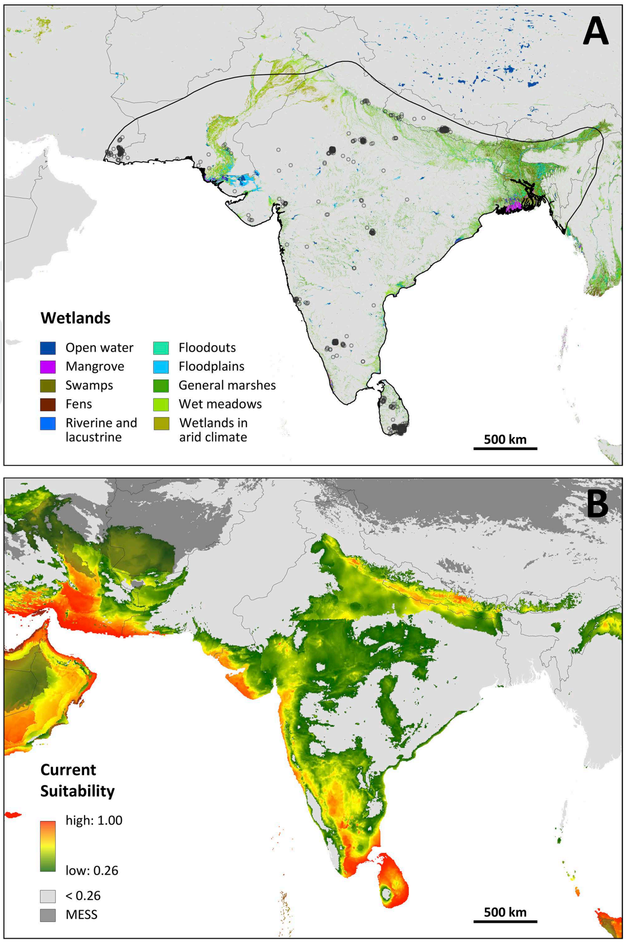

Figure 2. (A) Distribution of various types of wetlands and the Mugger Crocodile. The Global Range polygon for the species according to the IUCN Red List is indicated. (B) Predicted potential distribution of the Mugger Crocodile in the current climate. Warmer colours represent higher environmental suitability. Areas requiring extrapolation beyond the training range were identified via MESS and are indicated in grey.

ture scenarios (Fig. 1A). These stable climates seem to occur mainly in large reserves (Fig. 1B). There appears to be a large number of areas with suitable climate in all future scenarios, particularly along the Himalayan range and in tropical forest along the west coast of India as well as in neighbouring dry broadleaf forests, and more importantly, in the border region between Iran and Pakistan (Fig. 4A). In these areas, we identified reserves of top conservation priority based on overall stability and habitat percentage: Madinduwa, Seooyaka Samudra, Parapuduwa Nun's Island in Sri Lanka, Cut Muorki Chach, Marho Kotri, Keti Bunder South, Mirpur Sakro and Keti Bunder North in Pakistan, Mapangyong Cuo in China, and Thamihla Kyun Wildlife Sanctuary in Myanmar (Fig. 4B).

Potential future scenarios of anthropogenic pressures showed a general pattern of higher variability in later years, with the P3 storyline turning out the highest variability of anthropogenic pressure at the end of 2100 (Fig. 1D). The expected anthropogenic pressures seem to be prominent and increasing in many regions of India, Bangladesh and Pakistan by the year 2100 (Fig. 5).

Discussion

This study identified the variables of highest contribution to the models and these agreed with previous findings from studies in other crocodiles (cf. Rödder et al. 2010, Ihlow et al. 2015) or other habitat suitability studies on crocodiles. On the one hand, the annual temperature range between the coldest and warmest months of the year can be an important factor for the presence of crocodile prey (fish and amphibian species). On the other, mean temperature of the driest quarter and annual precipitation might determine vegetation cover but also the existence of shallow ponds, both of which are used by crocodiles (Da Silva & Lenin 2010, Abtin 2012). However, these crocodiles are known to use burrows as effective refuges from hot ambient temperatures. If habitats suitable for burrowing continue to exist, they could be favourable to the survival of the crocodiles (Whitaker et al. 2007). Basking sites are important for thermoregulation for crocodiles, too (Atigre et al. 2015).

The surprisingly low spatial extent of potentially suitable habitats that is currently predicted suggests that Mug-

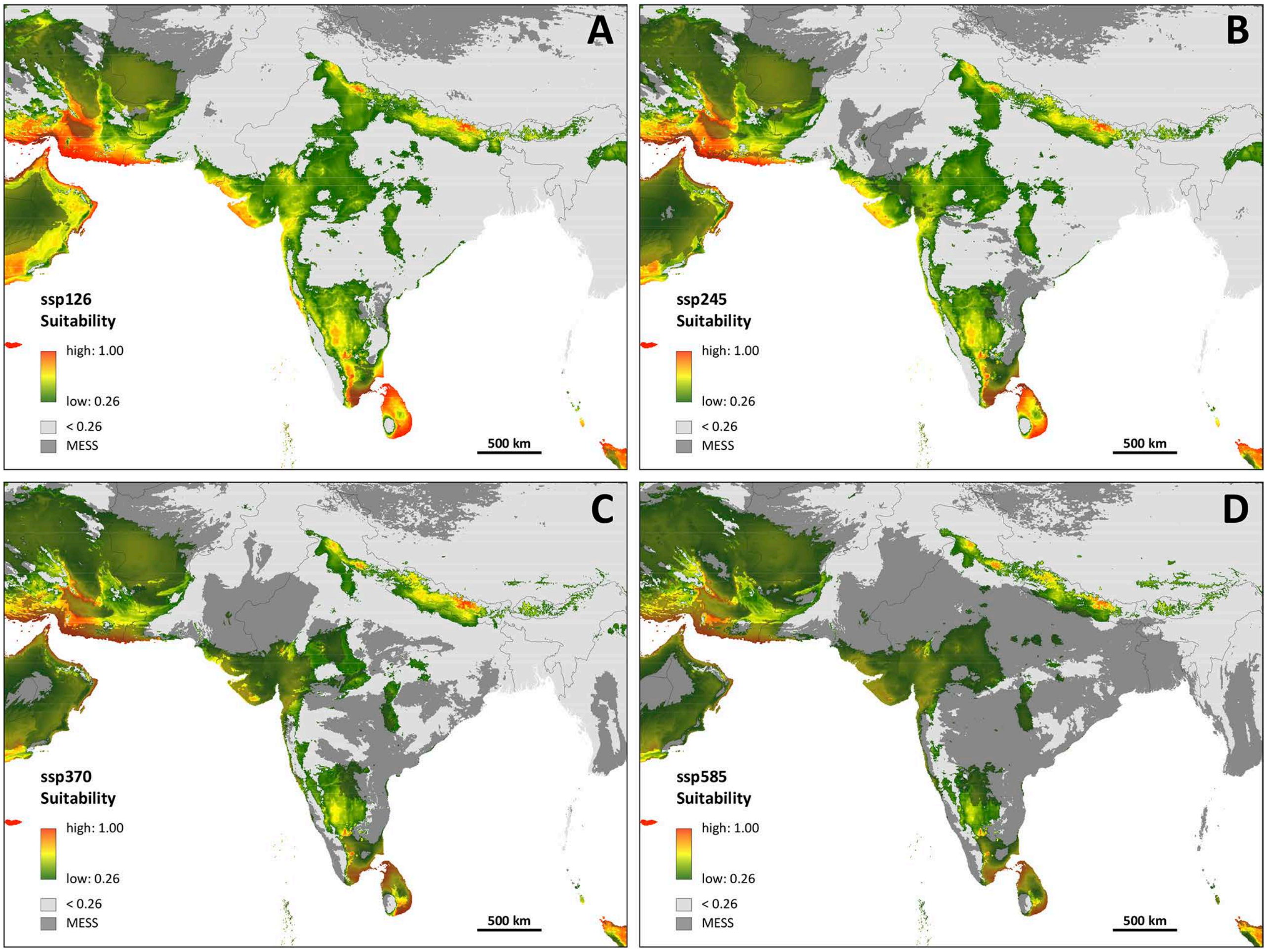

Figure 3. (A–D) Predicted potential distribution of the Mugger Crocodile in future climate change scenarios ssp126, ssp245, ssp370 and ssp585. Warmer colours represent higher environmental suitability. Areas requiring extrapolation beyond the training range were identified via MESS and are indicated in grey.

ger Crocodile populations are highly fragmented and degraded (Fig. 1). In fact, compared to their original distribution, these crocodiles do not have as much suitable habitat available as previously thought. One of the reasons explaining our results may be rapid urbanisation, especially in India with 5.33% growth between 2015 and 2020 (United Nations, Department of Economic and Social Affairs & Population Division 2019). Urbanisation is a form of habitat change that alters the entire environment from its native state (Elmqvist et al. 2016).

All countries in the distribution range of this species are developing countries in which population growth and urbanization are evident (Fig. 5). In Iran, urbanization and related activities like land use modification and agricultural development are prominent, but the most serious problems arise from local human/crocodile conflicts with the Mugger posing a serious threat to local people close to water bodies due to the former losing their natural habitats, due to increasing water shortage, and the latter needing water for daily living and agriculture (Mobaraki et al. 2018, 2021, Hill et al. 2018). This conflict will continue to escalate as anthropogenic activities increase within and around the crocodiles' habitats (Fig. 5).

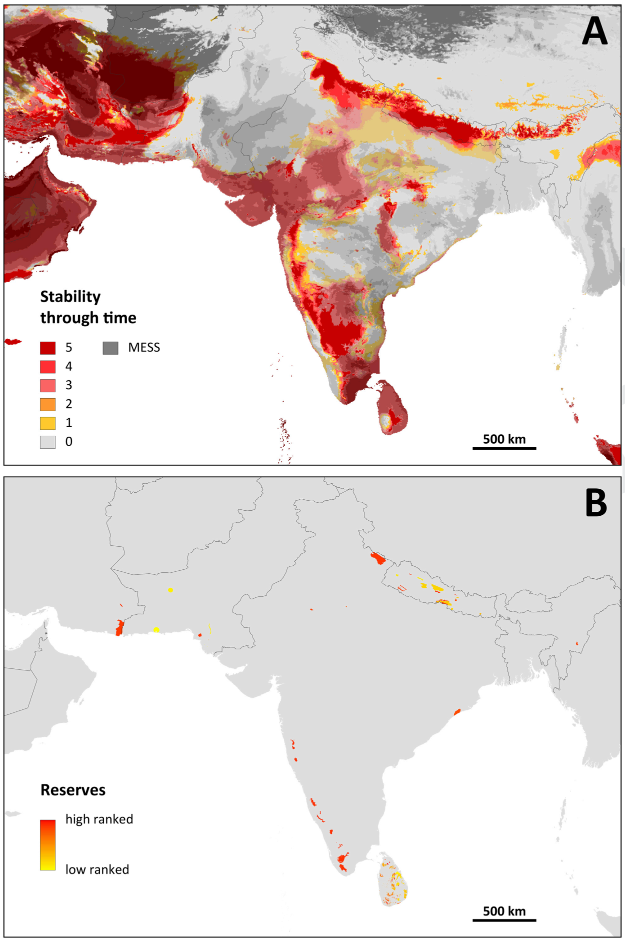

Figure 4. (A) Suitable areas that are stable at present and in the future scenarios. Numbers 0 to 5 indicate the number of scenarios (including current) that have a stable climate over time. (B) Ranking of protected reserves based on the proportion of suitable habitat and climate stability.

Our results suggest that Mugger Crocodiles will likely be affected by climate change in all future scenarios in the timeframe 2081–2100 (Fig. 1C), no matter whether the first scenario with the most optimistic situation for the future will apply or the fourth scenario with the worst situation in the future. There might be a similar trend where potentially suitable habitats are greatly reduced across their ranges, especially when uncertain predictability (MESS) areas are removed (Figs 2A–D). Such changes can be expected if temporary watercourses and ponds during the rainy season disappear as a result of rising global temperatures and intensive droughts become more frequent in the region. Loss of potentially suitable crocodile habitats in the coastal areas of Iran could be a major concern as most of the current Iranian populations are found near the coast. They are driven to the north and west where there are no water resources for the Mugger crocodile. Studies on other species such as the Asiatic black bear (*Selenarctus tibetanus*), Persian spider gecko (*Agamura persica*), Caucasian agama (*Paralaudakia caucasia*), and Iraqi Spiny-tailed Lizard (*Saara loricata*) in Iran reported similar results (Kafash et al. 2015, Yousefkhani et al. 2017, Farashi & Erfani 2018).

In terms of climate stability over time and possible future human/crocodile conflict, very few suitable areas (with large protected reserves) are found to be stable enough for the crocodiles in the future.

We therefore propose to focus future conservation efforts on the reserves with the highest rankings as shown in the results of this study (Fig. 4B). These reserves contain the best possible future refuges for the Mugger Crocodile. Two major areas are to be highlighted in this regard: a larger reserve in northern India (Nanda Devi National Park) and the westernmost area in Iran, especially within the Gando Reserve. Although climatically comparatively stable, the surroundings of the Nanda Devi National Park are expected to come under severe human pressure in the near future (Fig. 5), leaving the most important habitats in terms of conservation in Iran. These are located along two major rivers in the region, the Bahu-Kalat and Kaju. Here, crocodiles live in close contact with local people and conflicts are quite common (Mobaraki et al. 2015), but these are predicted to remain comparatively stable in the near future because human population growth is expected to be rather low in this area (Fig. 5). In the isolated, western extension of its distribution, the Mugger Crocodile is restricted to limited freshwater habitats in Sistan and Baluchistan provinces. The population of this species is small here, estimated at more than 500 individuals, and fragmented into several scattered sub-populations (Mobaraki et al. 2015, 2018) with only some level of intrapopulation connectivity (Campos et al. 2018). Improving the connectivity of the meta-population network will be of utmost importance for the survival of the crocodiles in the near future.

Conclusion

Our findings provide first insights into habitat suitability for Mugger crocodiles (*C. palustris*) in the Indian subcontinent and West Asia derived from climate data. The future for this crocodile species appears to be uncertain and in despair due to the loss of suitable habitats with stable climate and ever-increasing anthropogenic pressures. New surveys are required to identify potentially undiscovered populations of Mugger Crocodiles in potentially suitable habitats as predicted by our suitability models. Studies focussing on the behaviour and physiology of the Mugger Crocodile are urgently needed to improve our knowledge of the ecology of this species. These data would also be valuable for future niche models as well as the evaluation and management of current and future conservation areas for this species. Given the periodic water shortages and close contact with local people, human/crocodile conflicts may escalate and subsequently cause more problems from a conservation perspective. Defining sanctuaries and/or managing new suitable habitats would be beneficial to controlling those conflicts. Artificial ponds, irrigation drains, and reservoirs could be crucial to the survival of the crocodile in the face of ongoing climate change and urbanisation. Ex-situ conservation facilities would help in managing and conserving the Mugger Crocodile populations in the region.

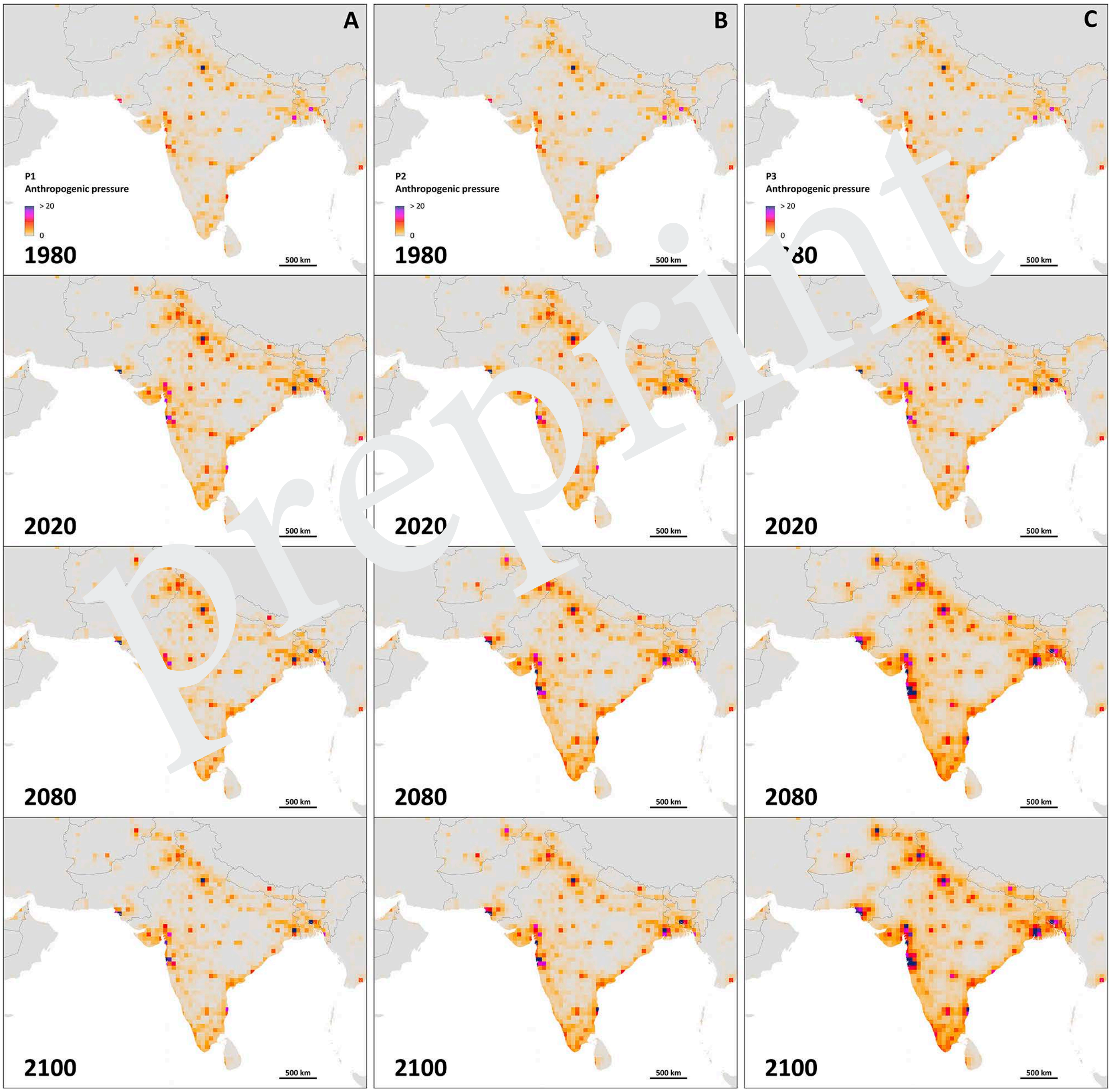

Figure 5. Distribution and intensity of anthropogenic pressures in the time slices 1980, 2020, 2080 and 2100 across 3 storylines.

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Disappearing archosaurs – an assessment of established protected areas in the Philippines to save the critically endangered, endemic Philippine Crocodile (*Crocodylus mindorensis*)

Sabine Harrer[1], Philipp Ginal[1,2], Wei Cheng Tan[1], Jake Wilson Binaday[3], Arvin Cantor Diesmos[4], Rainier Manalo[3], Thomas Ziegler[5,6] & Dennis Rödder[1]

[1] Herpetology Section, LIB, Museum Koenig Bonn, Adenauerallee 127, 53113 Bonn, Germany
[2] Aquazoo Löbbecke Museum, Kaiserswerther Str. 380, 40474 Düsseldorf, Germany
[3] Crocodylus Porosus Philippines Inc., Pag asa, Kapalong, Davao Del Norte, 8113, Philippines
[4] ASEAN Centre for Biodiversity, Domingo M. Lantican Avenue, Los Baños,Laguna 4031, Philippines
[5] AG Zoologischer Garten Köln, Riehler Str. 173, 50735 Köln, Germany
[6] Institute of Zoology, University of Cologne, Zülpicher Str. 47b, 50674 Cologne, Germany

Corresponding author: Philipp Ginal, e-mail: Philipp.ginal@gmx.de

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Abstract. Once distributed all over the Philippines, the endemic Philippine Crocodile (*Crocodylus mindorensis*) is nowadays threatened with extinction. It is estimated that less than 140 mature individuals live in the wild. Human activities like fishing and poaching, as well as land-use change and habitat conversion cause a continuing threat to the remaining populations. Therefore, designated protected areas (PAs) were evaluated with species distribution models (SDMs) and also to see if most suitable areas are covered by PAs in order to improve future conservation efforts. For this purpose, the existing IUCN-reserves were analysed for potential habitat suitability (combining bioclimatic and remote sensing variables), wetland occurrences and the human footprint index by using MaxEnt and QGIS. Based on species records, our final SDM showed high performance and revealed the climatically most suitable areas for the species, which were mostly on Luzon and Mindanao. However, only small parts of the climatically suitable wetlands are currently covered by reserves (0.3–46.3%). In addition, none of the species' records was located within a PA. The anthropogenic pressures in the reserves measured by human footprint index (considering eight variables i.e. 'population density', 'navigable waterways', 'crop lands' and 'roads') were diverse and varied between a low and moderate level. Most of the records were found in areas with a moderate human footprint. Considering the three criteria, 'Lake Lanao Watershed Reservation', 'Angat Watershed Forest Reserve District (Metro Water District)', 'Northern Sierra Madre Natural Park', 'Talaytay Protected Landscape' and 'Agusan Marsh Wildlife Sanctuary' revealed to be the most suitable conservation areas for *C. mindorensis*, whereas suitable areas outside PAs are highly recommended for further surveys. We recommend to declare Ligawasan Marsh, Mindanao as a PA as this area harbours a large population of *C. mindorensis*. The declaration of more climatically suitable areas with low level of human footprint to PAs is a necessary step for the long-term conservation of this endemic crocodile species. The current network of existing PAs needs improvement in order to provide well-suited and long-term protection for *C. mindorensis.* More surveys are also necessary to find hidden, so far overlooked populations and to assess *C. mindorensis* tolerance level for human impacts.

Key words. Crocodylia, species distribution modelling, human footprint index, wetlands, IUCN, MaxEnt, conservation, reptiles.

Introduction

The Philippines are one of the 20 global megadiverse countries and a major biodiversity hotspot in Southeast Asia due to its isolated location and diverse topography (CBD 2018, Peria 2014, UNDP 2021, von Rintelen et al. 2017). These megadiverse countries are home to about 70–80% of the plant and animal species on the planet, of which more than 20,000 are endemic (Ambal et al. 2012, FPE 2013). Almost half of the terrestrial animals occurring in the Philippines are also endemic to the country and in the case of reptiles, ~ 70% (244 of the 352 known species in 2017) of native species are endemic (PSA 2019). According to the categories of the International Union for Conservation of

Nature's (IUCN) Red List of Threatened Species, 652 native species of animals and plants are classified as 'Vulnerable', 542 as 'Endangered', 309 as 'Critically Endangered' and 15 of those (all members of the fish genus *Barbodes*) are already extinct (IUCN 2021a).

The Philippine Crocodile *Crocodylus mindorensis* Schmidt, 1935 has been classified as 'Critically Endangered' on the IUCN Red List since 1996, while the latest assessment was in 2012 (van Weerd 2016). Unlike the Indo-Pacific Crocodile, *Crocodylus porosus* Schneider, 1801, also known as Saltwater Crocodile, which is native to the Philippines but extends as far as South Asia, Southeast Asia and Australia (Uetz 2021), the Philippine Crocodile is endemic to the Philippines (van de Ven et al. 2017). Originally, *C. mindorensis* was distributed over almost the entire archipelago and inhabited islands of Mindoro, Masbate, Samar, Negros, Busuanga, Luzon and Mindanao (Ross 1982, Ross & Alcala 1983). Since the late 1990s and in the 2000s, more surveys have been conducted, but information on the actual distributional range of the crocodile remains scarce. Although it is protected by law since 2001, there are only about 92–137 estimated mature individuals left in the wild to date (van Weerd 2016), and populations are estimated to decline. These are highly fragmented populations in 'Dalupiri Island', 'Northern Luzon' and 'Ligawasan Marsh' on Mindanao (Manalo et al. 2013, Manalo et al. 2015, van Weerd 2016).

The habitats of the relatively small Philippine Crocodile are wetlands with freshwater occurrences such as creeks, ponds, man-made water reservoirs, mangrove areas and marshes, but also fast-flowing rivers with caves made from limestone cliffs (van de Ven et al. 2017). These caves are used as hiding places just as the ones in sandy and clay river banks. Similar behaviour has also been documented with the introduced population of the species in Paghungawan Marsh, Siargao Island which was part of the government's effort to repopulate the species in the wild (Binaday et al. 2020). The species' altitudinal range extends from the favoured inland wetlands up to 850 m (sea level vs. Cordillera Mountains on Luzon) (Manalo 2007).

The Philippines face several environmental problems like deforestation and forest degradation, water pollution, poaching and illicit wildlife trade (USAID 2021). The national desire for more sustainability, environmental protection and species conservation is often contrasted by the poor income situation of local communities (Adams et al. 2004, Jaisankar et al. 2018). Furthermore, large parts of protected areas (PAs) overlap with the ancestral domains (Perez 2018). Local communities living close to or even within these areas rely on the local resources and will be socio-economically harmed by strict environmental regulations, especially if there are no alternative livelihoods (Adams et al. 2004). In fact, some of the greatest threats for the Critically Endangered *C. mindorensis* is the use of its natural habitat by rural people, as well as habitat destruction. In addition, the crocodiles are often persecuted and their nests destroyed or plundered by humans. Fishing is also considered a danger to these crocodiles as they are likely caught in fishing nets as bycatch (Akmad & Pomares 2008, van Weerd 2016).

As early as 1992, the Philippine government committed itself to the international goals of the Convention on Biological Diversity (CBD). This resulted in several national environmental laws such as the National Integrated Protected Area System (NIPAS) Act of 1992 and the Wildlife Resources Conservation and Protection Act (2001), which are intended to protect the country's natural resources in the long term (DENR-BMB 2021). Currently, 248 areas have been recognised by the Philippine government as PAs, covering a cumulative area of 7.8 million ha (DENR-BMB 2020). However, it is currently unknown if these PAs provide climatically suitable habitats for the Philippine Crocodile. Species distribution models (SDMs) have been widely used and proven to be very useful in habitat analyses of other species and are used for prioritisation in conservation planning (Binaday et al. 2020, Fois et al. 2018, Ihlow et al. 2015, Rödder et al. 2010, Tan et al. 2022, Tsuyama et al. 2015). SDMs attempt to predict potentially environmentally suitable habitat by linking documented presence records of species to environmental variables and spatial characteristics such as human footprint and availability of surface water based on the species' ecological niche. In this study, it was investigated whether the existing PAs (1) provide suitable wetland habitats and (2) are climatically suitable for the Philippine Crocodile. Furthermore, we (3) included anthropogenic impact measured as human footprint index to identify these PAs where low anthropogenic pressure occurs.

Methods

For the evaluation of suitable PAs for the species, the 248 current PAs, availability of wetland areas, the climatic suitability and anthropogenic pressure were considered. Since the first two criteria are decisive for the basic survival of the ectothermic species, the final ranking involved three steps. In the first step, the wetlands were evaluated. In a second step, the climatically suitable areas of the remaining 117 sites were identified. Anthropogenic pressure to the remaining 114 sites was assessed in the third step. A final ranking was calculated based on the combined proportions of suitable wetland area and climate suitability ('wet-sdm-ranking') and anthropogenic pressures ('hfp-ranking'), which were multiplied with each other. Below we describe our workflow in detail.

PAs and wetlands data

As it is easier to implement *in situ* conservation measures of *C. mindorensis* in areas that are subject to minor anthropogenic influence, the coverage of the species range with PAs was assessed in addition to the assessment of available potential habitats. PAs are defined as geographical areas and classified by IUCN standards (categories I–

VI) to achieve the long-term conservation of nature and the corresponding ecosystems (IUCN 2021b). The World Database of Protected Areas (WDPA) polygon shapefiles were obtained from UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC; UNEP-WCMC & IUCN 2021).

The importance of wetlands was evaluated based on assessed tropical and subtropical wetlands with a resolution of 232 meters downloaded from the Global Wetlands Map (https://www2.cifor.org/global-wetlands/) (Manalo et al. 2018, van Weerd & van der Ploeg 2012). Gumbricht et al. (2017) developed a mapping method combining different data sources and methods, and classified wetlands into three key biophysical attributes: 'long-term water supply', 'annually or seasonally water-logged soils' and 'a geomorphological position where water can be supplied and retained'. Seven categories were selected for *C. mindorensis*: 'open water', 'mangrove', 'riverine', 'floodplains', 'marshes', 'swamps' and 'fens'. Furthermore, an additional category was added by importing a high-resolution water layer from the Global Runoff Data Centre (GRDC) to assess the suitability of river networks for the crocodile (GRDC 2020).

Species records and predictor variables

Species occurrence records were collected by JWB and RM between 2003 and 2021. The dataset was examined for outliers in QGIS, ver. 3.16.3 with GRASS 7.8.5 (QGIS.org 2021), but not corrected for potential spatial autocorrelation due to the few occurrence records. Habitat suitability was predicted using SDMs based on a combination of 46 environmental variables (Supplementary Table S2; Cord & Rödder 2011). The 19 bioclimatic variables were obtained from Worldclim database, ver. 1.4 and contain interpolated elements from different climate conditions collected over a period of 30 years (1960–1990) with a resolution of 30 arc seconds (Hijmans et al. 2005). The remaining 27 environmental predictors were derived from Moderate Resolution Imaging Spectroradiometer (MODIS) sensors of two NASA satellites. The spatial resolution of the pre-processed remote sensing variables amounts to 30 arc seconds and the temporal resolutions are 8-day averages (MOD11A2) and 16-day averages (MCD43B4) (Mu et al. 2007, Scharlemann et al. 2008). Since SDMs are sensitive to multicollinearity of predictors (De Marco & Nóbrega 2018, Merow et al. 2013), we calculated Variance Inflation Factor (VIF) in R (ver. 4.0.3; 'usdm package') (Naimi et al. 2014, R Core Team 2020) to exclude highly correlated variables, when one of them exceeded the value of 10. The final variables were temperature ranges, precipitation and isothermality (Supplementary Table S2).

Species distribution modelling

For SDM, MaxEnt was chosen as this machine-learning programme (Phillips et al. 2006, Phillips et al. 2016) is shown to be more reliable than other modelling tools especially when dealing with small sample sizes (Elith et al. 2006). As the historic distributional range of *C. mindorensis* covers large parts of the Philippines (Uetz 2021), the whole country was chosen as background area. In addition, the records used for SDM construction were reduced to one per grid cell to reduce sampling bias (Phillips et al. 2009).

Model fitting and selection followed the procedure described in Ginal et al. (2022) and is based on testing multiple regularisation multipliers (0.5 to 2.5 in steps of 0.1, as well as 5 and 10) and feature classes (LP, LQ, LH, LT, LQP, LQH, LQT, LPH, LPT, LHT, LQPT, LQHT, LPHT, LQPHT; L = Linear, P = Product, Q = Quadratic, H = Hinge, T = Threshold)). MaxEnt's raw output format was used for further processing and model selection, and the averaged AICc [corrected Akaike Information Criterion (Warren & Seifert 2011)] and AUC (Elith & Graham 2009, Lobo et al. 2008, Phillips & Dudík 2008) were calculated across ten replicates. Further, AUC was used as an evaluation of the model performance (Elith et al. 2010). For AUC calculation, the presence data were randomly divided for model training (80%) and testing (20%) using the bootstrap approach. For model selection, the lowest average AICc and an $\mathrm{AUC}_{\mathrm{Test}}$ above 0.7 were used (Phillips & Dudík 2008, Warren & Seifert 2011). The final model was replicated 100 times, again with an 80:20 split for training and testing. Finally, the average over the 100 replicates was calculated and evaluated using a combination of AUC (Elith et al. 2006) and True Skills Statistics (TSS) (Allouche et al. 2006, Shabani et al. 2018). For the final model, cloglog format was used as output. Considering the limited number of available occurrence records and the historical distribution of the species, the 'minimum training presence'-threshold was chosen for presence/absence.

The above mentioned wetland shapefile was overlaid with the reclassified MaxEnt-output (settings '0 – threshold = NA; ≥ threshold = 1') and then analysed together with PAs using the 'zonal.histogram'-raster function in QGIS (QGIS.org 2021). The obtained numbers of grid cells per category were summed up per reserve in proportion to the total area of the reserve.

To obtain sums and counts from the final model, the MaxEnt output was subjected to a second but separate classification in a first step (settings '0 – threshold = NA'). Then this reclassified MaxEnt output was rescaled within the range 0–1 before it was analysed with the shapefile generated in the 'zonal.histogram-analysis' using the 'zonal.statistics'-raster function in QGIS. The generated data provided information on how well the habitat is suited for the Philippine Crocodile in terms of climatic conditions ('sum'). Furthermore, it was possible to calculate the area of suitable habitat within a PA using 'count', which calculates the number of grid cells of the suitable area. The sum values were ranked in descending order. Since the resolutions of the MaxEnt-map (~ 1000 m) and the wetlands map (232 m) differ, both rankings were multiplied and a new combined ranking was assigned ('wet-sdm-ranking', ascending order).

Table 1. Results of the ten best MaxEnt models used for model selection, ranked by the mean AICc values and with information on the regularisation multipliers, feature classes, number of parameters, AICc, AUC_{Train} and AUC_{Test}. The final model used for the following processes is shown in bold.

Regularisation	Features	nParameters	AICc	AUC_{Train}	AUC_{Test}
0.6	**LPT**	**7.5**	**253.40**	**0.92**	**0.86**
0.9	L	6.5	256.08	0.90	0.83
1.0	LP	6.5	260.48	0.93	0.89
0.8	LP	6	265.08	0.88	0.89
1.2	LPT	5.5	266.02	0.88	0.86
1.1	LPT	6	266.06	0.86	0.84
1.0	LT	7	266.30	0.90	0.87
1.1	L	5.5	266.67	0.87	0.83
1.0	L	6.5	266.94	0.88	0.83
1.3	LT	5	267.03	0.90	0.85

Anthropogenic pressure

To assess the potential effect of anthropogenic pressure on the crocodiles, the 2018 release of human footprint was obtained from SEDAC (NASA Socioeconomic Data and Applications Center) and added to our analyses. These maps comprise eight variables (i. e. 'population density', 'navigable waterways', 'crop lands' and 'roads') to measure the direct and indirect human pressure (Venter et al. 2018). The human footprint-ranking ('hfp-ranking') was computed based on means of the 'zonal.statistics'-raster function of the combined map of "wildareas v3 2009 human footprint" and previously mentioned PAs shapefile.

Results

Species distribution modelling

For model fitting, MaxEnt computed 3450 models in total (23 regularisation multipliers × 15 feature class combinations × 10 replicates) of which the ten best performing models were ranked according to the lowest average AICc (Table 1). The ten models revealed high AUC values [AUC_{Train} 0.86 – 0.93, AUC_{Test} 0.83 – 0.89]. The values of the final model, which was replicated 100 times, were: regularisation multiplier 0.6, feature classes LPT, AUC_{Train} 0.92, AUC_{Test} 0.86 and TSS 0.45 ± 0.18. 'Mean diurnal range of temperature' had the highest contribution to the final SDM (36.4%), followed by 'isothermality' (16.8%), 'seasonality' (8.5%), 'precipitation of coldest quarter' (8.4%) and 'annual range of NDVI' (7.9%). The remaining variables contributed only less to the model performance (Table 2).

Availability of wetlands, climatic suitability and anthropogenic pressure

Only 57 of the 248 national PAs are currently designated by the IUCN. The areas of the 248 PAs strongly differed and ranged from 0.04 km² ('HinuluganTaktak Protected Landscape', Luzon) to 10,881.81 km² ('Palawan Game Refuge and Bird Sanctuary', Luzon). In the first step of ranking, 131 PAs were excluded from further evaluation due to the lack of habitat availability (Supplementary Material S1). In the second step another three areas were excluded as they did not provide suitable climatic conditions. The remaining 114 PAs were included in the final ranking.

Considering the results of the 'sdm-ranking', the PAs 'Northern Sierra Madre Natural Park' (North Luzon),

Table 2. MaxEnt variable contribution of the final species distribution model for *Crocodylus mindorensis*.

Variable	Abbreviation	Derived variable	Variable contribution [%]
V39	ED15078_bio2	Mean Diurnal Range of Temperature	36.4
V40	ED15078_bio3	Isothermality (Bio2/Bio7) (*100)	16.8
V41	ED15078_bio4	Seasonality	8.5
V19	bio_19	Precipitation of Coldest Quarter	8.4
V26	ED1514_bio7	Annual Range of NDVI	7.9
V37	ED1515_bio11	Mean EVI of Coldest Quarter	5.2
V14	bio_14	Precipitation of Driest Month	4.2
V18	bio_18	Precipitation of Warmest Quarter	3.9
V35	ED1515_bio7	Annual Range of EVI	3.8
V27	ED1514_bio10	Mean NDVI of Warmest Quarter	2.9
V13	bio_13	Precipitation of Wettest Month	1.9
V43	ED15078_bio6	Min Temperature of Coldest Month	0.1
V31	ED1515_bio3	Isothermaility (BIO2/BIO7) (*100) of EVI	0.0
V30	ED1515_bio2	Mean Diurnal Range of EVI	0.0
V22	ED1514_bio3	Isothermaility (BIO2/BIO7) (*100) of NDVI	0.0
V21	ED1514_bio2	Mean Diurnal Range of NDVI	0.0

Table 3. Top 5 reserves suitable for the Philippine Crocodile: reserve name, reserve category (assignment according to IUCN), reserve area, climatically suitable area [relative to reserve area in %], climatically suitable wetland area [relative to reserve area in %], and ranks according to the wet-sdm-ranking, hfp-ranking, and final-ranking.

Name	Reserve category	IUCN	reserve area [km²]	climatically suitable area [km²]	wetland area [km²]	wet-sdm-ranking	hfp-ranking	final-ranking
Lake Lanao Watershed Reservation	Watershed Reservation	not assigned	1712.93	946.87 [55.3%]	113.82 [6.6%]	2	34	1
Angat Watershed Forest Reserve District (Metro Water District)	Watershed Forest Reserve	not assigned	545.74	191.96 [35.2%]	2.83 [0.5%]	38	2	2
Northern Sierra Madre Natural Park	Natural Park	II	3569.69	1664.39 [46.6%]	96.22 [2.7%]	1	86	3
Talaytay Protected Landscape	Protected Landscape	V	35.98	1.44 [4.0%]	0.09 [0.3%]	100	1	4
Agusan Marsh Wildlife Sanctuary	Wildlife Sanctuary	IV	409.41	247.32 [60.4%]	189.43 [46.3%]	3	37	5

'Lake Lanao Watershed Reservation' (West Mindanao), 'Quirino Protected Landscape' (Luzon), 'Allah Valley Watershed Forest Reserve' (South Mindanao) and 'Upper Agno River Basin Resource Reserve' (Luzon) revealed the highest scores with climatically suitable areas between 549.29 and 1,664.39 km² (Table 3, Supplementary Material S1).

According to the 'wet-sdm ranking', the top five reserves with the highest scores were 'Northern Sierra Madre Natural Park' (North Luzon), 'Lake Lanao Watershed Reservation' (West Mindanao), 'Agusan Marsh Wildlife Sanctuary' (East Mindanao), 'Mindoro Island's Mangrove Swamp Forest Reserves as per Presidential Proclamation 2152' (South Luzon) and 'Allah Valley Watershed Forest Reserve' (South Mindanao). This coincided with the distribution of the species records, which were also identified on the Northern portion of Luzon Island and Mindanao Island (Figs 1 and 2). However, none of the species' occurrence records laid inside the top five reserves. Only two records were located on the edge or close to a reserve ('Northern Sierra Madre Natural Park'). Following the IUCN categories, three PAs were not assigned to any IUCN category ('Lake Lanao Watershed Reservation', 'Mindoro Island's Mangrove Swamp Forest Reserves' and 'Allah Valley Watershed Forest Reserve'), while 'Agusan Marsh Wildlife Sanctuary' belongs to category IV 'habitat/species management area', and 'Northern Sierra Madre Natural Park' is classified as 'national park' (category II). 'Lake Lanao Watershed Reservation' and 'Allah Valley Watershed Forest Reserve' are two reserves proclaimed by the national government through Presidential Proclamations No. 871 and 2455, respectively. Governance and management of these reserves are also covered by the NIPAS Act of 1992. Meanwhile, the Presidential Proclamation 2152 declares several mangrove areas throughout the country as 'Mangrove Swamp Forest Reserves', this includes the mangroves areas of Mindoro Island mentioned in this study. Our analysis showed that there are generally few areas with low anthropogenic pressure except for the mountain ranges on Luzon (Fig. 3). Not surprisingly, high human activity was found around the capital Manila. On the main island of Palawan, the human footprint was low, whereas in the Visayas, except for 'Samar Island', there were only a few contiguous areas with low human footprint. Mindanao, meanwhile, has a very homogeneous pattern distributing between high and low anthropogenic pressure. The reserves with the lowest human footprint were 'Talaytay Protected Landscape' (Central Luzon, IUCN category V = 'protected landscape/seascape'), 'Angat Watershed Forest Reserve District (Metro Water District)' (Luzon, not assigned), 'Mt. Mantalingahan Protected Landscape' (Luzon, IUCN category V), 'Amro River Protected Landscape' (Central Luzon, IUCN category V) and 'Mt. Pulag Protected Landscape' (Luzon, not assigned) (Supplementary Material S1).

Considering the availability of wetlands, the climatic suitability and the anthropogenic pressure, the final ranking revealed 'Lake Lanao Watershed Reservation' (West Mindanao, not assigned), 'Angat Watershed Forest Reserve District (Metro Water District)' (Luzon, not assigned), 'Northern Sierra Madre Natural Park' (North Luzon, IUCN category II), 'Talaytay Protected Landscape' (Central Luzon, IUCN category V) and 'Agusan Marsh Wildlife Sanctuary' (East Mindanao, IUCN category IV) as most suitable reserves for the Philippine Crocodile. The reserves covered a total area of between 35.98 km² and 3,569.69 km², with climatically suitable areas of between 1.44 km² and 1,664.39 km², and finally consisted of between 0.09 km² and 189.43 km² climatically suitable wetland habitats. The anthropogenic pressure strongly varied between low (ranks 1, 2, 34 and 37 in the 'hfp-ranking') and moderately high (ranks 86; Tables 3 and S1).

Discussion

General results

The assessed PAs strongly differ in size, IUCN/reserve category, climatic suitability, habitat availability and anthropogenic pressure, and therefore a trade-off is necessary to identify the most suitable PAs to protect the Philippine Crocodile *in situ*. Our SDMs indicated an average daily temperature range (36.4%), temperature fluctuations during the course of the day and year (16.8%), and seasonality (8.5%) to be most relevant climatic parameters for the Philippine Crocodile (Table 2). Ambient temperature influences the nest temperatures for reproduction and long-term maintenance for the species (Akmad & Pomares 2008). The amount of precipitation in the coldest quarter was also found important for the crocodiles (Table 2). Specific weather or climatic events such as floods can cause mortality to juveniles when they are still vulnerable (van de Ven et al. 2009, van de Ven et al. 2017). Furthermore, prolonged dry periods limit food resources and are therefore a threat for all age groups (Mazzotti et al. 2009).

Assessment of top five PAs and recommendations to establish new reserves

'Lake Lanao Watershed Reservation' (not assigned) is a watershed reservation located in the province of Lanao del

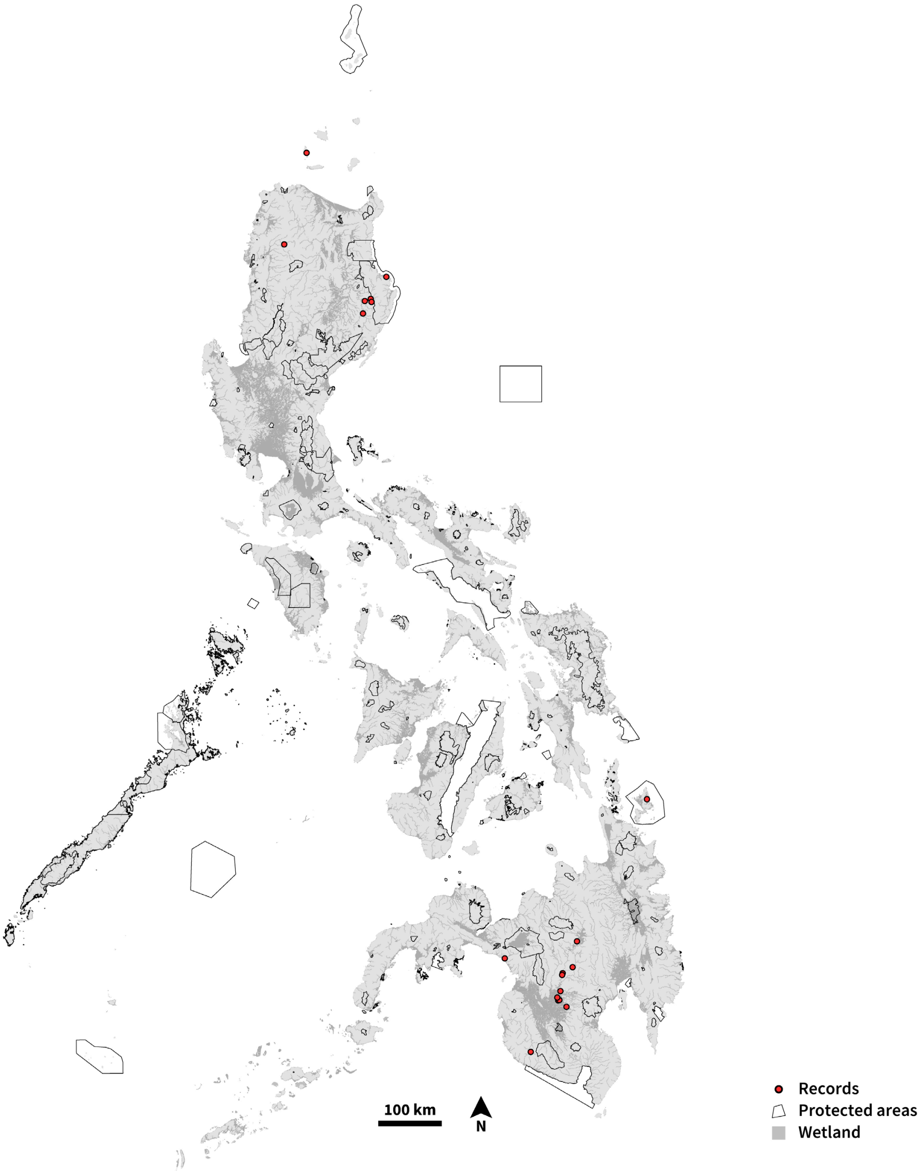

Figure 1. Map of the Philippines including species records of the Philippine Crocodile (*Crocodylus mindorensis*), wetland habitats, and national PAs.

Sur of the Bangsamoro Autonomous Region in Muslim Mindanao (BARMM) on the island of Mindanao. With a total reserve area of 1,712.93 km², covering 113.82 km² of climatically suitable wetland habitats, it is the second largest of the top five. Lake Lanao is Mindanao's largest lake (36.300 ha) and has five watersheds with rivers and major tributaries stretching over a total length of 431 km (DENR 2023). Its wetlands border the lake to the east for the most part and mainly consist of general marshes (39%), swamps (26%), fens (16%) and rivers (14%). The hydropower plant built along the lake and the Agus River is responsible for a significant contribution to Mindanao's electricity supply (70%) (DENR 2023), which also reflected by high anthropogenic pressure. The PA is also recognised as key biodiversity area (KBA) by IUCN and is therefore of crucial global importance. The lake is home to 18 endemic freshwater fish and supports a large number of waterfowl and other birds such as *Halcyon chloris* (White Collared Kingfisher) (DENR 2023). Moreover, a healthy population of *C. mindorensis* is inferred to be thriving in the rivers of Miundas, Maladi and Matling in Lanao del Sur with a recent discovery of individuals in 2019 and affirmation of its presence by the local community (Manalo et al. 2019). The headwaters of these three rivers are located in the vicinity of Lake Lanao.

The 'Angat Watershed Forest Reserve District (Metro Water District)' (not assigned to IUCN categories) protects the watershed of the Southern Sierra Madre north of Manila, where surface water flows into the Angat River and its tributaries. The rivers hold a proportion of 74% of the total wetlands in the PA. The reserve covers an area of 545.74 km² in the eastern part of Bulacan Province and the northern portion of Rizal Province at elevations between 490 to 1,206 metres a.s.l. The PA extends to the provinces of Nueva Ecija and Quezon and is centred on an artificial lake created by the Angat Dam which, together with the Ipo Dam (7.5 km downstream), supplies the majority of Metro Manila's water requirements. Despite this fact,

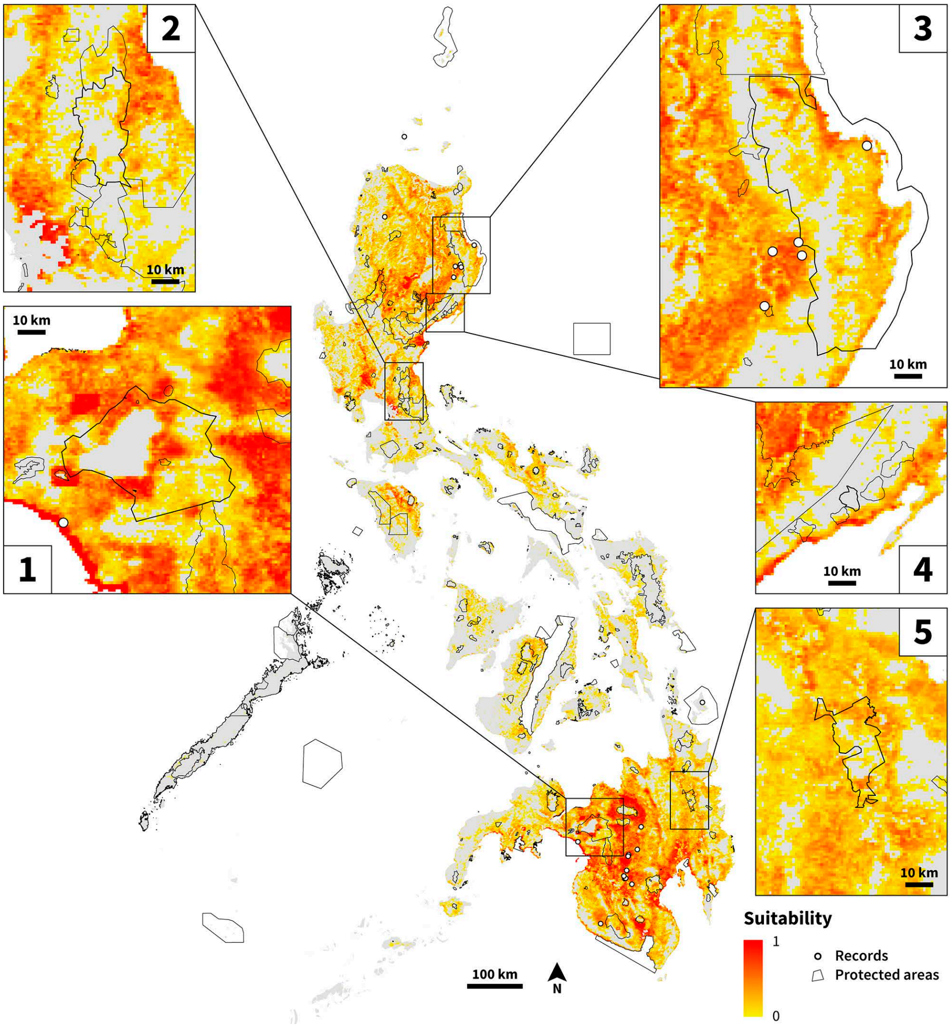

Figure 2. Suitable climatic space for the Philippine Crocodile *(Crocodylus mindorensis)* according to the results of our species distribution model as well as species records and national PAs. The five best suitable PAs according to our final ranking are highlighted.

the PA has a homogenous low human footprint. The watershed is a popular birdwatching site and a biodiversity hotspot, containing most of the remaining closed canopy forests in Central Luzon. A herpetofaunal survey conducted by McLeod et al. (2011) documented 19 frog, 22 lizard, two turtle, and 20 snake species within the PA, but survey efforts were mostly focused on low elevation sites (200–600 m a.s.l.). However, the presence of *C. mindorensis* in this PA is still unknown and needs further surveys. Although the area is highly suitable for the crocodile, large dams may restrict movement of the animals and the separation of populations would have a detrimental effect on the long-term conservation of the species (McAllister et al. 2001) or would require management or assisted migration. Nevertheless, the Philippine Crocodile has been documented to be able to climb steep slopes (Binaday et al. 2020) and studies are yet to be done on whether such infrastructures will have a significant impact on the species' population.

'Northern Sierra Madre Natural Park', a large national park, covers 3,569.69 km² of the north-east coast of Luzon. About 21.02% of the park is highly suitable. The wetland area, covering 17 km², is mainly consisting of rivers, swamps and marshes. The areas of the Sierra Madre Mountains on the east coast and the Cordillera Mountains on the middle-west side are exposed to little or no anthropogenic pressure. Only the settlements and human activities along the branches of the Palanan River possess medium to high human footprint. In the east of San Mariano, there are already several crocodile sanctuaries for this species (Manalo et al. 2018, van de Ven et al. 2017). However, the sanctuaries are currently located outside the PA where three of the species occurrences were found (Fig. 1). We highly recommend the extension of the designated reserve to cover areas surrounding the sanctuaries and especially the area north along the foothills of the Dicatian River as a potential reserve, where there is high climatic suitability and low human footprint (Figs 2 and 3). This park contains

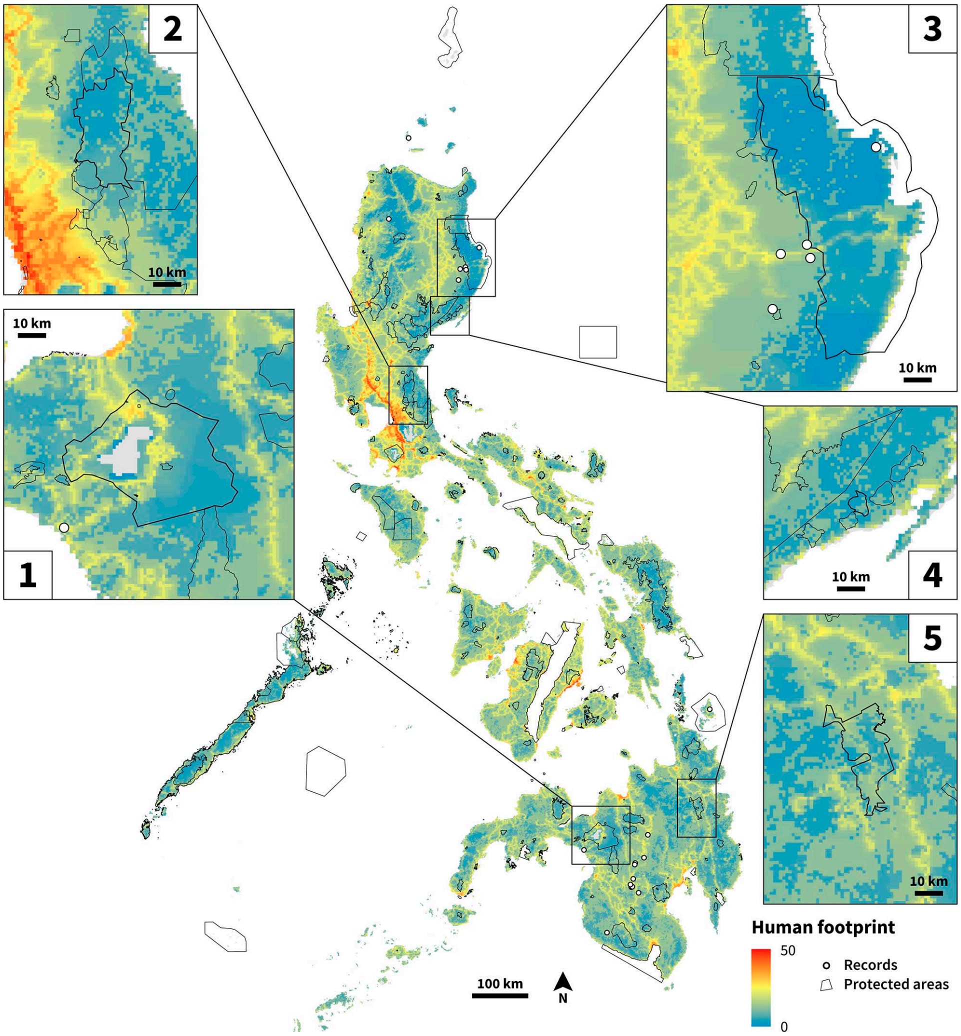

Figure 3. Anthropogeneic pressure in the Philippines measured as human footprint index as well as species records of the Philippine Crocodile (*Crocodylus mindorensis*) and national PAs. The five best suitable PAs according to our final ranking are highlighted.

the highest species richness of the Philippines, a wide variety of habitats (DENR 2015) and is home to many indigenous people (CEPF 2001). Among the Philippine endemic species, about 30% of all bird species and 62% of all mammal species are found here. It is also home to 35 threatened species (van der Ploeg et al. 2011), including *C. mindorensis*, Philippine Eagle (*Pithecophaga jefferyi*), Isabela Oriole (*Oriolus isabellae*) and Sierra Madre Forest Monitor (*Varanus bitatawa*) (DENR 2015). A herpetofaunal survey was conducted by Brown et al. (2013) in the PA and documented a total of 101 species of amphibians and reptiles, including the two species of crocodiles in the Philippines – *Crocodylus mindorensis* and *C. porosus*. Although much of the PA is covered by forest, it is reducing by about 1,400 ha per year (DENR 2015). Van der Ploeg et al. (2011) estimated that between 20,000–35,000 m^2 disappear from the national park each year due to illegal timber logging, but little action has been taken against this so far.

'Talaytay Protected Landscape' is located in northern Aurora (province) and covers the Talaytay River watershed in the Sierra Madre range of the island of Luzon. The PA comprises an area of 35.98 km^2, making it the smallest of the top five PAs, but like 'Lake Lanao Watershed Reservation' it is a KBA. This Protected Landscape (IUCN category V) stretches from the rugged interior including the source region of the Talaytay River to its mouth at the lowlands of the municipality of Dinalungan. Some important bird and mammal species are native to this PA, such as *Penelopides panini* (Tarictic Hornbill) or *Macaca fascicularis philippensis* (Philippine Long-Tailed Macaque). The wetlands there consist exclusively of rivers, and anthropogenic pressure is low. 'Northern Sierra Madre Natural Park' and 'Talaytay Protected Landscape' are PAs that are close to the coast or include parts of it. These habitats might also be suitable for the much larger *C. porosus*, which might outcompete the Philippine Crocodile for food, nesting sites or basking sites. Furthermore, hybrids between both species are known from captivity, which should be considered for conservation actions in these areas.

Almost 60% of Agusan area are climatally suitable of climatically suitable area and has 189.43 km^2 of suitable wetland habitat. The main parts of the wetlands are marshes, swamps and flood-outs. The persistence of wetlands is essential as they store atmospheric carbon in the plant roots and filter upstream pollutants, thus protecting coral reefs by holding back sediments (Gibbens 2021, Kumar et al. 2017). The Agusan River is accessible by small boats and therefore shows high anthropogenic pressure from northwest to southeast portion of the marsh (Gibbens 2021). The conversion of nearby areas along the river into fish ponds, rice fields, and/or settlements by the indigenous Manobo people result to areas with slightly increased anthropogenic pressure (Fig. 3) (Ramsar Sites Information Service 1999). The remaining part of the PA is exposed to low to moderate human pressure. In fact, it is even known to be the 'least disturbed freshwater wetland' in the Philippines (ASEAN CHM-ACB 2022). Having low human pressure and high suitability, the surrounding areas of Lake Mambagongon appear to be a hotspot for crocodiles and the lake is already known as a crocodile reproduction site (Tomas et al. 2009, van Weerd 2010). This PA is also a significant transit point for wild birds in Asia (DENR 2022) and home for 197 bird species as well as 53 reptile and 240 vascular plant species (ASEAN CHM-ACB 2022). Among the threatened species native to the area are the two crocodile species, the Philippine Duck (*Anas luzonica*), Golden-Crowned Flying Fox (*Acerodon jubatus*) and Philippine Sailfin Lizard (*Hydrosaurus pustulatus*) (DENR 2022). Philippine Crocodile populations were reported to occur in this PA but actually this revealed to be a *C. porosus* locality (Ross 2008). The coexistence of both species in the Agusan Marsh is still uncertain (Manalo et al. 2012).

Legislated PAs offer a large natural habitat for the species with the absence or minimal presence of anthropogenic pressures. The governance of such reserves is through the Protected Area Management Board (PAMB) whose members include several stakeholders from public and private sectors. This management board ensures that activities that will be conducted within the PA's boundaries abide with the national laws, particularly with the NIPAS Act. The strict regulation of anthropogenic activities within these reserves provide a safeguard for these habitats to remain intact and ensure its ecological integrity. Moreover, legislated PAs have allocated government funds for their management and protection. Additionally to the top five reserves, we recommend Ligawasan Marsh Game Refuge and Bird Sanctuary on Mindanao for the establishment of a new reserve, which is not a declared PA yet, but in reality there is a large population of *C. mindorensis* present. The area also shows high climatic suitability and low level of human footprint. The declaration as a PA is highly important for the conservation and existence of the Critically Endangered Philippine Crocodile.

Most of the species occurrence records in this study were outside declared and legislated PAs. Establishment of these habitats into PAs would entail a large sum of funds and efforts, which usually takes years to be established. Under the Philippine Wildlife Resources Conservation and Protection Act of 2001, public and privately owned areas outside PAs which serve as a habitat for threatened species can be declared as a Critical Habitat. Similar to legislated PAs, the declaration provides a layer of protection through a management board which regulates activities within the Critical Habitat, but takes shorter time to establish.

Crocodiles role in the ecosystem and human-wildlife conflicts

Crocodiles may serve as umbrella species for their ecosystems, which enables the protection of other threatened species and entire ecosystems. In the case of the Philippine Crocodile, there are many other wetland-dependent species with threatened status that would benefit from the expansion of existing PAs or the establishment of new ones in order to better protect crocodiles, including Philippine natives or even endemics such as *Pelochelys cantorii* which is Critically Endangered (Brown et al. 2013), *Anas luzonica, Hydrosaurus pustulatus, Limnonectes parvus, Platymantis sierramadrensis, Sanguirana tipanan* (Brown et al. 2013, Sanguila et al. 2016), which are Vulnerable, as well as diverse migratory birds.

Bucol et al. (2020) and Corvera et al. (2017) have shown that crocodile species native to the Philippines might have positive impact on the fish stocks. Brown et al. (2021) suggests *C. mindorensis* as a potential natural pest control agent based on analyses of the digestive tract. Invasive species such as *Pomacea canaliculata* (Golden Apple Snail) or *Rattus tanezumi* (Asian House Rat) are agricultural nuisances which are preyed by *C. mindorensis*.

The increase of protected reserves suitable for the Philippine Crocodile is also necessary to prevent future extinction of the species in the wild. Unfortunately, the main threat for *C. mindorensis* concerns its habitat, particularly fragmentation, use and destruction. The human footprint index can be a useful indicator of anthropogenic expansion and habitat loss, even if it is assessed remotely and can slightly differ from a local scale. Our results reveal that many protected reserves also have larger proportions with moderate to high human footprint (Fig. 3). The expansion of agricultural land for aquaculture or for the cultivation of rice and sugar cane, human-settlement growth, energy production and lucrative mining are destroying the habitats of this species (Corvera et al. 2017, Manalo et al. 2018, Sarmiento 2022, van Weerd & van der Ploeg 2012). Deforestation deprives them of shelter and prey resources (van Weerd & van der Ploeg 2012), which is intensified by fishing activities and can have a particularly negative impact on hatchling survival (Manalo et al. 2015, Somaweera et al. 2018). As a result, crocodiles are being displaced from their former habitats. They are now found more frequently in rice fields and near settlements, increasing the risk of human-crocodile conflicts (Corvera et al. 2017). Therefore, home ranges observed in studies by van Weerd et al. (2006) and van de Ven et al. (2017) should be taken into account when selecting areas for in situ conservation measures and appropriate buffer zones. More space is necessary than is available now to deescalate the aggressive intraspecific, territorial behaviour in particular of young Philippine Crocodiles (Mauger et al. 2017, van Weerd 2010, van Weerd & van der Ploeg 2012).

Unlike the larger and more aggressive species *Crocodylus porosus*, there has only been a single record of human–crocodile conflict in *C. mindorensis* in the country (Corvera et al. 2017). For the Critically Endangered *C. mindorensis*, repopulating the species in the wild can be considered a priority conservation action. Nevertheless, regardless of the species, crocodiles are generally feared by most Filipinos which is a major problem for introducing crocodiles in suitable habitats in the country. This makes the conservation introduction programs for the species highly complex involving political aspects and gathering the communities' support (Manalo et al. 2015). Such complexities would still arise if a decision has been made to introduce the species in suitable habitats within the identified PAs. On the other hand, the low human footprint in PAs makes them ideal as introduction sites with fewer human-crocodile interactions. In spite of such difficulties, there have been two conservation release programs already for the species (Manalo et al. 2015, van de Ven et al. 2009) which proves that it is not impossible to introduce and repopulate the species in the wild.

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Supplementary data

The following data are available online:

Supplementary Table S1. Final ranking containing detailed information on all 248 PAs including wetland categories, lower rankings, and further statistical values.

Supplementary Table S2. List of pre-processed variables obtained from WorldClim and MODIS before calculating multi-collinearity.

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RESEARCH ARTICLE

High freshwater turtle occupancy of streams within a sustainably managed tropical forest in Borneo

Wei Cheng Tan[1] | **Victor Vitalis**[2] | **Julsun Sikuim**[3] |
Dennis Rödder[1] | **Mark-Oliver Rödel**[4] | **Sami Asad**[5]

[1]Herpetology Section, Museum Koenig - Leibniz Institute for the Analysis of Biodiversity Change (LIB), Adenauerallee 127, Bonn 53113, Germany

[2]Panthera Malaysia, Petaling Jaya, Selangor 46200, Malaysia

[3]Forest Research Centre, Sabah Forestry Department, Sandakan, Sabah 90009, Malaysia

[4]Museum für Naturkunde - Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, Berlin 10115, Germany

[5]Tomorrow University of Applied Science, Platz der Einheit 2, Frankfurt am Main 60327, Germany

Correspondence

Wei Cheng Tan, Herpetology Section, Museum Koenig - Leibniz Institute for the Analysis of Biodiversity Change (LIB), Adenauerallee 127, Bonn 53113, Germany.
Email: n.tan@leibniz-lib.de

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Abstract

Despite suffering dramatic declines due to habitat loss and overexploitation, tortoises and freshwater turtles in Southeast Asia remain understudied. Sustainable forest management offers a promising approach for advancing the conservation of threatened turtle populations. This study examines the effect of reduced impact logging (RIL), a sustainable forestry method, on 2 freshwater turtle species. We examined detectability patterns and habitat relationships for the threatened Malayan flat-shelled turtle (*Notochelys platynota*) and the non-threatened Malayan soft-shelled turtle (*Dogania subplana*) in 8 streams within a commercial forest reserve between March and July 2019, in Sabah, Malaysian Borneo. Using single-species occupancy models, we identified covariates associated with the detection and occupancy probabilities of these species across a post-harvest recovery gradient (1–21 years since logging). Covariates used in the models were obtained directly from the field or from open-source remote sensing data. Results for soft-shelled turtles were inconclusive. In contrast, we found a negative association between monthly rainfall and flat-shelled turtle detectability. The occupancy probability of flat-shelled turtles was positively associated with greater distance from logging roads and higher stream flow accumulation. Occupancy probability for flat-shelled turtles and soft-shelled turtles was relatively high throughout the reserve (0.79 ± 0.1 [SD] and

0.57 ± 0.22, respectively). These results, suggest that appropriately managed forests, could serve as invaluable conservation areas for imperiled freshwater turtle species in the region.

KEYWORDS

Chelonia, detectability, *Dogania subplana*, forest management, logging roads, *Notochelys platynota*, reduced impact logging

Freshwater turtles and tortoises are currently considered the most threatened vertebrate taxa, with more than half of all 356 species classified as threatened (Stanford et al. 2018). While Southeast Asia represents a freshwater turtle diversity hotspot with high levels of phylogenetic endemism (Roll et al. 2017, Gumbs et al. 2020), the region also faces widespread species declines (Böhm et al. 2013, Roll et al. 2017). Turtle populations within Southeast Asia are currently being extirpated because of urban development, commercial logging, agriculture, pollution, and climate change (Stanford et al. 2018, Cox et al. 2022). Additionally, the region serves as both a source and market for a thriving turtle trade, with the majority of species facing unsustainable levels of harvesting for regional and international pet, medicine, and food markets (Dijk et al. 2000, Cox et al. 2022, Mohd Salleh et al. 2022). The growing demand and increased market prices for freshwater turtles and tortoises drive an ever-expanding, highly lucrative trade in many Southeast Asian countries (Van et al. 2019, Shepherd et al. 2020, Nijman and Shepherd 2022). In Kalimantan, Indonesia alone, up to 45,000 Southeast Asian box turtles are traded annually (Nijman and Shepherd 2022). While trade in the region is well documented, quantitative data on freshwater turtle responses to anthropogenic disturbance are lacking. Many studies (mainly conducted in America and Australia) of native freshwater turtles have shown negative physiological and behavioral responses to anthropogenic disturbances such as agriculture (Čapkun-Huot et al. 2021, Fulton et al. 2022), urbanization (Selman et al. 2013), and roads (Cassel et al. 2019). Determining the effects of human-induced land use change in Southeast Asia is essential for quantifying these impacts, damage mitigation, and identifying conservation priority areas for the region's threatened freshwater turtles.

Commercial logging activities occur in more than half of the remaining tropical forests (Food and Agriculture Organization [FAO] and United Nations Environment Programme [UNEP] 2020) and represent one of the greatest potential threats to freshwater turtle habitats in Southeast Asia (Huth and Ditzer 2001, Gaveau et al. 2014). Unsustainable management of these timber concessions has led to widespread habitat degradation and declining biodiversity throughout the region (Gibson et al. 2011, Burivalova et al. 2014).

Whilst many logging reserves in the region have been subject to conventional selective logging since the 1970s (Gaveau et al. 2014), the implementation of sustainable forestry methods could present a promising, economically viable alternative (Pinard et al. 1995). Although various sustainable forestry methods are available, reduced impact logging (RIL) has been the most widely adopted and tested in the tropics (Dykstra 2007). This method implements strict timber harvesting guidelines including reduced harvest rates ($< 30\,m^3$ timber per ha) compared to conventional logging, and a series of best practice techniques including directional felling, reduced skid trail construction, pre- and post-harvest planning, and 30-m riparian buffer zones along both sides of permanent water courses >5 m in width (Pinard et al. 1995, Putz et al. 2008, Sabah Forestry Department 2024). These methods result in 50% less damage to remnant forests, thus maintaining watersheds while reducing sedimentation and riparian habitat disturbance (Pinard et al. 1995, Sabah Forestry Department 2024). As such, RIL-managed forests maintain higher biodiversity compared to conventionally logged sites (Bicknell et al. 2014, Brozovic et al. 2018, Bohnett et al. 2022). While responses of various taxa to RIL practices are documented (amphibians, Asad et al. 2021*a*; mammals, Brozovic et al. 2018, Guharajan et al. 2021, Bohnett et al. 2022; birds, Edwards et al. 2012), the impact of RIL on Southeast Asia's freshwater turtles remains unstudied but should prove valuable for informing future conservation measures (Cox et al. 2022).

Quantifying abundance and occupancy are an effective approach for determining the effects of disturbances, such as logging, on turtles (Horn and Gervais 2018, Čapkun-Huot et al. 2021). However, the detection of turtles is typically imperfect because of observer error (Nichols et al. 2000), low population density, cryptic behaviors of individuals, or environmental conditions that influence the likelihood of detection (Gu and Swihart 2004). As such, failure to correct for imperfect detection can result in biased estimation of habitat associations and thus erroneous conclusions (Gu and Swihart 2004, Kellner and Swihart 2014). Temporal or climatological variables have been previously identified as factors associated with detection probability in diurnal (e.g., weather conditions, air and water temperature; Brown 2001, Armstrong 2016, Ocock et al. 2018, Buchanan et al. 2019), and nocturnal freshwater turtles (e.g., lunar phases and cloud coverage; Jensen and Das 2008). These climatological factors may influence the availability of food resources, shelters, nesting sites, and predator activity (Parlin et al. 2018, Escalona et al. 2019, Geller et al. 2022). Thus, it is essential to incorporate detection probability when studying the responses of freshwater turtles to disturbance, and their compatibility with sustainable forest management (Buchanan et al. 2019).

In Malaysian Borneo, Deramakot is a sustainably managed forest reserve using RIL techniques and is occupied by several freshwater turtle species. The Malayan soft-shelled turtle (*Dogania subplana*) is a non-threatened (least concern; Cota et al. 2021), soft-shelled Trionychidae and the Malayan flat-shelled turtle (*Notochelys platynota*) is a threatened (vulnerable; Kusrini et al. 2021) hard-shelled Geoemydidae. Both are harvested throughout the region for local food markets (Walter 2000, Jensen 2006, Jensen and Das 2008), while flat-shelled turtles are also traded internationally (Cheung and Dudgeon 2006, Gong et al. 2009). Several other freshwater turtle species (spiny turtle [*Heosemys spinosa*], Southeast Asian box turtle [*Cuora amboinensis*], and Asian leaf turtle [*Cyclemys dentata*]) occur in the reserve but are detected less frequently. The Malayan soft-shelled turtle is a medium-sized (maximum carapace length = 310 mm) predominately aquatic, omnivorous species (Lim and Das 1999, Pritchard 2001). Although limited ecological information is available, the species is primarily nocturnal and commonly found in small, silted forest streams and fast-flowing rivers (Premono et al. 2015, Mohd Ibrahim et al. 2019, Asad et al. 2021*b*). The Malayan flat-shelled turtle is a medium-sized (maximum carapace length = 360 mm) primarily herbivorous species, although it is reported to occasionally prey or scavenge on animals (Manthey and Grossmann 1997, Lim and Das 1999). This species is diurnal and nocturnal, preferring shallow, clear, sandy-bottomed streams in forested areas and is less aquatic than soft-shelled turtles (Lim and Das 1999, Asad et al. 2021*b*). Previous research indicates that potential fine-scale spatial separation of the 2 species may occur along sedimentation gradients within the same stream (Asad et al. 2021*b*).

In the face of rapid economic development and accompanying road expansion in Borneo (Sloan et al. 2019) and throughout the region (Bradshaw et al. 2009), we attempted to determine detectability and occupancy associations of these 2 freshwater turtle species within Deramakot. Our first objective was to examine the effect of climatological covariates on the detectability of these 2 species. We predicted that temperature and rainfall would be important covariates, as found in previous studies (of other species in other geographic regions; North America, Rowe 2003, Rowe et al. 2009, Anthonysamy et al. 2013; Oceania, Roe and Georges 2008). We also expected lunar phases to play a significant role in the detectability of these nocturnally active turtles (Jensen and Das 2008). Our second objective was to examine the effects of habitat and RIL-associated covariates on the occurrence of these 2 species. We expected that occupancy would be negatively influenced by covariates associated with logging (proximity to logging roads and time since logging). Our final objective was to determine the occupancy probability of the 2 species at sites within an active sustainable logging reserve. Because RIL affects forest structures less than other practices, and thus freshwater turtle habitat quality, we estimated moderate occupancy probabilities (<50%) in the reserve for both species.

STUDY AREA

We conducted this study between March and July 2019 in the Deramakot Forest Reserve (5°14-28′N, 117°19-36′E), in the Malaysian state of Sabah, on the island of Borneo (Figure 1). The climate is humid equatorial (average annual temperature = 26°C) and heavily influenced by both northeast (Nov–Feb) and southeast (May–Aug)

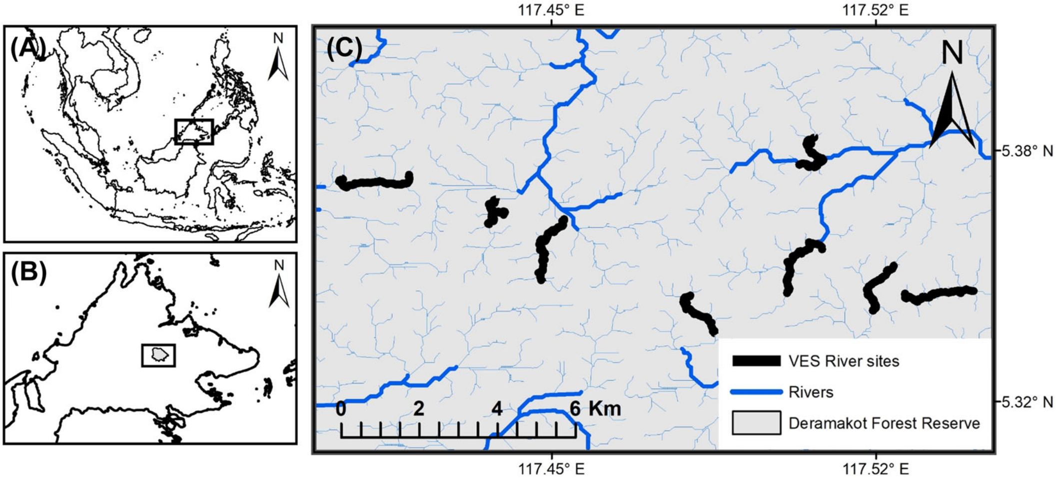

FIGURE 1 Location of A) Sabah, Malaysian Borneo, B) the Deramakot Forest Reserve in central Sabah, and C) the visual encounter survey (VES) stream sites within the center of the reserve used in single-species occupancy modeling of flat-shelled turtles and soft-shelled turtles in 2019.

monsoons with annual precipitation ranging between 1,700 mm and 5,100 mm (Kleine and Heuveldop 1993, Huth and Ditzer 2001). Geologically, Deramakot is characterized by tertiary sediments, mostly mud and sandstone (Huth and Ditzer 2000). The predominant Acrisols are poor in nutrients and easily eroded, especially when plant cover is removed (Sabah Forestry Department 2024). The reserve encompasses a 550-km² area of predominantly hilly, lowland (50–350 m above sea level) dipterocarp forest, dominated by *Dipterocarpus*, *Shorea*, and *Parashorea* species (Sabah Forestry Department 2024). Sustainable forest management techniques (predominately RIL) have been implemented in the reserve since September 1989 (Huth and Ditzer 2000). In 1997, Deramakot became the first tropical production forest to receive Forest Stewardship Council (FSC) certification and has been recognized for its sustainable forest management (Lagan et al. 2007). Since 1997, RIL techniques have been used throughout the reserve in accordance with the certified FSC guidelines (Pinard et al. 1995). The reserve now contains a mosaic of dipterocarp forests at varying levels of regeneration following logging (0–25 years). Previous research indicates that Deramakot contains a high diversity of mammals and amphibians despite logging (Sollmann et al. 2017, Asad et al. 2022).

METHODS

Freshwater turtle sampling and covariate collection

Within Deramakot, we established 8 standardized visual encounter survey (VES) sites (800–3,000 m in length) along separate river reaches (Figure 1). We selected these 8 sites within forestry compartments at varying levels of forest regeneration following RIL (1, 2, 6, 10, 11, 19, and 22 years since logging; Table A1). To ensure standardization of survey effort across reaches varying in length, we divided all VES sites into contiguous subplots 200 m in length (with varying widths depending on the river). We surveyed each VES and nested subplots on 3 occasions between March and July 2019, with 30–55 days between surveys. Two surveyors conducted surveys between 1830 and 2200 hours by walking the length of each subplot (0.33–0.66 m/sec), along opposite banks of the river. We recorded all flat-shelled turtles and soft-shelled turtles detected within or directly adjacent to the water body (<1 m removed). For detected turtles, we collected global positioning system location and time of observation. We hand-captured all flat-shelled turtles and determined adult or juvenile status, curved carapace or straight plastron length, and parasite (e.g., freshwater leeches and nematodes) burden at the point of capture (pausing the survey during processing). We took photographs of the carapace and plastron of flat-shelled turtles for individual identification. Only 8 flat-shelled turtles were not captured (because of escape) during the study (roughly 5%). We did not capture soft-shelled turtles because of the difficulty in handling this species. Following processing, we released turtles behind the observers to reduce the possibility of counting individuals repeatedly. Because of the speed of these species and our personal observations in the field, we find it highly unlikely that our study species swam past the observers and were thus double counted. For both species, we also recorded the stream width, depth, and siltation cover at each turtle detection locality. As these data were not collected systematically throughout each subplot, we could not include them in the modeling process, but we conducted non-parametric testing to determine variation between stream width, depth, and siltation at flat-shelled turtle and soft-shelled turtle detection localities. This data, along with other observations of the species' natural history can be found in Asad et al. (2021*b*).

We collected covariates associated with the detectability or activity of other freshwater turtle species in Borneo (Jensen and Das 2008), and other geographic regions (Rowe 2003, Roe and Georges 2008, Rowe et al. 2009, Anthonysamy et al. 2013): daily average temperature (°C) and humidity (%), maximum daily rainfall (MDR; mm), 30-day rainfall (mm), and lunar phase (%). We collected temperature and humidity daily averages and maximum daily rainfall from the Sabah Forestry Department (SFD) weather station located 0.4–13.5 km from survey sites. As 3 of the sampling months coincided with conditions caused by a dry El Niño event, we summed rainfall to represent total rainfall over a 30-day period before each survey to determine the impact of longer-term rainfall patterns on species detection probability. At the start of each transect visit, we recorded the moon phase (0–100% of lunar disc visible).

To determine habitat associations and responses to RIL in flat-shelled turtles and soft-shelled turtles, we collected environmental covariates previously linked to freshwater turtle occurrence, and covariates that have direct or indirect associations with RIL. These latter covariates were time since RIL (in years), which was recorded for each VES stream survey, and distance to logging road (m), forest height (m), and stream flow accumulation value, which we recorded at each 200-m-long subplot. We obtained time since RIL (1–21 years) from SFD logging records. As logging roads have a direct (Laurance et al. 2009, Yamada et al. 2014) and indirect (Kreutzweiser et al. 2005, Mollinari et al. 2019) impact on biodiversity, we obtained a logging road map (shapefile) from the SFD Deramakot management team. We then determined distance to nearest logging road from each VES subplot as a function of Euclidean distance (m) calculated in ArcGIS 10.3.1 (Esri, Redlands, CA, USA). For quantification of forest height (m), we used a recent model of forest canopy height estimation for the year 2019 provided by Potapov et al. (2021). This new 30-m resolution global forest canopy height dataset was derived from the integration of the Global Ecosystem Dynamics Investigation (GEDI) lidar forest structure measurements and Landsat analysis-ready data time-series (Potapov et al. 2021). It provides a measure of forest disturbance and vegetation structural complexity (Potapov et al. 2021). We computed an average forest height (m) within each VES subplot. Flow accumulation reflects the total flow into a downslope stream (Jenson and Domingue 1988, Manchado et al. 2021) and may be used to identify stream channels and quantify their size (i.e., width and depth); streams with high flow accumulation are areas of concentrated flow. As such, we used flow accumulation as a rough proxy for river size. We calculated flow accumulation values from a 30-m Shuttle Radar Topography Mission (SRTM) digital elevation model using the hydrology tool kit within ArcGIS 10.3.1. The result is a raster of accumulated flow value to each grid cell, as determined by accumulated weight for all cells that flow into each downslope cell. Subsequently, we extracted the highest flow accumulation value within each VES subplot for our analysis. Unfortunately, we were unable to collect measurements such as stream width, depth, siltation, speed, and substrate at consistent intervals along the length of VES river reaches and their subplots. However, based on stream width and depth measurements collected at each turtle capture location, all rivers within the study exhibit similar structural dynamics (Table A1).

Data analysis

To determine the association of flat-shelled and soft-shelled turtle detection and occupancy probability associations with environmental metrics, we used single-species occupancy models within a Bayesian framework. This method allows the estimation of occupancy where species may be detected imperfectly whilst allowing occupancy and detection probability to be modeled as a function of covariates (MacKenzie et al. 2018).

We scaled all climatological, environmental, and logging-associated covariates to have a mean of 0 and a standard deviation of 1 prior to modeling. We tested collinearity between covariates using Spearman's rank correlation in the package Hmsic version 4.2-0 (Harrell 2019) and removed all correlated covariates ($|r| > 0.7$) from subsequent analysis. Additionally, as our data set consisted of 82 subplots (sampling units), with unique covariate values nested within 8 VES river reach sites, we included a random effect in all models to account for the nested spatial effect among subplots within the same VES river reach. Additionally, we treated the 3 survey periods as separate survey occasions in subsequent analysis.

We conducted all single-species occupancy models in the R package ubms version 1.1.0 (Kellner et al. 2022) and used default vague priors for all models: normal distribution with mean = 0, and standard deviation = 10. We ran 3 parallel Markov chains with 10,000 iterations each discarding the first 5,000 as burn-in. We assessed model convergence via the Rhat statistics, whereby values between 1.05 and 1 indicate convergence. As occupancy models assume a linear relationship between coefficients and covariates, we visually confirmed the direction of effects prior to model selection. If species detections exhibited a non-linear association with a covariate, we used a squared version of the scaled covariate in place of the original.

For each species, we conducted model selection via a 2-step process. First, we created single covariate models for each detectability covariate (including a null model with no covariate effects on detection) to determine the optimum detectability model for each species. Following this, we created single-covariate models for each occupancy covariate (including a null model with no effects on occupancy) in combination with the previously selected optimum detection covariate to determine the optimum single-covariate occupancy model for each species. We used single covariates during model selection to determine individual associations between covariates and species occupancy and detectability to avoid the masking of covariate associations, which can occur with additive and interactive models.

For each model's covariate selection stage, we ranked candidate models in ubms using expected log pointwise predictive density (elpd) as a measure of each model's predictive power. To calculate elpd, we used leave-one-out cross validation for pairwise model comparisons (Vehtari et al. 2017). To assess model support in relation to the top model, we calculated pairwise differences in elpd (Δelpd) between each model and the top model along with each model's standard error (SE Δelpd). We considered models with an elpd difference greater than their standard error to be less supported than the top model, and hence we considered the predictive inference of the associated covariate to be limited.

To determine the significance of covariate effects on detection and occupancy probabilities for optimum models, we generated 95% credible intervals of the posterior distributions. We considered 95% Bayesian credible intervals that did not overlap zero to indicate strong, significant support for covariate effects.

RESULTS

We detected 127 hard-shelled turtles and 30 soft-shelled turtles (all for turtles within water) during the study period (Table A1). Although determining recaptures for soft-shelled turtles proved unsuccessful, we recaptured 4 flat-shelled turtles (within 2 sites on different surveys) during the study (details of recaptures and movements can be found in Asad et al. 2021*b*). Hard-shelled turtle and soft-shelled turtle detections occurred at least once in

64.6% and 28.1% of the 82 subplots, respectively, and in 100% of all sampled VES river reaches. Based on Spearman rank correlations, no covariates were strongly correlated; thus, we included all covariates in the model-selection process.

Prior to the development of single-species occupancy models, we determined that soft-shelled turtle detections exhibited a non-linear relationship with time since RIL, with the majority of detections occurring in areas subject to RIL 10–11 years ago (Figure B1). As occupancy models assume linear relationships between species occurrence and covariates, we squared time since RIL to account for this non-linear relationship, and included this covariate in the subsequent model-selection process.

Malayan flat-shelled turtle

Within detection model selection, 30-day rainfall had higher predictive power compared to other detectability covariates (Table C1). Pairwise Δelpd values for the remaining single-covariate (and null) models were greater than their respective SE(Δelpd) values. Therefore, the detectability model based on 30-day rainfall was the best supported for this species; 30-day rainfall exhibited a negative association with flat-shelled turtle detection probability (Figure 2A), with detectability reduced by approximately 15-20% per 100-mm increase in monthly rainfall.

Within occupancy model selection, distance to logging roads had the highest predictive power (Table C1). Pairwise Δelpd of the second ranked model (flow accumulation), was lower than its respective SE(Δelpd); thus, flow accumulation and distance to logging roads were equally effective at predicting flat-shelled turtle occupancy. In the first ranked model, occupancy probability exhibited a positive relationship with distance to logging roads. Sites adjacent to roads (<50 m) exhibited an almost 50% lower probability of occupancy than those >1 km from roads (Figure 3A). In the second ranked model, flow accumulation was positively associated with occupancy probability (Figure 3B), indicating that flat-shelled turtles occurred more frequently in wider or deeper river stretches (with higher flow volume).

Despite negative associations with logging roads, the average occupancy probability (ψ) of flat-shelled turtles predicted by the distance to logging road model was relatively high (ψ = 0.79 ± 0.1 [SD]) at surveyed sites within the reserve (Figure 4A).

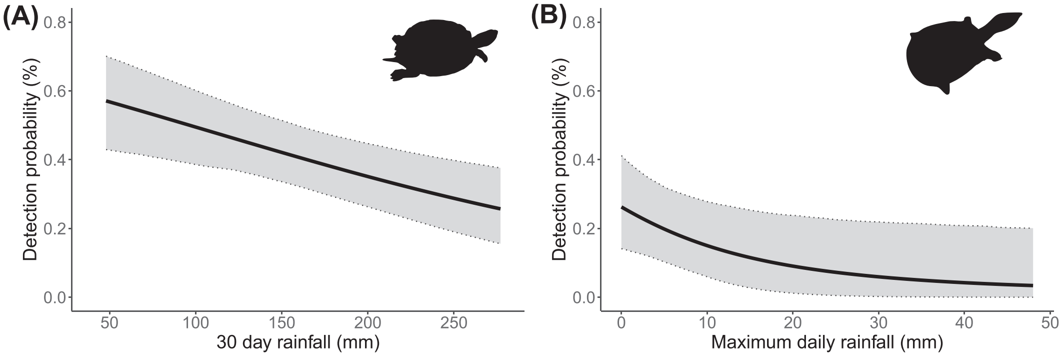

FIGURE 2 Marginal effect plots (posterior means and 95% credible intervals) displaying optimum detection model associations for each of the turtle species in Deramakot Forest Reserve, Sabah, Malaysian Borneo, 2019: A) effects of 30-day rainfall on flat-shelled turtle detection probability and B) effects of maximum daily rainfall on soft-shelled turtle detection probability.

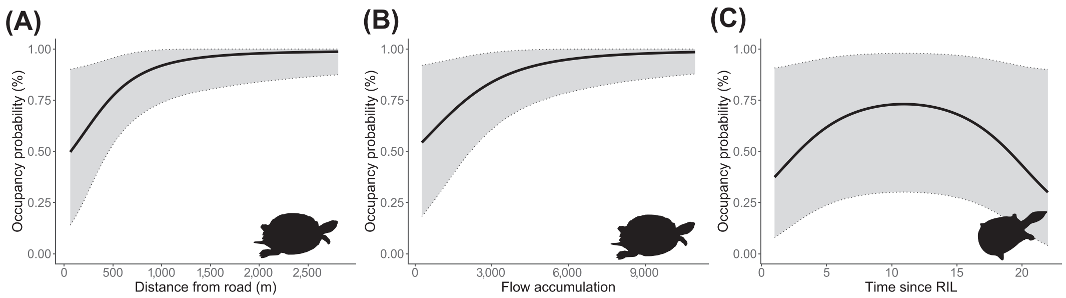

FIGURE 3 Marginal effect plots (posterior means and 95% credible intervals) displaying optimum occupancy model associations for each of the turtle species using data collected on 3 occasions in 8 sites using visual encounter surveys between March to July 2019, in Deramakot Forest Reserve, Sabah, Malaysian Borneo: A) effect of distance to nearest logging road on flat-shelled turtle occupancy probability, B) effect of stream flow accumulation on flat-shelled turtle occupancy probability, and C) effect of time since reduced impact logging (RIL; in years) on soft-shelled turtle occupancy probability.

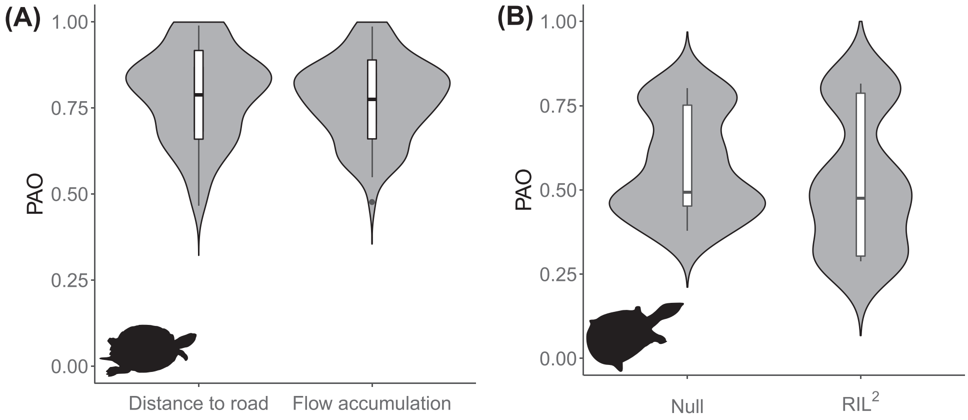

FIGURE 4 Probability of average occupancy (PAO) violin plots generated from the 2 best supported occupancy models for each species using data collected on 3 occasions in 8 sites using visual encounter surveys between March to July 2019, in Deramakot Forest Reserve, Sabah, Malaysian Borneo: A) flat-shelled turtle occupancy based on models including distance to logging road or flow accumulation, and B) soft-shelled turtle occupancy based on the null model and a model including the quadratic effect of time in years since reduced impact logging (RIL^2). White bar represents the interquartile range with the black bar in the middle representing the median and the thin black line representing the rest of the distributions. Grey shades on each side of the bar constitutes a kernel density estimation indicating the distribution of the data with wider sections reflecting higher concentrations or probabilities for occurrence of individuals.

Malayan soft-shelled turtles

Within detection model selection, maximum daily rainfall (MDR) displayed higher predictive power than the other covariates (Table C2). This covariate exhibited a negative association with soft-shelled turtle detection probability, but 95% credible intervals overlapped zero indicating there was little to no evidence of an effect (Figure 2B). All other detection covariate models (including the null model) produced Δelpd values that were lower than their respective SE(Δelpd) values. Overall, the power of MDR (and other covariates) describing soft-shelled turtle detectability was low. Despite its weak performance, we used MDR as the detectability covariate in subsequent models to improve model fit.

Within occupancy model selection, the quadratic form of time since RIL (RIL^2) had the greatest predictive power (Table C2). This covariate displayed a weak negative relationship with occupancy but indicated a slightly higher probability of soft-shelled turtle occurrence 8–12 years after RIL (Figure 3C). However, as with the detection covariates, the Δelpd of the null model (no effects of covariate on occupancy) was lower than its SE(Δelpd). The Δelpd of all other occupancy covariates were only slightly higher than their respective SE(Δelpd). Therefore, although the model containing time since RIL had similar predictive power as the null model, its performance was considerably higher than all other covariates.

Although Rhat values for soft-shelled turtles were within the parameters of model fit (1-1.05), support for optimum detection and occupancy models was considerably poorer than flat-shelled turtle models. Our models did suggest that soft-shelled turtles occupied roughly half ($\psi = 0.57 \pm 0.22$ [SD]) of all surveyed sites within the reserve (Figure 4B).

DISCUSSION

Our study is the first to examine the impacts of RIL practices on freshwater turtles and could provide an essential foundation for future studies and management decisions. While we could not determine detectability or occupancy patterns for the soft-shelled turtles, we successfully identified detection and occupancy relationships for the globally threatened flat-shelled turtle. This turtle exhibited a negative association between its detectability and monthly rainfall. Occupancy was positively associated with higher stream flow accumulation and greater distance from logging roads and was more common in wider or deeper stream stretches, suggesting that flat-shelled turtles may be negatively affected by roads. Regardless, our models predicted high levels of occupancy (> 50%) for both species throughout the reserve.

Influence of rainfall on detectability

Long-term (30-day) rainfall patterns appeared to be the best predictor of detectability for flat-shelled turtles in this study. Higher rainfall is generally expected to decrease the risk of desiccation while increasing the availability of aquatic and fossorial prey, thus favoring increased turtle activity (Rowe 2003, Roe and Georges 2008). Flat-shelled turtles were also encountered during periods of low rainfall in our surveys. This observation could be attributed to the exposure of riverine sandbanks suitable for nesting during low water volume periods caused by low precipitation. This, in turn, could increase rates of nest establishment and related behavior (Eisemberg et al. 2015). A recent review showed that nests of some species of freshwater turtles experience enhanced survivorship if constructed before rainfall (Geller et al. 2022), possibly owing to the removal of olfactory and physical signs of nest deposition. Although the authors also observed potential lekking behavior in flat-shelled turtles (Asad et al. 2021*b*), we cannot determine if rain-associated shifts in breeding caused increased detection during periods of low rainfall.

Although the relationship was weak, maximum daily rainfall was the covariate that best described soft-shelled turtle detectability. Water turbidity and increased silt deposition may have reduced visibility of this species immediately after rainfall. However, more data and further analysis would be required to confirm this linkage. Based on the literature (see Introduction), we assumed both species to be nocturnal. More nocturnal (*n* = 151) compared to diurnal (*n* = 7) encounters with flat-shelled turtles during 3 years of co-occurring amphibian and habitat sampling (S. Asad, Tomorrow University of Applied Science, personal observation) support this assumption. Although primarily nocturnal (Lim and Das 1999), we encountered soft-shelled turtles much less frequently during our surveys (only 30 sightings vs. 127 for flat-shelled turtles). Lower detection rates could accurately reflect lower occurrence of soft-shelled turtles in the reserve consistent with our models. However, such rates could also reflect the difficulty in detecting this species with visual surveys because it can bury itself in sand to hide or ambush prey (Lim and Das 1999, Asad et al. 2021*b*). During surveys, we observed disturbed individuals rapidly burying themselves within sandy substrates. As such, future surveys should combine visual survey methods with traditional trapping to quantify the utility of visual sampling methods for detecting this species.

Habitat and disturbance associations with occupancy

Although habitat associations of flat-shelled turtles are poorly documented, previous research by the authors identified this species in moderately sized, relatively shallow rivers, with an average width of 459 cm (104–964) and depth of 37 cm (11–100; Asad et al. 2021*b*). Shallow, fast-flowing streams with sandy bottoms and an abundance of water plants have been associated with previous records of this species (Lim and Das 1999, Mohd Ibrahim et al. 2019). Data presented herein suggest an association with relatively larger streams as flat-shelled turtle occupancy was positively associated with higher flow accumulation. However, the broadest stream section surveyed was <12 m in width; thus, flat-shelled turtle associations with even wider, higher order streams is untested. The morphological adaptations and ecology of the species are poorly suited to large rivers. Our results likely pertain to streams within hilly forest areas rather than large rivers in lowland or swamp forest areas (>20 m in width). Regardless, larger streams in similar land cover types (hilly, lowland dipterocarp forest) may serve as an important habitat for this species, and as such should be protected for its conservation. We recommend habitat measurements (e.g., stream depth, width, siltation) at finer spatial scales to clarify its habitat associations.

Most records of flat-shelled turtles are restricted to clear streams of undisturbed forests (Sharma and Tisen 2000, Mohd Ibrahim et al. 2019). Our findings somewhat support this, we recorded lower flat-shelled turtle occupancy closer to logging roads, suggesting that roads negatively affected the species. Roads result in mortalities during overland movements, create dispersal barriers, and elevate predation risk (Laurance et al. 2009, Rytwinski and Fahrig 2012, Steen et al. 2012). Although logging roads support less traffic than wider or paved roads, they can cause major changes to the soil, hydrology and water quality of surrounding habitats (Kleinschroth and Healey 2017, Laurance, Goosen and Laurance 2009). Furthermore, logging roads often provide easier accessibility for poachers (Laurance et al. 2006, Kleinschroth and Healey 2017).

Although our results for soft-shelled turtles were less conclusive, we detected the greatest number of soft-shelled turtles in sites subject to RIL 10–11 years earlier, consistent with predicted increased occupancy of these sites (although support for this pattern was weak). Previous research identified a preference by this species for sites experiencing heavy siltation (Asad et al. 2021*b*), which could align with an intermediate level of disturbance. More data and analysis are required to confirm these relationships. Exploring other potential habitat covariates (such as siltation cover and substrate type) that may better describe the occupancy patterns of this species could be useful in future studies.

Freshwater turtle responses to RIL

Although our lack of data from undisturbed primary forests undermines our ability to determine baseline occupancy patterns of these 2 species, they exhibited high occupancy of streams throughout Deramakot Forest Reserve. Previous research indicates that RIL has less impact on forest structure compared to conventional logging methods (Zarin et al. 2007, Putz et al. 2008), and subsequently maintains higher biodiversity (Bicknell et al. 2014, Bohnett et al. 2022). Additionally, the preservation of 30-m riparian buffers throughout the reserve potentially reduces the negative impacts of logging on sensitive aquatic habitats (Asad et al. 2021*a* 2022). Our findings support these conclusions and suggest that sustainably managed forests using RIL methods maintain habitat for some turtle species at the landscape scale. Although logging impacts may penetrate into adjacent buffer zones and streams (Gomi et al. 2006), the terrestrial habitat features assessed in this study (forest height, time since RIL, proximity to logging roads) did not appear to affect adjacent riparian areas, and therefore may not affect the ecology or behavior of primarily aquatic freshwater turtles (particularly for soft-shelled turtles).

Besides forestry practices, another explanation for the high occupancy probabilities of the 2 turtle species in Deramakot Forest Reserve is reduced poaching activities. Thanks to passive (secured gates on reserve borders and forest department presence within the reserve) and active (frequent river and ground patrols and aerial surveillance) site security within the reserve (Lagan et al. 2007), trade-driven poaching of freshwater turtles appears to be minimal.

CONSERVATION IMPLICATIONS

Our study suggests that soft-shelled turtles and particularly flat-shelled turtles can thrive within sustainably managed forests using RIL methods in Southeast Asia. This could be due to the creation of riparian buffers, maintenance of forest structure, and reduced poaching pressure. We recommend that logging roads should be carefully managed in reserves, for example, placing them at a greater distance from larger stream networks, to reduce their negative impact on flat-shelled turtle occupancy. Our detectability results suggest that weather conditions (namely long-term rainfall) should be incorporated into further monitoring of turtle populations (particularly flat-shelled turtles) to ensure reliable population and occurrence estimates. Finally, we strongly recommend that future comparative studies examine occupancy between RIL, conventionally logged, and primary forest sites to resolve the impacts of logging and the role of key habitat features on the distribution of turtles on forest streams in Malaysia.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All animal handling and welfare during this study was compliant with a license granted by Sabah Biodiversity Council (SaBC; permit number: JKM/MBS.1000-2/2 JLD.7 (63)).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

ORCID

Wei Cheng Tan http://orcid.org/0000-0002-6067-3528

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APPENDIX A: SITE AND SURVEY SUMMARY

TABLE A1 Summary of the 8 visual encounter survey (VES) river reaches surveyed on 3 occasions between March and July 2019 in Deramakot Forest Reserve, Sabah, Malaysian Borneo, including their time since reduced impact logging (RIL), averaged covariates values (± SD) from each VES, averaged stream width and depth (recorded at turtle detection locations), and number of soft-shelled turtle and flat-shelled turtle detections (with detections during each occasion presented in parentheses).

VES river ID	Length (m)	Number of subplots	Time since RIL (years)	Stream flow accumulation	Forest height (m)	Distance to logging road (m)	Stream width (m)	Stream depth (m)	Soft-shelled turtle detections	Flat-shelled turtle detections
DF18-28_C64	2,400	12	1	3,642.54 ± 1,766.19	31.54 ± 1.39	463.01 ± 144.86	517.25 ± 156.65	37.72 ± 12.6	1 (0) (0) (1)	11 (5) (4) (2)
DF30_C72	2,000	10	2	1,295.45 ± 631.56	27.55 ± 2.65	394.54 ± 153.88	385.05 ± 123.67	36.1 ± 19.65	4 (1) (3) (0)	16 (3) (8) (5)
SDC43_C63	1,800	9	6	1,705.33 ± 510.17	30.94 ± 2.88	649.08 ± 92.9	395.33 ± 158.02	41.42 ± 27.82	2 (2) (0) (0)	19 (6) (11) (2)
DF40_C71	2,200	11	10	1,290.23 ± 725.71	26.95 ± 2.86	314.62 ± 50.88	354.29 ± 126.1	31.93 ± 16.79	6 (2) (1) (3)	11 (5) (4) (2)
SDC42_C61	2,400	12	11	1,991.67 ± 782.6	31.71 ± 0.72	682.34 ± 161.38	465.48 ± 156.44	42.63 ± 17.95	10 (4) (3) (3)	13 (9) (1) (3)
DF41_C43	2,000	10	19	6,735.45 ± 3,668.57	31.2 ± 1.38	1,004.02 ± 178.38	557.26 ± 192.04	33.68 ± 12.27	2 (0) (2) (0)	36 (7) (26) (3)
SDC31_C53	1,200	6	19	3,010 ± 305.12	32.33 ± 1.08	488.82 ± 197.26	396.43 ± 147.32	34.09 ± 20.84	3 (2) (1) (0)	4 (3) (1) (0)
SDC29_C55	2,400	12	22	2,589.08 ± 1,246.19	29.12 ± 2.65	590.36 ± 390.89	416.74 ± 154.94	33.02 ± 11.9	2 (1) (1) (0)	17 (5) (6) (6)

APPENDIX B: DETECTION AT SITES VARYING IN YEARS SINCE RIL

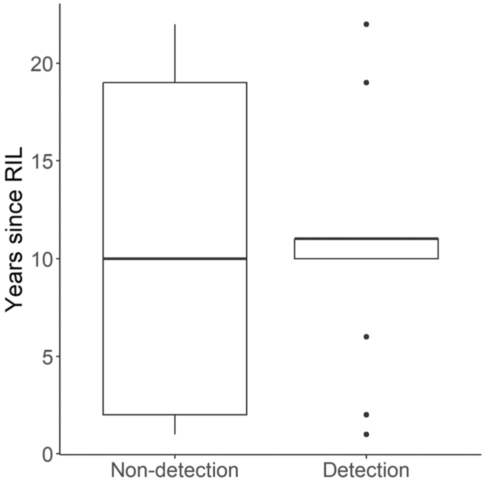

FIGURE B1 Soft-shelled turtle detections and non-detections throughout all 82 surveyed subplots within the 8 visual encounter survey transects at varying levels of regeneration following reduced impact logging (RIL; 1–22 years since logging). Survey data were collected on 3 occasions between March and July 2019 in Deramakot Forest Reserve, Sabah, Malaysian Borneo.

APPENDIX C: MODEL RESULTS

TABLE C1 Model covariate selection by ranking single-species occupancy models using expected log pointwise predictive density (elpd), number of parameters (nparam), and pairwise differences in elpd (Δelpd) between each model and the top model along with their standard errors (SE Δelpd) for flat-shelled turtle in Deramakot Forest Reserve, Sabah, Malaysian Borneo, 2019. We obtained the estimated effect sizes (estimate) of each covariate on the detection and occupancy probability from the models, with an asterisk (*) indicating significant evidence of an association (95% credible intervals not overlapping zero). Covariate abbreviations are as follows: MDR = maximum daily rainfall and RIL = years since reduced impact logging.

Covariate	elpd	nparam	Δelpd	SE Δelpd	Weight	Estimate
Detection						
30-day rainfall	152.887	3.927	0.000	0.000	0.999	−0.493 *
Temperature	156.455	4.211	−3.568	2.494	0.000	0.301
Humidity	−156.65	4.399	−3.763	2.152	0.000	−0.299
Null	157.179	3.011	−4.292	2.804	0.000	
MDR	157.642	4.211	−4.754	2.742	0.000	−0.193
Lunar phase	158.235	4.118	−5.348	2.799	0.000	−0.008
Occupancy						
Distance to logging road	150.064	4.325	0.000	0.000	0.609	2.058 *
Flow accumulation	150.347	4.513	−0.282	1.665	0.391	1.373 *
30-day rainfall	152.887	3.927	−2.823	1.879	0.000	
RIL	153.681	4.696	−3.617	1.987	0.000	0.0417
Forest height	153.736	4.961	−3.672	2.045	0.000	−0.225
Null	157.179	3.011	−7.115	3.277	0.000	

TABLE C2 Model covariate selection by ranking single-species occupancy models using expected log pointwise predictive density (elpd), number of parameters (nparam), and pairwise differences in elpd (Δelpd) between each model and the top model along with their standard errors (SE Δelpd) for soft-shelled turtle in Deramakot Forest Reserve, Sabah, Malaysian Borneo, 2019. We obtained the estimated effect sizes (estimate) of each covariate on the detection and occupancy probability from the models. Covariate abbreviations are as follows: MDR = maximum daily rainfall and RIL = years since reduced impact logging.

Covariate	elpd	nparam	Δelpd	SE Δelpd	Weight	Estimate
Detection						
MDR	−85.084	6.395	0.000	0.000	0.731	−0.749
Null	−85.594	5.006	−0.510	2.084	0.269	
Humidity	−86.038	5.964	−0.954	2.211	0.000	−0.246
30-day rainfall	−86.219	6.159	−1.135	2.321	0.000	−0.230
Lunar phase	−86.311	6.167	−1.227	2.276	0.000	−0.178
Temperature	−86.56	6.302	−1.476	2.198	0.000	0.104
Occupancy						
RIL^2	−83.739	5.523	0.000	0.000	0.836	−1.076
MDR	−85.084	6.395	−1.345	1.203	0.000	
Null	−85.594	5.006	−1.855	2.420	0.164	
Forest height	−85.699	6.774	−1.961	1.548	0.000	−0.524
Distance to logging road	−85.751	6.800	−2.013	1.393	0.000	−0.033
Flow accumulation	−86.710	7.940	−2.971	2.657	0.000	−0.373