BIOGEOGRAPHY AND CONSERVATION OF REPTILIAN DIVERSITY IN WEST INDONESIA

by

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Abstract

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Uncovering and analyzing the distributional patterns of species across the landscape is central to biogeography, but these same patterns and explanations for those patterns are also critical to proper conservation and management of wildlife. Here, I use two model systems to address different aspects of challenges regarding conservation and management of natural resources across the globe. First, I use draconid lizards of the Greater Sunda Region to highlight the extent to which diversity remains undescribed in biodiverse tropical regions, and how continued biological inventory and taxonomic evaluation of those speciose groups will improve conservation strategies in the future. I also show how testing questions about historical biogeography of these diverse groups may provide important insight for conservation biologists, ecologists, and evolutionary biologists. Second, I use crocodilians of Sumatra to highlight the impacts of human pressures on the contemporary biogeography of species. In a short evolutionary time-scale, humans have drastically reshaped the distributions of species by restricting or expanding the ranges of some, while completely reshuffling the distributions of others. The ramifications of these practices to the effected ecosystems are not yet fully understood, but this work addresses questions which will hopefully contribute to a deeper understanding of human impacts on distributions, and the conservation and management response measures to be prioritized.

Table of Contents

List of Illustrations

List of Tables

Chapter 1

Conservation and Biogeography of Reptilian Diversity in West Indonesia

INTRODUCTION

Earth's biodiversity is fascinating for biologists from a variety of disciplines and holds intrinsic value for people across the world. Thus, biological research which seeks to uncover and preserve biodiversity holds long term scientific, economic, ecological and social importance. Yet, current human practices are rapidly resulting in widespread species extinctions and loss of habitat across the globe. It is imperative to conserve and manage Earth's remaining intact ecosystems, particularly the world's remaining biodiversity hotpots. However, conservation efforts require in depth knowledge of evolutionary and ecological process, as well as thorough understanding of floral and faunal distributional patterns across the landscape (i.e. biogeography). This highlights the importance of understanding how natural historic pressures have shaped distributions through time and how humans continue reshaping them. I have chosen to focus my dissertation on the biogeography and conservation of reptilian diversity of Indonesia for four distinct reasons: (1) Indonesia is one of the world's most complex and fascinating geographic landscapes in the world, (2) Indonesia is currently facing one of the world's most rapid rates of forest loss and species extinctions are believed to be significantly high, (3) Indonesia's reptilian diversity is largely unexplored and expected to be highly underestimated, (4) uncovering biogeographic patterns and taxonomic relationships allows biologists to understand species' distributions and define clear-cut management and conservation schemes.

Based on Indonesia's need for biogeographic and conservation attention, I selected two model systems and have three distinct aims: (I) assess the importance of unravelling historical biogeography and taxonomic relationships for applied conservation biology, (II) describe unknown diversity and unravel interspecies relationships to advance evolutionary and ecological research, (III) assess how contemporary human practices continue to alter species distributions. I will address these aims from two standpoints—*historical* and *contemporary* biogeography.

To address *historical biogeography* and underestimated diversity, I selected highland agamid lizards of the Sunda Region (details on Sunda Region found below). Because, the world and specifically Indonesia's landscapes are changing so drastically in contemporary times, I chose crocodilians for understanding *contemporary biogeography* and conservation challenges. Crocodilians make an excellent model system for examining contemporary biogeography because they have clearly defined taxonomic boundaries. Thus, changes in distribution in response to human pressures are more easily identifiable.

1.1 Historical Biogeography of the Sunda Region

Tropical Southeast Asia and Australasia form the world's largest archipelago, consisting of over 20,000 islands. The region spans multiple biogeographic barriers and encompasses the western edge of the Pacific Ring of Fire (a series of volcanoes around the perimeter of much of the Pacific Ocean). Yet, the geologic and climatic pressures that shaped floral and faunal diversity across the region are not yet fully understood, nor is the extent of biological diversity. Alfred Russel Wallace was among the first to explore the Indo-Australian archipelago during the mid-1800's and described many of the region's fascinating species (Wallace 1869). Wallace first identified the Strait of Lombok as a key dividing feature between the Australian and Oriental faunal zones, forming a portion of Wallace's Line (Huxley 1868), which bisects the straight between Sulawesi and Borneo, extending along the western edge of the Philippines. Wallace defined distinct distributional boundaries between eastern and western species.

Huxley's modified line extends beyond the Sulu Archipelago and divides the Philippines from the Sunda Shelf, but branches south and westward to include a larger portion of the China Sea. Eventually other distinct biogeographic barriers were also defined throughout the region, including: Lydekker's Line on the western edge of New Guinea and Weber's Line on the western edge of the Moluccan Islands. Murray's and Muller's Lines were also defined as slight variations of Wallace's Line.

The Sunda Shelf lies directly West of Wallace's Line and is often referred to as the Greater Sunda Region or Sundaland (GSR). The GSR is considered one of the world's biodiversity hotspots and encompasses Peninsular Malaysia and the islands of Bali, Borneo, Java, Sumatra and hundreds of small islands. Only the island of Borneo has been in contact with mainland Asia since the early Miocene Period, while other islands were cut off at various stages of high sea levels. Other large Sunda Islands were pushed into the Sunda Shelf by shifting tectonic plates approximately 40 MYA, coinciding with the collision of the Indian subcontinent with Asia. This collision caused intense subduction along fault lines forming the Himalayan Mountain Range on mainland Asia, as well as the Barisan Mountain Range in Sumatra. In turn, a series of volcanoes formed along the backbone of Java and Sumatra. Subsequent volcanic blasts through time may have wiped out local diversity in some areas, while diversity in other areas remained unchanged. Thus, isolation and recalibration of species composition from volcanic blasts are two potential explanations for high rates of floral and faunal endemism across the Barisan Range.

When climatic conditions reached a suitable state, cloud forest appeared in the upper elevations of the Barisan Range; however, the spatiotemporal extent of cloud forest during previous epochs is not yet fully understood. Hall et al. (2011, 2015) suggest that rising sea levels may have covered much of Sumatra's lowlands during the terminal Miocene epoch. Hall et al. (2012) hypothesize that highland forests were not present until approximately five MYA and only small pockets of terrestrial habitat remained above sea level between 10 and 20 MYA. Although Hall et al. (2015) hypothesize the time and extent of mountain range which remained above water, these hypotheses are yet to be tested in comparison to faunal relationships. One fascinating question to test, is can genetic relationships of modern highland species provide more precise estimates of mountain forest extent and isolation during the terminal Miocene, Pleiocene and Pleistocene epochs?

Previous biogeographic studies of floral and faunal species in the Sunda Region have uncovered interesting patterns shaped by the Pleistocene epoch, approximately 1.8 Ma to 12 ka years ago. Glacial spikes are believed to have occurred approximately 1.8 Ma, 920 ka, 630 ka, 430 ka, 350 ka, 140 ka, 18 ka (Chappell and Shackleton 1986, Chappell et al. 1996), followed by subsequent drops in sea level. Low sea levels allowed connectivity between major land masses across the globe, including Beringia (Russia and North America), the Sahul Shelf (Australia and New Guinea) and the Sunda Shelf (Greater Sunda Islands). Despite the known connectivity between the Sunda Islands, researchers are yet to determine exactly which geologic factors are responsible for modern day floral and faunal distributions. Morley and Flenley (1987) suggest the Sunda Shelf may have been divided by a dry, grassland belt which acted as a barrier between Sumatran and Bornean Forest dwelling species and allowed for the movement of grassland species from Peninsular Malaysia to Java. Conversely, these dry grassland patches and large paleo-rivers branching out across the Sunda Shelf may have limited dispersal of some terrestrial species. Alternatively, recent evidence of dipterocarp tree distribution during glacial maxima suggests that the existence of a dry savannah corridor across the Sunda Shelf to be unlikely (Raes et al. 2014).

The watersheds of the Sunda Shelf are thought to have been historically interconnected, on and off during the time period between 250 ka and18 ka (the latter signifying the end of the glacial maximum). The theoretical location of where these rivers flowed during the Pleistocene is not exact, however it is obvious that many of the paleo-rivers would simply be a continuation of the large river systems we see today and bathymetric charts of the Sunda Shelf still show evidence of river corridors in some areas. Voris (2000) split the Sunda Region into four pale-river systems, which consisted of the Siam River System, North Sunda River System, Malacca Straits River System and East Sunda River System. The East Sunda River System ran through what is known today as the Java Sea. This system would have consisted of tributaries from all of North Java's modern day river systems, the rivers of South Sumatra and many of the Rivers from South Borneo. Based on bathymetric contours of the region, the most commonly accepted hypothesis is that all of the tributaries from the three main islands listed, would have met and created one single main channel. The Malacca Straits River System consisted of the paleo river extensions of what are known today as the Sungai Panai, Sungai Rokan and Sungai Siak rivers of northeast Sumatra, and four rivers from eastern Peninsular Malaysia known as the Sungai Perak, Sungai Bernam, Sungai Muar and Sungai Lenek. The Malacca Straits River System likely flowed toward what is now the Malacca Strait before changing trajectories and flowing towards the sea near the Andaman Islands. Some sources suggest these rivers met and created one large river which flowed North, while other sources suggest they flowed parallel to one another and never combined (Voris 2000). The North Sunda River System is considered to be the largest paleo-river of the Sunda Shelf and multiple rivers of East Sumatra and West Borneo are thought to have contributed to forming one large watershed. This watershed was thought to have met in the middle of the Sunda Shelf and then those flowed into the South China Sea. It would have flowed parallel to the East Sunda River System, separated by approximately 100 km of land. Last, the Siam River System was an extension of today's Kampar (Riau, Sumatra) and Johore (East Peninsular Malaysia) rivers. The Sungai Kampar currently drains one of the largest river systems in Sumatra, and when sea levels were lower this system likely continued directly East through the Singapore Strait, before it met the Johore. Many rivers from Thailand are also believed to contribute to this river system before eventually flowing into the South China Sea.

During glacial maxima, it is also hypothesized that the Sunda region was cooler and montane forests may have lowered 300 to 500 meters from their contemporary elevational limits (Walker and Flenley 1979, Maloney 1980, Morley 1982, Stuijts 1983, van der Kaars 1998, Kershaw et al. 2001, Harrison et al. 2006). Van der Kaars (1998) and Kershaw et al. (2001) hypothesized that the Sunda Region experienced a 30 to 50% decline in precipitation and reduction in temperature based on pollen species counts recovered from soil cores. If in fact montane forest extent was lowered, then species may have been able to disperse between what were previously isolated mountain peaks. Closely related species may have been able to hybridize, while distantly related species could have inhabited areas sympatrically. However, empirical tests of forest cover extent during the Pleistocene based on the distributions of faunal model systems are lacking. Phylogeographic relationships amongst systematically targeted mountain islands in the Barisan Range could yield answers regarding the extent of montane forest cover during glacial maxima.

Highland cloud forest agamid lizards are excellent for studying historical biogeography in the GSR for multiple reasons. First, a major agamid lizard radiation occurs in the GSR and is yet to be analyzed in depth. Second, the regions complex topography allows testing a series of impactful phylogeographic questions. Third, I have unprecedented access to broad sampling of agamid lizards from across the extent of Java, Sumatra and parts of mainland Asia. The importance of unravelling interspecific agamid lizard relationships is highlighted in Chapter 2 and the results of systematic and biogeographic analyses in chapter 3.

1.2 Contemporary Biogeography and Conservation in the Sunda Region

Examining contemporary biogeography is important for conservation initiatives, but also for understanding the ecological and evolutionary ramifications of human induced changes on the environment. Drastic shifts in native species distributions and the introduction of nonnative species across the globe is certain to have a series of cascading effects on ecosystems. However, it is not yet fully understood to what extent human alteration of distributions will continue to affect the environment. Thus, I briefly review human driven species extinctions, distributional shifts of species, and human induced global changes, and highlight the need for contemporary biogeographic studies in Sundaland.

Contemporary biogeography focuses on patterns of biodiversity in relation to modern times and largely on human induced change to the environment. Therefore, contemporary biogeography, as defined here, deals with species distributions and shifts since the approximate point at which human descendants branched off on their own evolutionary trajectory. Although humans have certainly affected biodiversity for hundreds of thousands of years, evidence for human induced change is largely limited to the terminal Pleistocene and Holocene epochs, following the last glacial maximum. Thus, I will focus specifically on contemporary biogeography from the terminal Pleistocene onwards; with an emphasis on changes since the expansion of European settlement for which documentation of human history is most available. Herein, this latter period will be defined as the Anthropocene; although this period has taken on a variety of defined time frames since the term was coined (including the onset of the Holocene period).

Terminal Pleistocene to Present—The onset of the Holocene is considered to be the post-glacial time frame following the Pleistocene encompassing the last 12,000 years. After glaciers receded, a series of mass extinctions took place across the globe. In North America and Asia, some of the most notable extinctions include the Wooly Mammoth, Mastodon, Saber Tooth Tigers, Short Faced Bears, Giant Sloth and a variety of horse species. In South America, 95% of megafauna species went extinct in the early Holocene; including multiple horse, camel, and carnivore species. Turvey et al. (2009) provide an in depth review of the early mammal and avian Holocene extinctions. Examples of amphibian, fish and reptile extinctions from that time period have been covered in less detail, but estimates of total extinctions within these groups are believed to be highly underestimated (Alroy 2015).

There are multiple hypotheses for the mass Holocene extinctions. Although climate change was likely a large contributing factor, it is unclear to what extent modern humans contributed, maybe synergistically. Some suggest human hunting pressures may have directly caused the extinction of most Holocene megafauna in North America (referred to as "Overkill" or "Blitzkrieg" Hypothesis). Firestone et al. (2007) show evidence for a major impact from a comet, which subsequently altered Earth's climate and led to the extinction of most North American megafauna. Smith et al. (2015) and Bartlett et al. (2015) suggest that human colonization during the terminal Pleistocene was correlated with the last known occurrence of many late Quaternary megafaunal species. Villavicencio et al. (2015) provide interesting evidence that suggests humans, climatic change and vegetation change all contributed to the extinction of late Quaternary megafauna species in southern Patagonia, Chile. Soil core samples taken during this study showed evidence of drastic shifts from grassland to *Nothofagus* forest cover during the early Holocene. Interestingly Villavicencio et al. (2015) suggest that the shift to forest habitat may have also been facilitated by the absence of megafauna and not solely on a shift in climate. This emphasizes the potential ecological cascade which may have incurred from the loss of a single species during the early Holocene. Using carbon dating, Villavicencio et al. (2015) also provide a chronology of likely herbivore and carnivore extinction dates. Interestingly, they found that the disappearance of horses and lamas was directly correlated with habitat shifts, and the disappearance of some carnivores was likely attributable to human hunting pressures. Researchers estimate that there were fewer extinctions amongst African megafauna, specifically because Africa is the place of origin of hominids and native African species had the ability to evolve alongside modern humans.

The loss of so many organisms at the top of the trophic cascade during the early Holocene has been shown to have significant effects on ecosystems. Doughty et al. (2016) has shown that savanna woody biomass in South America changes drastically depending upon which herbivore species are present.

Humans were responsible for the direct exploitation of a variety of species throughout the Holocene; however, *Homo sapiens* also began shaping contemporary species' distributions via nonnative introductions during this time. There are three reasons for early human induced species introductions: (1) Early agricultural practices, with evidence of early agriculture in Mesopotamia, the Yangtze river basin, northcentral Africa, the Andes Mountains, Central America, Mexico, and the plains of North America; (2) the domestication of animals and subsequent travel with them to new regions of the globe (e. g., Dingoes are believed to have been domesticated dogs released in Australia around 3500 years ago, resulting in the extinction of endemic Australian mammals, (3) accidental transport of species, via boats and travelling caravans. Regardless of the cause, nonnative introductions began effecting contemporary biogeography at an early stage in the Holocene.

Anthropocene—More recently, there has been a significant loss of biodiversity, mirroring human population growth across the globe. The IUCN estimates that 869 plant and animal species have gone extinct within the last 500 years. These include functionally extinct species, not in the wild, and those not even in captivity (https://cmsdata.iucn.org/downloads/species_extinction_05_2007.pdf). During the early 15th and 16th centuries, a variety of Pacific island species went extinct in response to exploitation from indigenous settlements. Loss of bird diversity may be the most well documented of these early oceanic extinctions and a variety of endemic rail, gallinules and parrots are believed to have disappeared from the Cook, Samoan and Tongan islands. Over a dozen Chiropteran species went extinct as well, including endemic Flying Fox Bats on multiple pacific islands. In New Zealand, human pressures drove a variety of endemic species to extinction as well, including at least five species of intriguing flightless birds known as Moas. The island of Madagascar and the smaller neighboring islands of Aldabra, Mascarene and Mauritius also suffered a tremendous loss of endemic biodiversity. Unique hippopotamus, tortoise and multiple rodent species from the islands went extinct in the 1800’s. Similarly a variety of extinct species have been documented from the Caribbean, Galapagos, Falkland and Mediterranean archipelagos as well. Turvey et al. (2009) provide a review of all documented mammal and avian extinctions during the holocene period, with a particular focus on species within the last 500 years. The collective result of these extinctions is a drastic reshuffling of contemporary biogeography.

The last 200 years in Earth’s history have seen mass extinctions across the globe, coupled with drastic habitat alteration, climate change and human induced introductions of nonnative species. In fact, the current time frame is considered one of the world’s top six extinction periods, emphasizing the rapid change in contemporary biogeography in modern times. Examples of extinctions or extreme shifts in species’ distributions are widespread. In North America, the majority of remaining mammalian megafauna were brought to the verge of extinction near the end of the 19th century and their distributions are only a fragment of what they were prior to European expansion. Plains Bison populations are estimated to have been around 30 million individuals before the year 1800 and by the beginning of the 20th century an estimated 300 individuals remained. Brown bears, gray wolves, and elk are a few other charismatic species that were also almost eliminated through mass market hunting pressures. In Australia, a variety of endemic marsupial species went extinct as well, including two species of Bilby and perhaps the most notable, the Tasmanian Tiger (or Thylacine). The Thylacine was a unique genus of carnivorous marsupials from the Australasian region. Although the systematics are currently unresolved, butat least one species was believed to have inhabited Australia, one in Tasmania and another single species on the island of New Guinea. The last known occurrence of a Thylacene is 1936 when the last captive individual died in Tasmania.

Further contributing to species extinctions and shrinking species ranges, has been a significant increase in introductions of invasive species across the globe. Human induced dispersal of species allows for intercontinental travel, completely altering biogeographic patterns across the globe. There are currently estimated to be thousands of invasive species introduced by humans across the globe, since the first recorded introductions in the mid Holocene. Invasive animals, bacteria, plants and viruses are believed to be responsible for hundreds of extinctions. In Australia, invasive cats and foxes are hypothesized to have driven multiple small mammals to extinction and on the island of Guam, the Brown Tree Snake has caused multiple endemic bird species to go extinct. The spread of infectious disease via human interactions with the environment has also taken a major toll on wildlife. For example chytrid fungus has been largely involved the global loss of amphibian diversity and the disease has now been documenting in most of the world's tropical regions. Diseases such as brucellosis and pneumonia are also believed to be passed from livestock to native species, including threatened Bison and Bighorn Sheep species. When invasive species do not lead to the extinction or local extirpation of native species, they may still completely change the evolutionary trajectory of species they interact with. Shine et al. (2012) provide interesting evidence which suggests black snake physiology is shifting in areas where they are sympatric with invasive cane toads. They hypothesize that selection for snakes more tolerant of toad toxins and with smaller heads (e.g. capable of eating smaller toads with less toxin volume) is occurring. Evidence of this is shown only in the last 100 years since the cane toad introduction to Australia, and the evolutionary and ecological consequences of invasive species remain completely unexplored fields.

Contemporary biogeography is heavily influenced by a loss of habitat, mass hunting pressures and more recently, significant climate change. Exploitation of vertebrates for meat, skins and pets has directly contributed to the extinction of a variety of vertebrates and fishing pressures have altered aquatic vertebrate populations across the globe as well. Habitat alteration may cause the most drastic shift in species' distributions, particularly in forest habitats. The loss of large forest tracts also contributes to climate alteration, coupled with increased greenhouse gas emissions in the last 200 years. In response to shifts in atmospheric gases, Earth's average polar temperatures and overall global average temperatures have risen nearly 2 degrees C. Because of climate change, coral bleaching is currently a significant concern, as much of the oceans biodiversity is found in coral reefs throughout Earth's tropical ocean waters. Small shifts in ocean temperature caused by global change has directly caused the bleaching of massive coral beds throughout the world and particularly in Caribbean and Australian waters.

The negative trophic cascade which may incur from inserting or deleting entire species from the ecosystem is not yet fully understood. A few studies have identified drastic changes to the environment following human induced local extirpations. Ripple et al. (2014) reviews the cascade effects associated with the loss of top carnivores from the ecosystem. For example, the loss of wolves from the Greater Yellowstone Ecosystem led to increase in elk populations and a subsequent overconsumption of aspen shoots by elk. Memmott et al. (2004) used empirical data to estimate plant species loss in response to pollinator species extinction. Biesmeijer et al. (2006)

showed that the loss of plants will often directly lead to a loss of specialized pollinators. In absence of large empirical datasets, researchers have also generated coextinction and community viability models, which essentially explore the potential ramifications incurred from a species being lost to the food web (Koh et al. 2004, Turvey 2009). Although progress has been made in understanding cascade effects, scientists are only beginning to understand the full effects associated with human-induced shifts in contemporary biogeography. Thus, it is essential to understand the ecological, evolutionary and conservation related consequences that may incur from human induced alterations to the landscape and associative ecosystems.

Wildlife of Indonesia and particularly the Greater Sunda Region has been drastically affected by anthropogenic driven global change. Forest loss in the GSR is occurring more rapidly than any other region in the world. In turn species distributions are being shaped and altered at an unprecedented rate. As humans reshape the environment, patterns of contemporary species distributions must conform to the remaining suitable landscapes.

In order to examine the effects of Earth's changing landscapes on wildlife, it is essential to choose a model system for which species status is well defined. Shaney et al. (2016) highlights the negative management and conservation ramifications incurred when taxonomic verification is lacking (Chapter 2 of this thesis). Furthermore, obligate wildlife species' distributions are likely to follow landscape alteration much more so than generalist species. Large vertebrate fauna are expected to be under the greatest threat. Therefore, we chose a unique model organism, which could be used to examine the effects of human pressures on the contemporary biogeography of wildlife in today's world.

Crocodilians of Indonesia are an excellent model system for examining contemporary biogeography, because measurements of historical and modern crocodilian distributions can often be done accurately. This is partially because of relatively low crocodilian diversity and a better resolved phylogeny amongst Crocodylia. Furthermore, documentation of many species is present from the late 1700's forward, prior to a boom in human populations and drastic habitat alteration across the globe. Crocodilians are also considered extremely important and relevant for conservation and management initiatives for four specific reasons: (1) Crocodilians are considered a keystone species, yet the cascade effects on their associated ecosystems caused by their absence are not understood, (2) Crocodilian skins and parts generate billions of dollars annually across the globe and developing a long-term sustainable harvest requires further ecological and population related data, (3) Crocodilians are believed to be responsible for more attacks on humans than any other group of large carnivores; thus thorough population data is critical for improving management strategies, (4) 26% of crocodilian species are endangered or critically endangered, thus conservation attention is critically needed. Therefore I chose two species of crocodile native to Indonesia for which to assess contemporary biogeography and answer interesting questions regarding the effects of human pressures on wildlife in modern times.

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Chapter 2

Conservation Challenges Regarding Species Status Assessments in Biogeographically Complex Regions: Examples from Overexploited Reptiles of Indonesia

Abstract

IUCN Red List assessments are important for conservation and management initiatives. However, due to poor sampling between many biogeographic regions, status assessments are often quite challenging. In turn, researchers sometimes assess poorly known species, which can have unforeseen ramifications, including the trade of rare and cryptic species under common species names. Here we address this issue with economically important species of reptiles in Indonesia. We review specific examples of single species assessments identified as “Least Concern”, which in reality likely encompass multiple closely related species. We also examine Red List assessments which utilize species distribution modelling techniques and identify biogeography as a major barrier to using such methods. To test how biogeography may affect status assessments, we use our own model lizard system from Indonesia and take an integrative phylogeographic approach to quantify status assessments under contrasting scenarios. We show that failure to account for major biogeographic breaks leads to drastic red list status variation and our model system fluctuates from “Least Concern” to “Endangered” depending upon whether taxonomic evaluations consider biogeographic boundaries. We identify Sauria (lizards) and Serpentes (snakes) as major lineages requiring taxonomic and conservation attention in Indonesia. We also suggest: (1) Indonesia’s trade quotas should further subdivide management zones to account for gaps in taxonomic evaluations; (2) genetic sampling should be considered high priority during exportation processes from poorly studied geographic areas; and (3) continuation of thorough biological inventory is critical for conservation initiatives across heterogeneous mountain and island landscapes.

1.0 Introduction

The ability of wildlife officials to accurately manage a given species or population depends on the quality of data available. Wildlife officials require this information to set harvest quotas, establish protected areas and propose management regulations (Margules & Pressey 2000). Many officials rely on the IUCN Red List, which reports the conservation status for a broad range of species world-wide, (http://www.iucnredlist.org/). However, because information is lacking, many species are left unassessed or given the status of "Data Deficient (DD)" until more information is available. Broad sampling and population relationships must be obtained to accurately determine species conservation status, particularly when dealing with potentially cryptic species (undescribed, similar species). This is especially important when assessing the status of species inhabiting large geographic ranges and multiple habitat types. Without a detailed systematic analysis, cryptic species are harvested and traded under the name of closely related common species, which may lead to the extinction of undocumented species, subspecies or genetically distinct populations. Brown et al. (2007) describe an example of cryptic Giraffe lineages diminishing in population size in Africa, because they were hidden under a common species "lower risk" status. Lohman et al. (2010) provide examples of cryptic, island bird lineages in the Philippines which are under threat of extinction, because they are hidden under common species' names. Bernardo (2011) summarizes other detailed examples as well. Despite this major conservation concern, status assessments are sometimes decided upon in geologically complex regions where little is known about the extent of biological diversity.

Loss of cryptic species may be acute in countries such as Indonesia, where an absence of data across many islands or mountains makes accurate Red List assessment difficult to accomplish. The Pacific Ring of Fire includes much of Indonesia, and this unique geology has allowed widespread diversity to develop. The country of Indonesia also encompasses many, major biogeographic breaks, including Huxley's Line, Lydekker's Line, Wallace's Line and Weber's Line. In turn, taxonomic relationships are quite difficult to resolve across the region. Further complicating the issue, anthropogenic pressures are causing a rapid decline in diversity across the country. Sodhi et al. (2004**),** stated that agricultural practices across the Greater Sunda Islands (Borneo, Java and Sumatra) have produced one of the world's highest rates of deforestation. Agricultural workers are rapidly converting forests across the islands into oil palm, rubber, tea and coffee plantations (Miettinen et al. 2014, Myers et al. 2000). These practices, in combination with a lack of wildlife management resources and personal, have led to unregulated over-harvesting of resources. The islands of Java and Sumatra are of particular concern. Achard et al. (2002), Brooks et al. (1997) and Margono et al. (2012) have quantified forest loss across the islands and estimate that six percent of Java's and 35 percent of Sumatra's original forests currently remain.

The Greater Sunda Region (or Sundaland) is also considered one of the world's biodiversity hotspots (http://www.cepf.net/resources/hotspots/Asia-Pacific/Pages/Sundaland.aspx). A variety of endemic and Endangered (EN) species call these islands home (Shepherd et al. 2004), yet many vertebrate groups remain poorly studied; particularly reptiles of the region. Iskandar and Erdelen (2006) note that few herpetofaunal surveys have been conducted throughout the Greater Sunda Region in recent times and the extent of reptilian diversity in Java and Sumatra is unknown. This lack of knowledge leaves large gaps in taxonomic assessments. Compounding this issue, Natusch and Lyons (2012), Nijman et al. (2012) and Shepherd (2000) have noted major exploitation of reptiles for skin, meat and pet trade throughout Indonesia, meaning quotas and other management decisions based on species status are critical. In fact, Indonesia is considered an epicenter for illegal wildlife trade and Natusch and Lyons (2012) state that reptiles are traded in higher volume than any other taxonomic group throughout the region. Böhm et al. (2013) describe the reptile extinction risk across the Indo-Malayan region as one of the highest in the world. Although CITES has implemented export quotas for multiple reptile species in Indonesia, species are constantly misidentified and quotas are often applied across vast regions and distinct biogeographic lines. In turn, these practices sometimes neglect to account for geographic isolation and potentially unrecognized lineages.

In this paper we highlight taxonomic and biogeographic challenges impeding conservation status assessments in Indonesia. We start by reviewing previous Red List assessments throughout Indonesia and identify “Least Concern” (LC) species which are likely large species complexes (multiple species assessed as one) in reality. Then, we use a model organism, *Pseudocalotes tympanistriga* (lizard native to Indonesia) to test and contrast species status simulations under different species distribution modelling scenarios, and quantify the effects complex biogeography may have on Red List status outcomes.

2.0 Methods

2.1 Reptile Statuses of West Indonesia

We gathered information on the status of all currently recognized reptiles in Java and Sumatra, Indonesia to assess the current conservation knowledge of major reptilian lineages. We focus specifically on Javan and Sumatran reptiles because our own herpetofaunal surveys over the last three years focused on those islands and we are most familiar with that region of Indonesia. To generate a comprehensive list of all species of reptiles known to occur on Java and Sumatra we searched primary literature and available web databases (e.g., Das 2010, http://reptile-database.reptarium.cz/). For each species we obtained the conservation status afforded by the IUCN Red List. Species with no IUCN status were considered Not Evaluated (NE). Using these sources, we produced a summary of the IUCN status of Javan and Sumatran reptiles, by major taxonomic group (e.g. crocodiles, lizards, snakes and turtles).

2.2 Least Concern Species Assessments and Major Biogeographic Boundaries

The issue of species complexes is well understood by the IUCN and this is clearly defined in their guidelines for status assessment. Furthermore, the IUCN is not a taxonomic authority and those who conduct Red List assessments conduct the best assessments possible with the information available. However, the challenges of complex biogeography and lack of funding for biological inventory and taxonomic evaluations may lead to significant issues when conducting Red List assessments and these issues need to be further addressed. To understand the challenges of biogeography in conducting Red List assessments we searched for clear examples of previously assessed species complexes, spanning major biogeographic boundaries. To do this we widened our focus to include all reptile species that inhabit Indonesia (beyond the status assessments discussed above). We focused on "LC" species because their assessments are commonly based on a large distribution and ability to occupy multiple habitat types, which are also characteristics of species complexes, yet to be recognized. We further narrowed the list to include species that are commonly exploited in trade, because cryptic species are likely to be more heavily exploited in such scenarios. The final list identified multiple commercially traded species that are afforded the status of "LC", yet have ranges crossing distinct biogeographic boundaries. An exhaustive review is not realistic for all "LC" species that fall within this scenario; therefore, we focus on three species with sufficient background information to make our claims. These are *Bronchocela jubata, Varanus indicus* and *Varanus salvator*. We also discuss a fourth species *Varanus marmoratus*, but we include this in the discussion of the *V. salvator* complex, because of their recent split from one another.

2.3 A Model System for Status Simulations:

Here, we identify a model system to quantify potential status assessment miscalculations affected by complex biogeography. We use *P. tympanistriga* (Gray, 1831), a medium sized arboreal lizard of the family Agamidae (Manthey, 2010), to simulate status assessment under different scenarios. Based on biogeography and a lack of taxonomic work we inferred that *P. tympanistriga* was in fact a large species complex, therefore any attempt to determine status could result in inaccurate assessment. We collected historical information, which assumes that *P. tympanistriga* is a single species, ranging between the islands of Java and Sumatra and contrasted this with *P. tympanistriga* we collected during our own herpetofaunal surveys of Java and Sumatra between 2012 and 2014. During our surveys we systematically targeted geographically isolated mountain ranges to fill in sampling gaps. We then assess basic phylogeographic relationships of *P. tympanistriga*, in order to make contrasting simulations (discussed in section 2.4).

We used a combination of molecular and morphological characters in order to identify species boundaries. To identify specimens of *P. tympanistriga* we first used the methods of (Harvey et al. 2014). Our morphological analysis allowed identification of specimens closely related to *P. tympanistriga* for assessment. We took all similar individuals (tentative *P. tympanistriga*) collected from both Java and Sumatra and sequenced the mitochondrial gene ND4 for a subset of individuals from each unique locality. We used the ND4-LEU mitochondrial fragment, commonly used in other phylogenetic analyses of agamid lizards (Leaché et al. 2009). We decided upon a single gene analysis, because the morphological data in combination with a single gene analysis should provide corroboration of correct taxonomic placement prior to Red List assessment. Details on DNA extraction methods and PCR amplification protocols follow Leaché et al. (2009).

We included sequences from eight *Pseudocalotes* individuals and three out-groups in our phylogenetic analysis (out-groups were *Bronchocela, Calotes* and *Gonocephalus* genera). Harvey et al. (2015) provides specific details on sequence generation and analysis. We first conducted a UPGMA analysis, allowing raw sequence divergence visualization between samples and to check for potential sample mislabeling or contamination. Because genetic differentiation is commonly used to define species boundaries, this allowed context as to how divergent the individuals are from one another. Next, we conducted a Bayesian analysis following the protocols outlined in Harvey et al. (2015) to visualize phylogenetic relationships. Using morphological data and overall genetic divergence between individuals as a guideline, we allocated specimens to the species *P. tympanistriga* and to other species where necessary (previously cryptic species). All sequences have been deposited in Genbank under accession numbers KT180139 – KT180152 and KT211019 (Appendix B).

2.4 Quantifying Effects of Taxonomic Uncertainty

Here, we quantify the effect of complex landscapes on Red List assessments. The IUCN provides a clear set of guidelines for determining species status (http://www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria). The guidelines are based on a letter grading system (e.g. A – E). If an assessment meets specific criteria defined for any of the three threatened categories (e.g. Critically Endangered CE, Endangered (EN) or Vulnerable (VU), then that status is selected. If it does not fall into a threatened category then it may be assigned Near Threatened (NT), LC or DD. The IUCN suggests using the most conservative estimate possible if status can be assessed using multiple methods. In our simulation we chose a straightforward method for rapid assessment which focused on geographic range of the species in question. We used two metrics for which to emulate the Red List assessment of *P. tympanistriga*, Area of Occupancy (AOO) and Extent of Occurrence (EOO).

After identifying true *P. tympanistriga* individuals for the final IUCN Red List assessment (Methods Section 2.3) we uploaded collection GPS coordinates into a program designed for IUCN status assessment known as GeoCAT (Geospatial Conservation Assessment Tool; http://geocat.kew.org/). Bachman et al. (2011) support this program, because of its ability to accurately and rapidly make assessments. The program plots locality data on a map interface and IUCN Red List assessment suggestions are provided based on the EOO and AOO for the species in question.

We ran two separate analyses to visually contrast possible conservation status outcomes. In our first analysis *(Simulation 1),* we used all confirmed *P. tympanistriga* samples and uploaded their localities into GeoCAT. We specified an AOO of 15 km^2 (per individual) which is the approximate extent of highland forest habitat on mountain islands they inhabit in West Java and GeoCAT produced a recommended status. Next, we analyzed all *Pseudocalotes* samples from Java and Sumatra *(Simulation 2),* which would have all been considered *P. tympanistriga* prior to our taxonomic work (without consideration of geographic boundaries). We uploaded their localities into GeoCAT and assigned an AOO as 25 km^2 (per individual). The larger AOO, accounts for larger mountain ranges in Sumatra and wider sampling gaps. It is important to note: these methods require a high degree of confidence in sufficient sampling effort, because failure to find individuals present across the entirety of their range can drastically alter the results. We believe we have surveyed sufficiently enough to record accurate presence absence information on *P. tympanistriga,* particularly because this is not a formal assessment.

2.5 Species Distribution Modelling

Niche modelling, or species distribution modelling (SDM), has been recently highlighted as a potential source for assisting in IUCN Red List assessments, particularly when occurrence data is limited (Pena et al. 2014, Syfert et al. 2014). Because SDM can be done with or without taxonomic work being carried out, incorrect SDM is a concern, as it may overestimate range and underestimate the threat on a species. We use our simulation species *P. tympanistriga* to emphasize these points.

We downloaded all 18 (30 second resolution) Bioclimatic variable files (Bioclim files) available at http://www.worldclim.org/formats, which provide current world wide data on multiple climate variables. We then used ArcMap 10.0 and ran “Clip” and “Raster to .ASC” tools in order to format the Bioclim files correctly for SDM modelling. We uploaded the 18 files in to the MaxEnt 3.3.3k niche modelling program (Phillips et al. 2006) and added locality data for *P. tympanistriga*.

We uploaded locality data for all *Pseudocalotes* individuals we collected, in conjunction with historical locality data (http://www.herpnet.org/, Manthey 2008). We used the “Auto Features” settings provided and altered the number of iterations to allow for convergence of data (changed from 500 to 5,000), changed the replicated run type to “Subsample” and set random test percentage to “25”. Using this setup we modelled the estimation of *P. tympanistriga* distribution. We assessed the omission data plot, area under the curve plot (AUC) and the species range map generated from the analysis. The range map provides probability of occurrence, ranging from 0.0 to 1.0. We arbitrarily considered high quality habitat to be 0.9 – 1.0, medium quality habitat to be 0.7 – 0.9 and low quality habitat to be 0.5 – 0.7. Anything less than 0.5 was considered unsuitable habitat. We did not consider these arbitrary cutoffs to be an issue for two reasons: (1) these estimates are conservative; and (2) these estimates are only used to provide a relative idea of how SDM’s can affect EOO estimates, not to determine the actual status.

3.0 Results

3.1 IUCN Status of Reptiles and Amphibians in Java and Sumatra

After a literature and web search, we found that there are currently 248 naturally occurring reptile species in Java and Sumatra (Appendix A), Indonesia and eight species of questionable occurrence (sightings based on unconfirmed reports or possibly introduced). Of these species, three are crocodiles (Crocodylia), 18 are turtles (Testudines), 90 are lizards (Sauria) and 145 are snakes (Serpentes). When the status for these was contrasted among each group, we found that lizards had a lower percentage of species assessed than other groups, whereas crocodiles and turtles have received the most attention (Figures 1A – E provide a breakdown for each group).

The IUCN Red List category statuses of all reptiles are as follows: four CE, six EN, seven VU, three NT, 110 LC, 28 DD, and 99 NE (Figure 1). In total 50.5% of the reptile species from these islands are DD or NE, 42.2% are listed as LC and 7.3% hold a near threatened or worse status. Although we only summarized the status for species in Java and Sumatra, this may provide context for how status assessments are distributed throughout Indonesia.

3.2 "Least Concern" Species in Question

Our results show that the three species we reviewed which are labelled as "LC" are likely species complexes (multiple species assessed as one), spanning across major biogeographic breaks. The first species, *Varanus salvator,* has been identified as the world's most heavily exploited animal in the international skin trade (Koch et al. 2013). The export quotas for this species are extremely high for Indonesia. Koch et al. (2013) summarize reports from 2000 – 2010, which estimate that 6.2 million skins were traded from wild caught *V. salvator*. Approximately 11,500 skins were confiscated in this time period. To a lesser extent the species is also captured and traded for consumption (Koch et al. 2013). In addition, an unknown number of wild *V. salvator* are harvested every year from across their range. This is of particular concern in an archipelagic nation like Indonesia, because of the high potential of the existence of undescribed species. The species complex is currently listed as CITES Appendix II and data on the known export of these animals is available at the Cites Trade Database (http://trade.cites.org/). We have provided a list of details on *V. salvator* exports from Indonesia for the most up to date year, 2013 (Table 1). Despite the high demand, there is little consideration for biogeographic barriers in current harvest quotas across Indonesia.

Varanus salvator was assessed as "LC" in 2009 (http://www.iucnredlist.org/details/178214/0), due to its wide distribution, abundance and ability to live in many habitats. However, at the time of assessment there were four recognized subspecies (specifically stated to be included in the assessment) and evidence of a large species complex *(V. s. salvator, V. s. bivittatus, V. s. macromaculatus, V. s. andamanensis)* and evidence of cryptic species was made clear by the authors during the assessment. A troubling example is that at the time of assessment, the subspecies *V. s. bivittatus* range extended through Java and across Wallace's line (major biogeographic barrier) to multiple small islands; including Bali, Lombok, Sumbawa, Flores, Ombai and Wetar (Figure 2B). Yet, there is no genetic or morphological data from these islands to confirm taxonomic relationships.

In 2007 (prior to IUCN Red List assessment in 2009) a morphological study of the *V. salvator* complex resurrected taxa and a population from Sulawesi was described as a distinct species, *V. togianus* (Koch et al. 2007). In 2010 a new subspecies (*V. s. ziegleri*) was described from the Moluccan Islands far to the east of Sulawesi (Koch et al. 2010b) and across another major biogeographic break (Huxley's line; Figure 2B). Therefore, one cryptic species was elevated to species status from the middle of *V. salvator's* distribution (*V. togianus* in 2007), while a new subspecies was described from a region which extended the distribution of the *V. salvator* complex (*V. s. ziegleri*) considerably (650 km due east across the ocean). *Varanus s. ziegleri* is a clear example of a questionable lineage being traded as *V. salvator*.

Although now considered distinct, *V. marmoratus* was split from the *V. salvator* complex in 2007 (Koch et al. 2007) and shows the same issues. After being described from the Philippine Islands, *V.*

marmoratus was assessed as "LC" in 2007 (http://www.iucnredlist.org/details/169844/0. However, in 2010 three years after an assessment, *V. marmoratus* was identified as a species complex as well and two species from small island chains were described and split from *V. marmoratus*. These species are currently recognized as *Varanus palawanensis and Varanus rasmusseni* (Koch et al. 2010a). Previously unrecognized *V. palawanensis* and *V. rasmusseni* had been traded as a "LC" species since 2007, under the name *V. marmoratus*. Recently, Welton et al. (2014) described two more species from the *V. marmoratus* complex (*V. bangonorum* and *V. dalubhasa*). Like the previous cases, these two species are still traded under a status of LC that is being applied to different species which were previously considered *V. marmoratus* as well.

Our second example, *V. indicus* (Daudin, 1802) occurs across much of eastern Indonesia (Figure 2C) and was assessed as "LC" in 2009 (http://www.iucnredlist.org/details/178416/0). *Varanus indicus* is traded heavily across Indonesia and is labelled as a CITES Appendix II species. Although it is protected in Indonesia, it is still traded in high numbers labelled as "bred in captivity". Unfortunately, it is difficult to differentiate between an animal that a breeder says is captive bred, or an animal that was captured in the wild and traders simply fake captive breeding without repercussions.

This group was noted to likely consist of multiple cryptic species upon assessment and populations range across a major biogeographic break (e.g. Lydekker's line; Figure 2C). Prior to the most recent assessment, Harvey and Barker (1998) described a new species from the Moluccan Islands, *V. yuwonoi*. Ziegler et al. (1999) described a new species from Halmahera Island, *V. caerulivierens*. Ziegler et al. (2007) also described a new species form Halmahera Island, *V. rainerguentheri* and summarized the taxonomy of many other species which had been previously split from *V. indicus*. Although these changes took place before assessment, they should have been red flags and major revisions also came after the "LC" assessment. A concrete example can be seen in the description of *V. obor*, described in 2010 from the northern Moluccas Islands (Weijola and Sweet 2010). This new species was named after the "LC" assessment in 2009, meaning that at least one cryptic species was hidden under the “LC” assessment of *V. indicus* during that time.

It was also noted by Koch et al. (2013) that *V. indicus* occurs on Savo Island, in the Solomon Archipelago, an island of only about 30 km^2. This archipelago is distant from other *V. indicus* populations and is a likely candidate for species recognition. This is yet to be determined, but high trade quotas applied across the region could wipe out that small island population before this question is answered.

Last, we address the species *Bronchocela jubata,* Duméril and Bibron 1837. This species has received less attention than *Varanus*, however its distribution alone suggests one of three potential scenarios: (1) *B. jubata* may be a large species complex, or (2) *B. jubata* has been introduced across major biogeographic regions. (3)The potential for *B. jubata* to be a single wide ranging species is present, however, is unlikely because other terrestrial vertebrates do not typically follow that distributional pattern across the same biogeographic barriers. No morphological or genetic studies have been done to determine within species population distinction or genetic isolation. Despite the taxonomy of this group never being studied, *B. jubata* is currently identified as “LC” on the IUCN Red List (http://www.iucnredlist.org/details/170378/0). This status was determined based on their large distribution, abundance and ability to live in multiple habitat types. *Bronchocela jubata* is currently stated to range across South-East Asia and across major biogeographic boundaries, including Wallace’s line and Weber’s line (Figure 2A), spanning across hundreds of islands, many in isolation for thousands or even millions of years from one another. Based on this and other species distributional patterns (Woodruff 2010), it is unlikely that all populations of *B. jubata*, belong to a single species.

Hallermann et al. (2005) addressed *B. jubata* in a review of the genus *Bronchocela,* highlighting the uncertainty in its distribution. It is quite possible that rare species are currently concealed under the blanket name *B. jubata* and traded in high numbers. Unlike many of the *Varanus* species, *B. jubata* is currently not of concern for CITES and there is no available information on trade quotas for this species. Although it is not traded nearly to the same extent as the *Varanus* species, this species is sold regularly in the pet trade (personal observations). *Bronchocela jubata* has simply not yet received the taxonomic evaluation necessary to uncover any of the relationships among populations.

Indeed, biogeographic barriers may act differently on the lizards discussed here, than they would on other lizard groups, or other reptile groups. However, these three examples highlight the main difficulties associated with status assessments across heterogeneous landscapes and these challenges are certainly applicable across other lizard and snake groups which could not be covered here (See Discussion).

3.3 Case Study Species Assessment Simulation

Pseudocalotes tympanistriga was previously thought to occur throughout the Barisan Mountain Range of Sumatra and the mountains of western Java. There are 83 specimens catalogued in the publicly available museum database herpnet.org (http://www.herpnet.org/), which includes specimens from multiple universities. All specimens from herpnet.org are listed as being found in various parts of west Java and none are currently confirmed *P. tympanistriga* from Sumatra.

During our herpetofaunal inventory, we collected 45 *P. tympanistriga* individuals from Java. From Sumatra, we collected 18 *Pseudocalotes*, all somewhat similar to *P. tympanistriga,* but based on morphological differences we questioned whether the Sumatran individuals were in fact *P. tympanistriga* (Figure 3 shows the distribution of our collections). After thorough morphological examination it was concluded that Sumatran specimens belonged to multiple “cryptic” species (Figure 4A – E), which Harvey et al. (2014) described as *P. cybelidermus*, *P. guttalineatus* and *P. rhammanotus*. All *Pseudocalotes* from Sumatra were only superficially similar to *P. tympanistriga*.

Our phylogenetic analysis confirmed our morphological taxonomic findings and clearly shows the genetic differentiation among the *Pseudocalotes* species (Figure 5). We find *P. tympanistriga* restricted to the island of Java, and that there are at least four distinct species of *Pseudocalotes* on Sumatra. This genetic analysis supports our hypothesis that *P. tympanistriga* does not occur on Sumatra. Using these data we parsed our simulations accordingly.

In our first Red List assessment simulation *(Simulation 1)* of taxonomically confirmed *P. tympanistriga* (Javan lizards only), we show that GeoCAT produced an EOO of 1,051 square km and recommended an “EN” status. The AOO produced was 1,200 square km with a recommendation of “VU” status. When contrasted with a hypothetical assessment, which included all specimens (Javan and Sumatran) previously considered *P. tympanistriga (Simulation 2)*, the results were quite different. The outcome was an EOO of 38, 605 square km and a recommendation of “NT” status. Although GeoCAT recommends “NT”, it is important to note that at nearly 40,000 square km, the status could even be considered “LC”. The AOO was 5,000 square km and a recommendation of “LC” based on that metric. These analyses simulate assessment before and after taxonomic verification (Figure 6). Without accounting for biogeography, we would have seriously underestimated the potential threat on *P. tympanistriga,* similar to specific examples discussed in section 3.2 above. We only consider geographic range to prove our point here; however, in a formal Red List assessment other considerations for sub conditions would be considered as well (i.e. levels of exploitation, fragmentation, evidence of decline, etc…; http://www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria), which is beyond the scope of this paper.

3.4 Species Distribution Modelling, P. tympanistriga

MaxEnt outputs estimated highest quality habitat (0.9 – 1) was to occur across the mountains of West Java, two small islands east of Java and south and central Sumatra. Medium quality habitat (0.7 – 0.9) was distributed across Java and small neighboring islands to the east of Java, throughout Sumatra and isolated patches in Borneo. Low quality habitat (0.5 – 0.7) was distributed across Borneo, Java (and islands to the East), Sulawesi and Sumatra (Figure 7). The AUC plot indicated a well fit model with training data=0.991 and test data =0.993 (where a random prediction is =0.5; Pena et al. 2014). Without taxonomic evaluation, the SDM approach would suggest that *P. tympanistriga* occurs across a wide range (throughout Sumatra), overestimating range and EOO drastically.

4.0 Discussion

4.1 Overview

We show clear evidence that complex biogeography may be leading to threatened species being listed under common species names, which can lead to extinction of unknown species. These issues are amplified when dealing with species of high economic value, particularly across an archipelago nation like Indonesia. We show that on the islands of Java and Sumatra alone, the majority of reptile species are labelled as “DD”, “NA” (~50% combined) or “LC” (~42%) and Lizards and Snakes represent the largest proportion of poorly studied reptiles in West Indonesia. Based on assessments discussed in this paper, we suspect a high number of species are being assessed prematurely as “LC”, because they have large ranges across major biogeographic breaks, yet have not been fully studied from a taxonomic standpoint. The three examples covered in the results highlight our point; however, there are certainly other “LC” species which likely fall in to the same scenario, but cannot be covered due to the scope of this study. Among the snakes, *Morelia amethistina* (Amethystine scrub python) may be a clear example, as it could be comprised of distinct species; particularly the population from the Aru Islands (http://www.iucnredlist.org/details/177501/0). Likewise, *Ahaetulla prasina* is considered a single “LC” species across a broad geographic range and multiple islands, yet the species lacks complete taxonomic evaluation.

Had we assumed that all similar *Pseudocalotes* lizards from Java and Sumatra were all truly *P. tympanistriga*, we would have reached a status of “LC” or at most “NT”. Our integrative analysis (considering biogeography beforehand) was enough to determine that *P. tympanistriga* was composed of multiple unrecognized species and that *P. tympanistriga* does not occur in Sumatra, and seriously diminished the known EOO and AOO for *P. tympanistriga*. We determined that *P. tympanistriga* should actually be considered "VU" or potentially "EN" in reality and cryptic *Pseudocalotes* species on Sumatra require additional attention. Our *Pseudocalotes* dataset also shows SDM methods can result in similarly biased outcomes, which exaggerate estimates of species range. Authors who suggest SDM's as a method for assisting in determining species status do make it clear that taxonomic verification is important (Pena et al. 2014, Syfert et al. 2014). However, it is clearly not trivial to ensure a single species is being included in SDM's, particularly across mountain or true island systems.

The Balai Konservasi Sumber Daya Alam (Natural Resources Conservation Agency; BKSDA) is currently responsible for determining provincial quotas for each species across Indonesia. However, these quotas are arbitrary if no scientific information is available. If a species in question (for red list assessment) ranges across major biogeographic boundaries and lacks recent taxonomic evaluation, then we suggest: (1) Indonesia's trade quotas should be further divided across separately managed zones. Rather than a one quota fits all model, which it seems is currently applied across vast areas, depending mostly upon species demand. We acknowledge this may be difficult to enforce in areas lacking the appropriate resources. If traders are not found with the animals in the location of origin, it is very difficult to ensure animals are coming from a specific area. To assist with this problem, conservation forensic techniques could help considerably. Wasser et al. (2004) used this method to determine the geographic origin of black market ivory in Africa. Welton et al. (2013A) used a similar barcoding method to successfully determine the origin of traded monitor lizards in the Philippines. Genotyping methods would work if applied to reptiles in Indonesia, but only if biological samples are collected from as many locations as possible, to determine genetic signatures in multiple geographic locations.

Aside from the challenges of biogeography and limited taxonomic sampling for researchers conducting conservation status assessments, researchers also have difficulties in obtaining the proper permits as well. Researchers may need to set aside a month and sometimes up to a whole year of bureaucratic time before any research occurs. This is simply not realistic for many researchers and those with restricted funding may be unable to afford the process. This problem is particularly acute for graduate and undergraduate students and researchers counting only on personal funds. Fees to enter National Parks for research have been raised considerably in recent years and are often very difficult to obtain. These areas are often some of the last patches of primary forest habitat (therefore the most intact), yet may not be affordable for work, or are outside of permitting possibilities for foreign researchers and even for local scientists with limited funding. Although countries follow strict guidelines to ensure that research is carried out appropriately, it in fact leads to less research being conducted in some cases.

4.2 Conclusions

Taxonomic relationships are constantly changing as well as researcher's perceptions on where species boundaries should be drawn. Therefore, we do not suggest that species status assessments hold off until samples are collected from every last possible locality (particularly in a place such as Indonesia). This is obviously unrealistic and conversely, labelling everything "DD" may also be harmful to species that are clearly under threat, but have not been included in taxonomic evaluations. However, there are many cases where species assessments need to be more conservative, because inaccurate assessment can be more detrimental than helpful. This is particularly the case in regions consisting of complex, heterogeneous landscapes and poorly sampled areas. Funding for broad scale biological inventory should absolutely be considered a priority in unexplored regions such as the Indonesian archipelago, which is critical for unravelling taxonomic relationships and subsequently results in improved conservation efforts.

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Tables

Table 1. *Varanus salvator* export data from Indonesia, during the year 2013 (most recent dataset). App, refers to CITES Appendix. Importers are CZ=Czech Republic, DE=Germany, ES=Spain, FR=France, GB=United Kingdom of Great Britain and Northern Ireland, IT=Italy, JP=Japan, MX=Mexico, NL=Netherlands, SG=Singapore, US=United States of America. Exporter is Indonesia (ID). Quantity is provided in number of total individuals. Term is the state in which animals were sold. Source is where individuals came from; W=Wild, C=Captive Bred, F=Born in Captivity, I=Confiscated or Seized Specimens.

Year	App.	Taxon	Importer	Exporter	Quantity	Term	Source
2013	II	*Varanus salvator*	CZ	ID	15	live	C
2013	II	*Varanus salvator*	DE	ID	74	live	W
2013	II	*Varanus salvator*	DE	ID	41	leather products	W
2013	II	*Varanus salvator*	ES	ID	25	live	W
2013	II	*Varanus salvator*	ES	ID	3,600	skins	W
2013	II	*Varanus salvator*	FR	ID	30	live	W
2013	II	*Varanus salvator*	FR	ID	563	leather products	W
2013	II	*Varanus salvator*	GB	ID	40	live	C
2013	II	*Varanus salvator*	GB	ID	55	live	W
2013	II	*Varanus salvator*	GB	ID	7	leather products	W
2013	II	*Varanus salvator*	IT	ID	104	leather products	W
2013	II	*Varanus salvator*	IT	ID	44,017	skins	W
2013	II	*Varanus salvator*	JP	ID	75	garments	W
2013	II	*Varanus salvator*	JP	ID	4	live	C
2013	II	*Varanus salvator*	JP	ID	270	live	W

2013	II	*Varanus salvator*	JP	ID	60	leather products	W
2013	II	*Varanus salvator*	JP	ID	36,094	skins	W
2013	II	*Varanus salvator*	MX	ID	47,500	skins	W
2013	II	*Varanus salvator*	NL	ID	248	leather products	W
2013	II	*Varanus salvator*	SG	ID	207,205	skins	W
2013	II	*Varanus salvator*	US	ID	75	live	F
2013	II	*Varanus salvator*	US	ID	1,916	live	W
2013	II	*Varanus salvator*	US	ID	17	leather products	C
2013	II	*Varanus salvator*	US	ID	3	leather products	I
2013	II	*Varanus salvator*	US	ID	113	leather products	W
2013	II	*Varanus salvator*	US	ID	8,223	skins	W

Figures

Figure 1. Summarized status assessments of all currently recognized reptiles found on the islands of Java and Sumatra. Graph A shows only the status of lizard species, Graph B shows only the status of snake species, Graph C shows only the status of turtle species, Graph D shows only the status of crocodile species and Graph E shows the status of all reptile species combined. The y-axis indicates number of species and the x-axis indicates each status. NE=Not Evaluated, DD=Data Deficient, LC=Least Concern, NT=Near Threatened, VU=Vulnerable, EN=Endangered and CE=Critically Endangered.

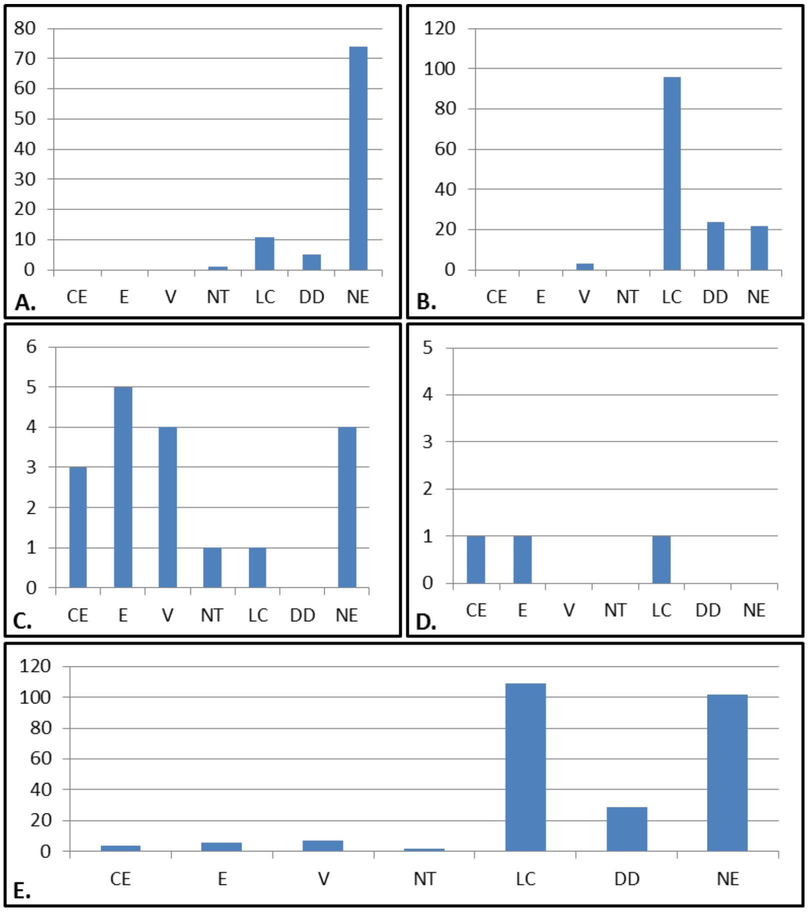


Figure 2. Range maps for the three “LC” species. Map A represents the estimated range of *B. jubata* and question marks indicate that occurrence is unknown in some areas. Wallace’s Line (black dotted) and Huxley’s line (red dotted) show the major bio-geographic breaks that fall within the range of what is considered to be *B. jubata*. Map B. represents the estimated range of *V. salvator* subspecies and the recently described species *V. togianus*. Wallace’s Line (black dotted) and Weber’s Line (orange dotted) show the major bio-geographic breaks that fall within the range of what is considered *V. salvator*. Map C. represents the estimated range of *V. indicus*. Lydekker’s Line (green dotted) shows the major bio-geographic break that falls within the range of what is considered to be *V. indicus*.

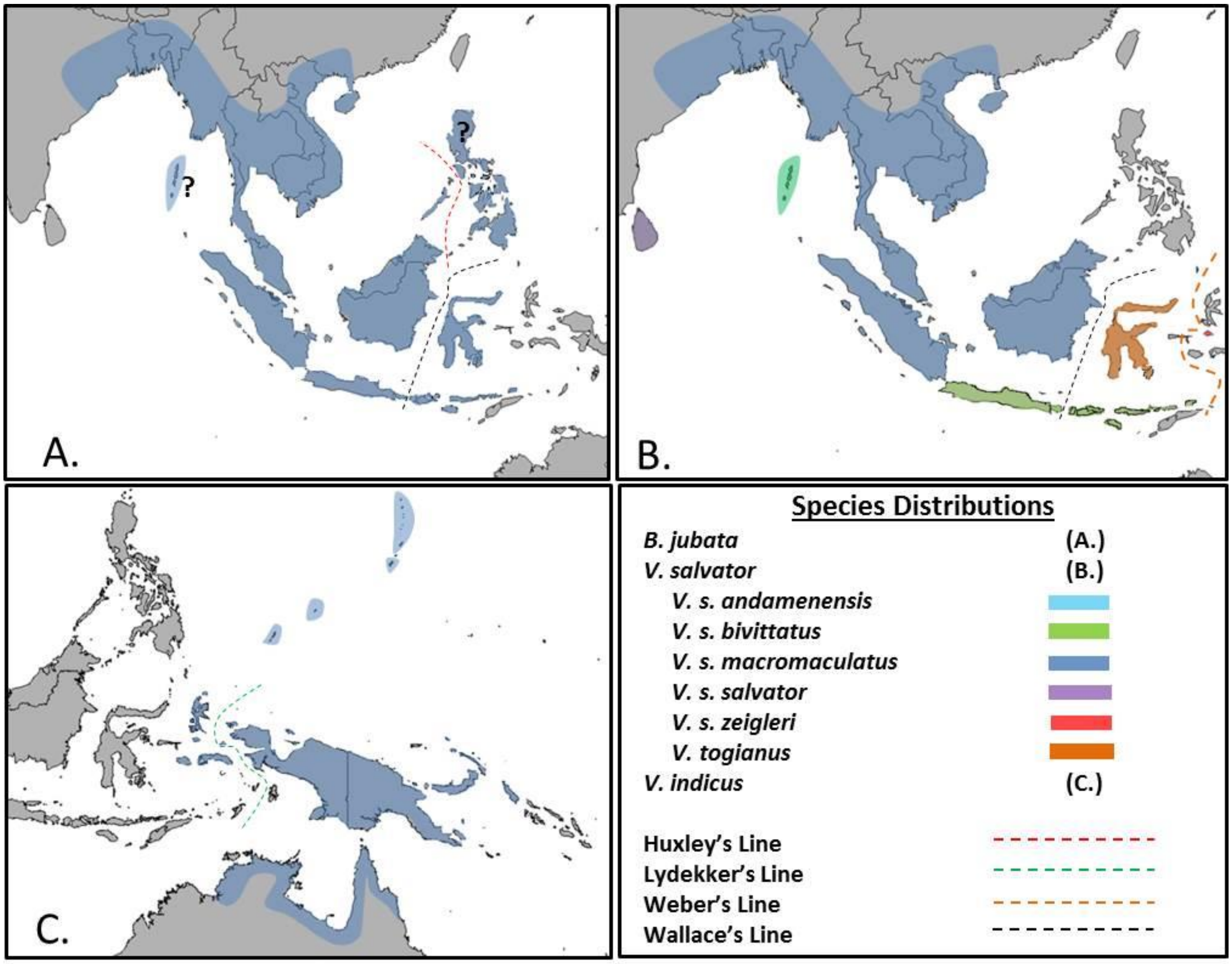


Figure 3. Collection localities of *Pseudocalotes*. Different colors represent species we have delimited based on morphological and genetic differentiation. See Appendix B for coordinates and specimen ID's.

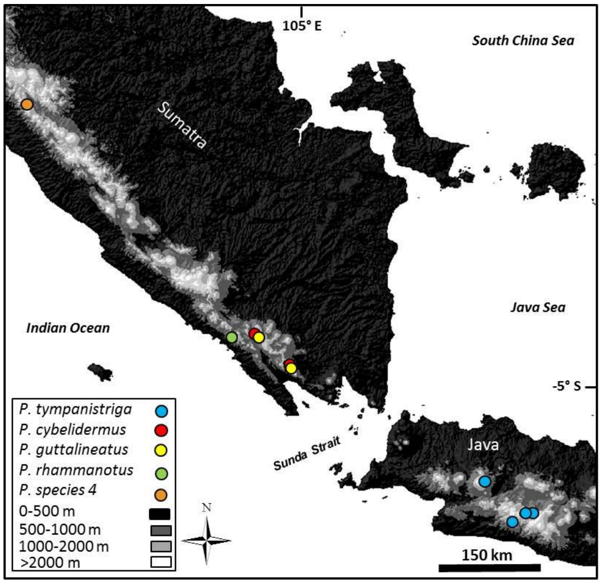


Figure 4. The five superficially similar *Pseudocalotes* species, which we delimited before conducting our IUCN Red List assessment simulation on *P. tympanistriga*. Image A is *P. rhammanotus*, Image B is *P. tympanistriga*, Image C is *P. species 4* (*Pseudocalotes baliomus;* Harvey et al. In Review), Image D is *P. cybelidermus* and Image E is *P. guttalineatus*.

Figure 5. Both phylogenetic analyses. The tree on the left shows our UPGMA analysis which indicates that there are four distinct lineages of *Pseudocalotes* other than *P. tympanistriga*. The scale bar represents the pairwise genetic distance (percentage) between individuals. The tree on the right shows our Bayesian phylogenetic analysis which shows very similar relationships to the UPGMA with some minor differences. The scale bar in the Bayesian analysis corresponds to the average substitutions/site. The red dots on each tree represent the *P. tympanistriga* group. The tree shows four strongly supported *Pseudocalotes* lineages other than *P. tympanistriga*.

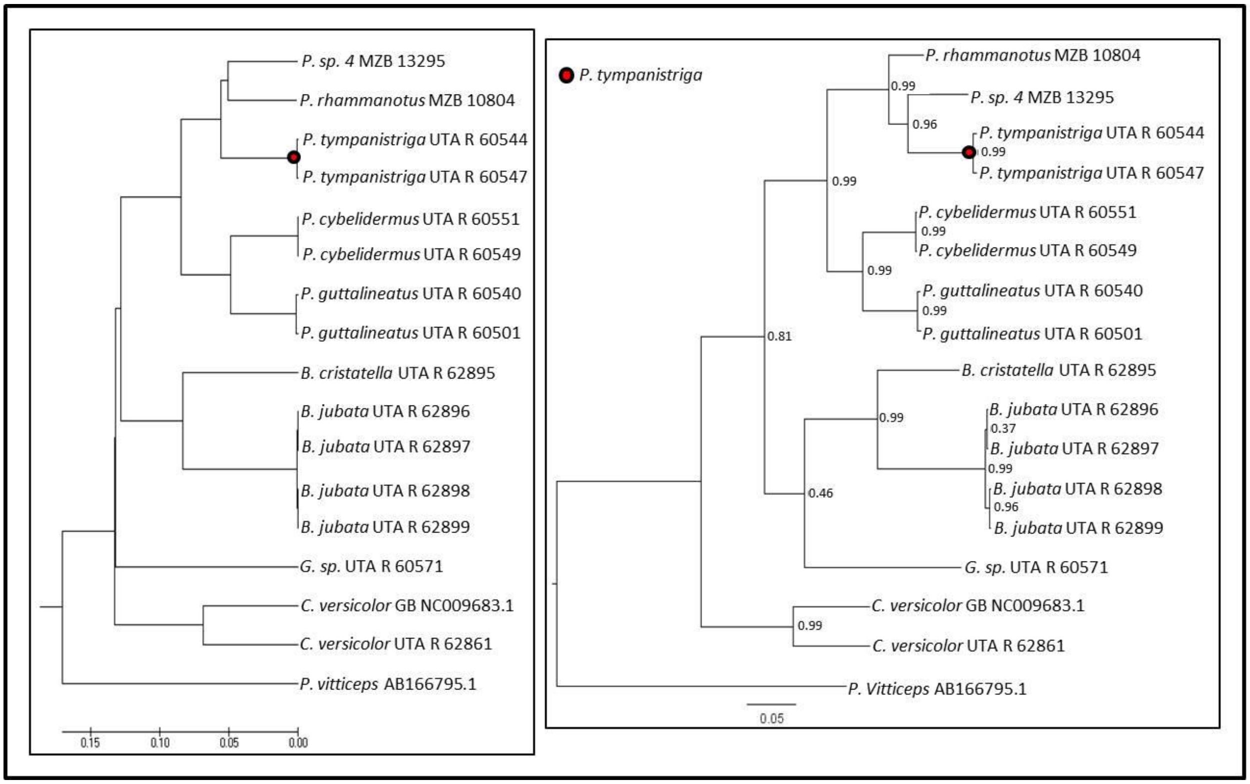


Figure 6. The IUCN Red List assessment produced from the analysis in the program GeoCAT. Image A represents what the Red List assessment would have produced prior to any taxonomic verification being conducted on *P. tympanistriga*. Image B represents the Red List assessment after taxonomic verification and only actual *P. tympanistriga* are included. This shows how using an integrative taxonomic approach can alter an IUCN Red List assessment.

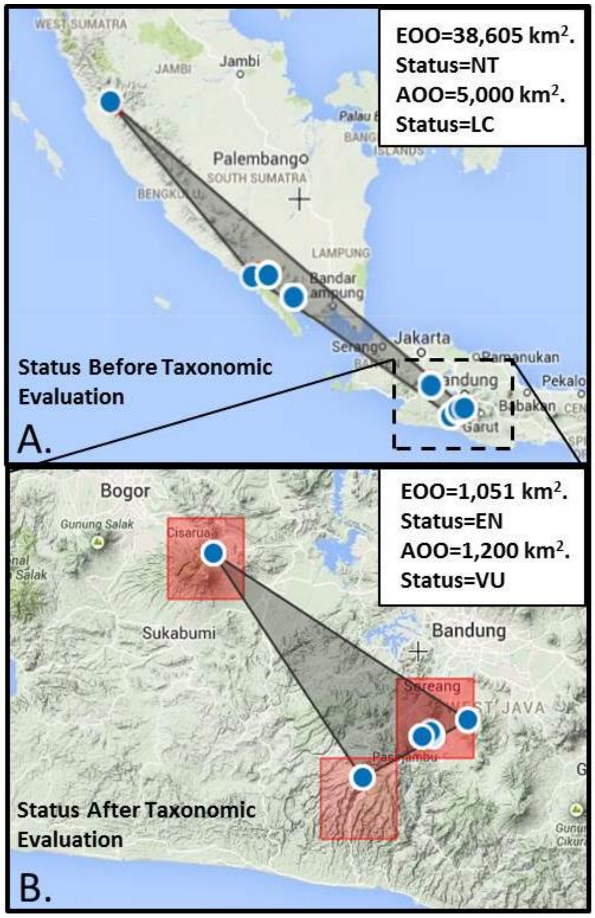
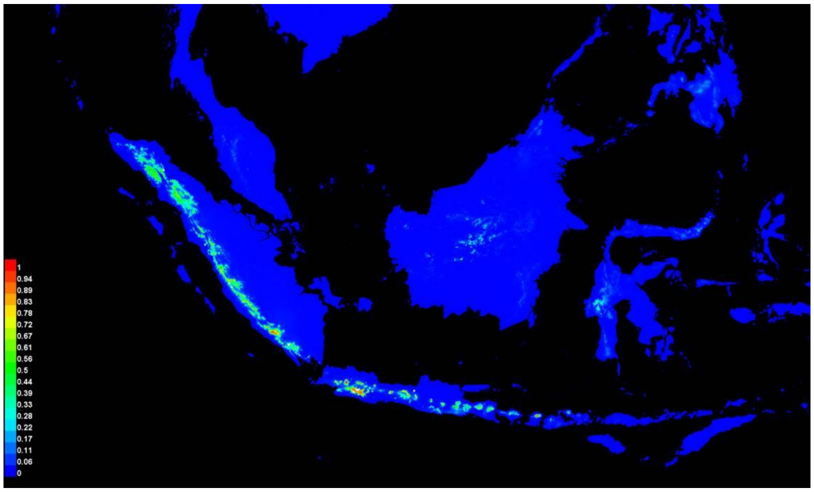


Figure 7. Species distribution modelling output from the MaxEnt analysis. The scale bar on the left hand side of the map indicates probability of occurrence. There are high probability areas (0.9 – 1.0) that extend across Java and Sumatra, well beyond our confirmed *P. tympanistriga* distribution in reality. There are medium probability areas (0.7 – 0.9) that extend across Borneo, Java and neighboring islands and Sumatra, which completely exceeds the confirmed range of *P. tympanistriga*. Lastly there are low quality areas (0.5 – 0.7) that extend across Borneo, Java and neighboring islands, Sulawesi and Sumatra. Overall this shows completely overestimated range of a *P. tympanistriga* in reality.



Chapter 3

Biogeography of Montane Forest “Island” Draconid Lizards in the Western Extreme of the Pacific Ring of Fire

Abstract- The “regional endemism paradigm” predicts that island biodiversity is driven via extinction amongst regionally endemic species, rather than allopatric diversification between isolated locations. Biogeographical evidence, both, for and against this hypothesis has been uncovered across the Greater Sunda Region (Sundaland) of southeast Asia. Additionally, several hypotheses have been put forth regarding the extent of Pleistocene refugia in Sumatra and the potential impacts of the Toba blast (71.6 ka) on Sumatran diversity. We analyzed nearly complete mitochondrial genomes and a single nuclear gene for montane forest lizards (subfamily: Draconinae) across Sumatran forest “islands”, examined genetic divergence between species, and analyzed contemporary distributional patterns. Using these data, we tested whether: (1) Sumatra’s highland draconid diversification fit the regional endemism paradigm, (2) draconid phylogeography provides evidence for Pleistocene forest extent, and (3) if there is evidence of loss of genetic diversity in montane draconids due to the Toba eruption. We uncovered cryptic species diversity, distributed allopatrically across montane forest “islands”. Deep genetic divergence between species suggests that highland refugia were more widely distributed than was previously hypothesized during the Pleistocene Epoch. We suggest that the contemporary distribution of point endemics and lack of sympatry between species provides biological evidence for the elevational lower limit of montane forests during glacial maxima of the Pleistocene Epoch. Within population genetic diversity in North Sumatra (near the Toba eruption site) suggests that genetic diversity within close proximity to the Toba blast 71.6 kya remained intact following the eruption. Our results suggest in situ diversification, not extinction amongst regional endemics, was the main

driver behind montane draconid lizard diversification in Sumatra. Furthermore, these patterns of endemic diversity in Sumatra can be used to identify potential locations for undiscovered lineages of other montane forest dwelling taxonomic groups.

Introduction

Extinction of local populations amongst regionally endemic species has been hypothesized as a significant driver of patterns of species composition in archipelagic regions, particularly amongst islands which have been connected by intermittent dry land connections (Demos et al. 2016, Whittaker & Fernandez-Palacios). Demos et al. (2016) describe this hypothesis as the "regional endemism paradigm" and tested for evidence of this pattern in shrews in the Greater Sunda Island chain of southeast Asia. Species' distributions across the Greater Sunda Islands are hypothesized to largely be driven by the "regional endemism paradigm" for two reasons: (I) Intermittent land bridge connections amongst the Greater Sunda Islands during periods of glacial maxima and minima, which allowed for floral and faunal dispersal between islands, (II) subsequent climate shifts incurred during the Pleistocene epoch, along with shifting forest distributions, rising sea levels and volcanic blasts, were likely responsible for a variety of species extinctions. Such events have been particularly regarded as drivers of extinction and faunal recalibration in Sumatra, which lies on the western extreme of the Pacific Ring of Fire. However, in situ diversification amongst other species may have played a greater role in driving patterns of faunal diversification in Sumatra than was previously hypothesized. For example, Demos et al. (2016) rejected the regional endemism paradigm as it pertains to shrews in their study.

Deep divergence between mammal species in Sumatra has been dated to the late Miocene and early Pliocene epochs, suggesting within island diversification when sea levels covered much of the islands of Java and Sumatra. However, reconstructions of lowland and highland forest cover during those time periods suggests there were few isolated patches of land, which may have acted as refugia for diversification. Hall et al. (2009, 2012), reconstructed hypothesized land cover extent across the islands of Java and Sumatra and suggest that most of northern Sumatra remained underwater during these time periods and highlands only covered a small section of South and Central Sumatra during the early Pliocene (~5 mya). Yet, limited strips of largely continuous land cover do not explain species radiations during the late Miocene to early Pliocene epochs, which may be an indication of wider spread highland or lowland refugia during those time periods than was previously hypothesized.

Montane forest cover, contemporarily occurring between 1200 and 2500 meters in elevation, extends across the upper altitudinal bands of Sumatran mountain ranges, forming montane forest “islands”. Hall et al. (2009, 2012) suggest glacial minima may have caused those forests to retreat downward 300–500 meters in elevation for intermittent periods of time during the Pleistocene. Depending upon how far forests retreated, this hypothesis could have caused montane forest islands to become intermittently connected, allowing for floral and faunal dispersal. This scenario may in fact support the “regional endemism paradigm”, but in a “montane forest archipelago” of Sumatra’s highlands. Further supporting this hypothesis, is a lack of montane forest endemism currently described from Sumatra and the evidence of significant volcanic blasts suspected to have driven extinctions in Sumatra’s highlands. For example Patou et al. (2010) suggest the Toba blast may have caused faunal extinctions in Sumatra 71.6 kya, which may explain higher described diversity in Borneo. Yet, Sumatra’s lack of described montane diversity may be an artifact of limited biological inventory rather than biogeographic history. Recent studies have uncovered a wide array of new montane forest species from Sumatra’s highlands (Achmadi et al. 2012, Harvey et al. 2014, Streicher et al. 2014, Shaney et al. in review). Demos et al. (2016) noted that fine-scale phylogeographic studies may be the most informative measure for determining the relative importance of speciation in generating β-diversity (e.g. the ratio between regional and local diversity) and only recently have studies started to uncover these fine scale patterns.

Here, we use nearly complete mitochondrial genomes and a single nuclear locus to estimate species boundaries and divergence dates of highland draconid lizards across Sumatra's montane forest "islands" and test whether: (1) draconid lizard distribution in Sumatra supports or rejects the "regional endemism paradigm", (2) contemporary draconid lizard distribution and composition provide biological evidence for the lower elevational extent of montane forest during the Pleistocene, (3) contemporary draconid genetic diversity supports evidence for extinctions or loss of genetic diversity near the Toba eruption site.

Materials and Methods

Biological Inventory and Study Area

A fine scale herpetofaunal survey was conducted across the highland forests of Java and Sumatra's Barisan Mountain Range, between 2012 and 2016, and sampling all draconid lizards encountered. We systematically targeted montane forests appearing to be geographically isolated, based on topographic variation in the landscape. We focused our analyses on two monotypic genera from within the draconid subfamily, previously excluded from any phylogentic study: (I) *Dendragama,* (II) *Lophocalotes,* and a single species previously considered to be the sole occurring insular member of its genus from Java and Sumatra (*Pseudocalote*s tympanistriga). Following collection in the field we grouped individuals based on preliminary species ID and locality. Next, we selected between one and six individuals from each geographic location, depending upon how many were collected and whether there was any evidence of sexual dimorphism or morphological variation. From this, we selected varying numbers of individuals from these genera and several other draconid genera representatives for our final phylogenetic assessment, depending on which loci we were sequencing.

Taxonomy of Sundaland *Dendragama*, *Lophocalotes* and *Pseudocalotes*

Previous studies have identified southern, central, and northern taxonomic clades in Sumatra (Demos et al. 2016, Oconnell et al. in press). These major clades are concordant with subaerial refugia put forth by Hall et al. (2009, 2012); however, they do not explain the extent to which refugia may have been further subdivided during the Miocene, Pliocene, and/or Pleistocene. After sampling, broadly within and between the southern, central, and northern branches of the Barisan Range, we grouped taxa by genus and by locality to test the extent of historical subaerial refugia in Sumatra.

Initially, we divided populations within each genus based on locality, predicting biogeographic divides. Thus, each mountain top has been treated as a separate population, until enough information has been collected to deme a population a new species, a separate population, or still requiring additional information for determination. Since collection between 2013–2016, we have described three new species of *Dendragama*, one new species of *Lophocalotes*, and three new species of *Pseudocalotes* (Harvey et al. 2014, 2015a,b, Shaney et al. In review). Considering each genus only represented one species previously from the islands of Java and Sumatra, draconid diversity has grown considerably within these three genera and we provide additional biogeographic and taxonomic information for the continuous evaluation of this group.

Whole Mitochondrial Genome Amplification

We used a protocol developed by Fujita et al. (in press) for whole mitochondrial genome amplification. We used 1 microliter of Plasmid Safe DNase enzyme that only digests linear DNA, allowing circular Mitochondrial DNA to remain undigested and absent of all nuclear DNA following this step. Next, we ran test PCR's with one mitochondrial primer set (ND4) and one nuclear primer set (BDNF) to test for amplification of mitochondrial and nuclear DNA in all samples. The nuclear DNA test was used as a control to ensure that all nuclear DNA had properly been digested and the mitochondrial DNA test was to ensure that each sample still contained mitochondrial DNA for sequencing. If nuclear DNA amplified, we backtracked and repeated the nuclear digestation step with Plasmid Safe DNase enzyme, then reran control PCR's. Once all nuclear DNA was removed we amplified all mitochondrial DNA using N10 oligos and Phi29 enzyme.

We used NENext DNA Library preperation kits for Illumina sequencing preperation, which followed four distinct steps: (1) we fragmented 7.5 microliters of DNA product for each sample using 0.5 μLof Fragmentase Enzyme, then incubated samples at 37 C for 15 min, (2) we conducted end-repair of fragments as outlined in the NEBNext kit, (3) dA-tailing was done, and finally (4) we ligated adaptors to the ends of digested fragments that contained unique molecular identifiers (UMIs; eight consecutive N's prior to the ligation site). Following adapter ligation, samples were pooled in sets of eight, size selected for a range of 500–700 bp using the Blue Pippin Prep (Sage Science, Beverly, MA, USA), and PCR amplified to complete attachment of flow-cell binding sequences and addition of a second index specific to each sub-pool. Sub-pools were pooled and submitted to the Genomics Core Facility at UT Arlington to be sequenced using 100 bp paired-end reads on an Illumina MiSeq.

Mitochondrial Sequence Analysis

We sequenced a total of 63 complete or nearly complete mitochondrial genomes, representing 9 genera, 76 ND4 sequences representing 10 genera, 43 BDNF sequences representing 8 genera. The larger ND4 dataset was generated to cover a wider number of intragenic taxa and to double check

ID’s of mitochondrial genome data, while the BDNF dataset was generated to test whether nuclear DNA was in concordance with mitochondrial DNA. The mitochondrial genomes selected for sequencing were chosen systematically to represent as many of the Sumatran agamids as possible.

We PCR’d a fragment of the NADH dehydrogenase subunit 4 (ND4) gene using the forward primer 5’CACCTATGACTACCAAAAGCTCATGTAGAAGC 3’(ND4) and reverse primer 5’CATTACTTTTACTTGGATTTGCACCA 3’(LEU) which targeted an 892 bp region of the gene, while mitochondrial genomes used the protocol above. The ND4 thermal cycle profile consisted of an initial denaturation at 94 C for three min, followed by 30 cycles of denaturation at 94 C for 30 sec, a 50 C annealing phase for 45 sec and a 72 C extension for one min, followed by a 72 C extension for seven min, then a holding phase at 4 C. We cleaned the products of amplification using Sera-Mag Speedbeads (Fisher Scientific, Pittsburgh, PA, USA), following the procedure outlined by Rohland and Reich (2012).

Gene sequence chromatograms were edited using Sequencher. We aligned sequences using ClustalW in Genious v6.2.6.; used Bayesian phylogenetic inference to estimate phylogenetic relationships among highland agamids in MrBayes v3.2.1 (Huelsenbeck and Ronquist, 2001); and chose *Draco* as an outgroup based on previous phylogenetic studies of draconid lizard relationships (Grismer et al. 2016). We used PartitionFinder v1.2.1 (Lanfear et al. 2012) to select best-fit models of evolution for implentation of phylogenetic analyses. Our three datasets were analyzed independently to test for concordance among mitochondrial and nuclear DNA, as well as amongst single mitochondrial markers and whole mitochondrial genomes. We used the program MITOS to annotate whole mitochondrial genomes, trimmed tRNA sections, parsed all mitochondrial genes from whole genome sequences, and concatenated genes before running the alignments through ParitionFinder (we did this for ND4 and BDNF separate from whole genome concatenations). Likewise, tRNA’s were trimmed from single locus data as well. Models selected for our three datasets were as follows: HKY for 1st and 2nd codon positions and GTR + I for the 3rd codon. We paritioned all three datasets by codon position and by gene when we analyzed whole mitochondrial genomes. We used four independent runs (nruns = 4) and four chains (three heated chains and one cold chain) for 10 million generations, sampling every 100 generations. Default temperatures for chains were used. Adequate mixing, appropriate amount of burn-in, andconvergence were assessed by inspecting the log files in the program TRACER v1.6 (Rambaut et al. 2014). 25% of trees were discarded in TreeAnnotator v2.4.6 (http://beast.community/treeannotator). We conducted UPGMA analyses and calculated uncorrected pairwise distances using Mega 5.1 (Tamura et al. 2011).

Divergence Dating

Divergence times were estimated using a concatenated data matrix with BEAST2 (Drummond and Rambaut, 2007). Given the major discrepancies in taxonomic sampling between our two mitochondrial datasets, we decided against concatenating the two loci and repeated the analyses with each locus separately, to see if we got concordant divergence times and HPD values. In both cases we calibrated the root of the tree with a secondary calibration and simultaneously provided the general rate for mitochondrial evolution of 0.001 to 1.0 substitutions per million year (mean = 0.5) (Drummond and Bouckaert 2015). To this end, we used the relaxed log-normal clock in conjunction with a Calibrated Yule tree prior and all other parameters were set to default values. For both datasets, we calibrated the root to 88.5 MYA (95% HPD = 85.0–92.0) after Grismer et al. (2016) using a Normal distribution.

In both instances, we ran two independent runs with a chain length of 1×10^9 and a sampling frequency of 1×10^4 resulting in ESS values >200. Convergence for both runs was diagnosed using TRACER v. 1.7 (Rambaut & Drummond, 2009). Both runs were then combined in LogCombiner (Rambaut & Drummond, 2009) before contructing a final maximum clade credibility tree using

TreeAnnotator v. 1.7.4 available within the BEAST2 package. FigTree v.1.4.0 (http://tree.bio.ed.ac.uk/software/figtree/) was used to visualize tree topology.

Sundaland Montane Refugia Reconstructions

Contemporary montane forests in Sumatra occur between approximately 1200–2800 meters. These forests are only isolated from one another where the topography dips down below this otherwise continuous band of forest across the Barisan Range, or where land clearing has occurred in the last several hundred or thousand years.

Montane forests are believed to have fluctuated up and down in elevational extent, following glacial maxima and minima during the Pleistocene. Periods of cooler temperatures forced montane forests to retreat downslope, while periods of warmer temperatures forced forests to retreat back upslope. Hall et al. (2012) suggest that montane forests retreated between 300–500 meters during cool periods of the Pleistocene. If in fact forests retreated to these elevational limits, we would expect periodic time periods where isolated montane forests became interconnected and allowed for dispersal of species between mountains. The extent to which dispersal would have been possible would depend on how far forests retreated. In other words, if forests retreated no more than 300 meters, then only some sections of montane forest across the Barisan Mountain Range would become interconnected. However, if forests retreated as much as 500 meters, the montane forests of the Barisan Range would have become one. Baring extinction events, we expect to see contemporary species distributions that correlate with Pleistocene montane forest connectivity. Species would occur across breaks of what are currently isolated mountains today (i.e., 2017) if they had the ability to disperse during periods of connectivity during the Pleistocene. We would also expect to see sympatry in sections of mountain range that become interconnected during periods of forest fluctuation, where divergent species were able to disperse freely.

We use (1) the presence of point endemic draconid species, (2) locations where draconid species occur sympatrically, and (3) genetic divergence (pairwise divergence and divergence dating) to test where montane refugia may have occurred historically and where the lower elevational limit of montane forest extent may have been during periods of glacial maxima. This may be used to identify broad scale biogeographic patterns that may apply to other taxonomic groups throughout the region.

Toba Blast

The latest Toba blast occurred 71.6 kya, and it is believed to be responsible for the extinction of species across the region. If the Toba blast caused the local extinction of the Karo highlands draconid species we would expect to see one of three scenarios: (1) an absence of endemic draconid lizards across the plateau due to isolation from other populations since the Toba blast, or (2) low intraspecific genetic diversity across the Karo highlands and the presence of the same species from either the Northern or Central clades of Sumatra. The presence of either the Northern or Central clades across the Karo highlands would suggest a recent invasion following the Toba blast and low genetic diversity would be indicative of such an event, or (3) a recent invasion from both, the North and Central clades, following the extinction of Karo population after the Toba blast. This latter case would show evidence of two sympatric species across the Karo highlands (the same species found today in the Northern and Central regions), maybe with evidence of hybridization.

Alternatively, if the Toba blast was not responsible for the extinction of the Karo highland species, we would expect Karo highland endemics still found across the highlands. In such a case the amount of population subdivision (or genetic diversity) preserved may indicate how much the Toba blast impacted the Karo lizard populations. For example, did one small population survive the blast? Or, did several populations survive the blast? We test for evidence of a highland draconid extinction event following the Toba blast using the only genus found across all sections of the Barisan range, *Dendragama*.

Results

Phylogenetic Analyses

We obtained high support for our Bayesian phylogenetic reconstruction of Sundaland draconids, particularly among our three target genera, *Dendragama*, *Lophocalotes*, and *Pseudocalotes*. As has been discussed in recent papers, we confirmed that mainland and insular *Pseudocalotes* are paraphyletic (Harvey et al. 2016), while insular *Pseudocalotes*, *Dendragama*, and *Lophocalotes* each form their own monophyletic clade. *Dendragama* and *Lophocalotes* are found to be sister to one another, while *Pseudocalotes* is basal to those genera.

Nearly all the mountains sampled have their own distinct lineage from each genus represented (e.g. point endemics). The *Pseudocalotes* group represents at least seven distinct lineages, previously only considered one species distributed across Java and Sumatra, *Lophocalotes* represents at least three distinct lineages, and *Dendragama* represents at least six distinct lineages. Harvey et al. (2014, 2015, 2016, in press, Shaney et al. in press) have described several of these new lineages, while the taxonomic evaluation of some are still in progress. Among intragenic populations there is distinct genetic diversity between mountains tops. *Dendragama* populations range between 1–11% pairwise genetic divergence. Where populations from the same regions of Sumatra (e.g. south, central, north-central, north clades) have low to moderate levels of genetic diversity (1–5%) and populations from different regions of Sumatra have higher levels of genetic diversity (5–11%). This same pattern holds for *Lophocalotes* and *Pseudocalotes* populations, although they are not distributed north of central Sumatra.

Biogeography

Among all three insular clades, we found a consistent pattern in levels of intragenic diversity and contemporary species distributions. Within *Dendragama*, *D. australis* populations form a distinct southern clade, *D. boulengeri* populations form a central clade, *D. schneideri* forms its own distinct clade in the Karo highlands, which we refer to here as the North-Central clade, and *D. diodema* forms its own northern clade. Within each of these large clades, there is widespread population subdivision, including many subpopulations with deep genetic divergence from one another.

Insular *Pseudocalotes* are divided into two subclades, *P. guttalineatus* and *P. cybelidermus* group, which were the only intragenic species distributed sympatrically within the same region (South in this case) across the mountains of Patah, Dempo, and Sumatera Selatan. While the other group consists of *P. tympanistriga* from Java and several sister taxa from Sumatra. We identified three distinct clades from Java (currently undescribed) and three other clades from Sumatra (*P. rhammanotus* (Mountains around Danau Ranau), *P. baliomus* (Mount Kerinci), and one undescribed clade from Mount Kunyit.

Lophocalotes species are restricted to the South and Central subregions of Sumatra. Following a recent description by Harvey et al. (in press) *L. ludekingi* is now considered to occur only in the mountains near Mount Kerinci, while *L. achlios* is found in the Mountains of Dempo and Patah. A separate, yet distinct, population is found on Mount Kaba, but has not yet been described.

Genetic Divergence—Where intergenic sampling overlapped, we identified concordant levels of mitochondrial divergence. Examples of this include, *Dendragama boulengeri* populations from Mount Kerinci and Mount Kunyit which vary by 4.8% across the ND4 gene between mountains, whereas *P. baliomus* populations from Mount Kerinci and Mount Kunyit vary by 4.7%. Similarly, *Dendragama* populations between Mount Dempo and Mount Patah vary by 3.2%, whereas *Lophocalotes* populations between Mount Dempo and Mount Patah vary by 2.8%.

Divergence dating—Fig. 1 shows the results of our divergence estimates, which suggest deep divergence between genera and interspecifically within genera. Interspecific breaks within each of the three focal genera, *Dendragama*, *Lophocalotes*, and *Pseudocalotes*, indicate splits between many populations prior to the initiation of the Pleistocene. Within *Dendragama*, *D. schneideri* (North Central clade), *D. boulengeri* (Central clade), and *D. australis* (Southern clade) are estimated to have split 19.83 mya from *D. dioidema* (Northern clade). *Dendragama schneideri* split from *D. boulengeri* and *D. australis* 13.45 mya, and *D. boulengeri* and *D. australis* split from one another 9.77 mya. Multiple splits between *D. schneideri* populations along the Karo highlands plateau are estimated to have occurred well before the Toba eruption 71.6 kya. In fact, most of these intraspecific splits within *D. schneideri* are estimated to be between 200 kya and 2.1 mya. Splits between the three focal genera are estimated to have occurred deep within the Oligocene (~29.15 mya between *Dendragama* and *Lophocalotes*) or even further in the past, during the Paleogene (37.56 mya between the *Dendragama*/*Lophocalotes* group and *Pseudocalotes*).

Forests

Breaks in the distributional extent of forest are consistent with breaks in topography and levels of genetic divergence across all three focal genera. There is a strong relationship between levels of genetic diversity and the elevation of topographic prominence. Where topographic prominence dips below 800–1000 meters (the point where shared topography between peaks goes no higher than 800 meters) genetic diversity increases considerably between populations (Fig. 2). Areas where topographic prominence is higher between mountain tops show less genetic diversity between montane draconid populations. Furthermore, the only location where we found sympatry between intragenic species was in South Sumatra, between *P. cybelidermus* and *P. guttalineatus*, which occur across mountains with higher limits of topographic prominence (e.g., ~1100 meters).

Toba Blast

Dendragama from the Karo highlands (or north central populations of Sumatra) were identified as their own distinct species, *D. schneideri* (Shaney et al. in press), endemic only to the Karo highlands. Additionally, we found no other sympatric species of *Dendragama* throughout the Karo highlands, which suggests that *D. schneideri* may be the only representative of that genus across the Karo highlands.

We found distinct population subdivision among the *Dendragama* populations that were collected from the Karo highlands. Populations from around lake Toba ranged between 0.8 and 1.2% pairwise genetic divergence from the other Karo populations. *Dendragama* populations from Samosir ranged between 1 – 1.4%. Divergence estimates suggest these populations split from one another between 800 kya and 1.2 mya. Those estimates suggest a division long before the Toba blast 71.6 kya. Fig. 3 shows *D. schneideri* sampling in relation to the Toba blast site, while Table 1 provides corresponding pairwise genetic divergence for those samples.

Discussion

Regional Endemism Paradigm—Montane agamids show consistent patterns in distribution and genetic diversity among isolated mountain peaks. Agamid lizards show high pairwise genetic diversity, a lack of sympatry among interspecific species, and point endemic distribution across Sumatra's highlands. These patterns were consistent across the three genera we focused on this study.

The high genetic diversity, lack of sympatry, and point endemic distribution of species suggest that highland agamids have remained isolated from each other for several million years, which was further supported by our divergence estimates. If the regional endemism paradigm explained contemporary distributional patterns, we posset that sympatric distributions would occur more often and more randomly, not in the point endemic arrangement that is seen today. Thus, we reject the regional endemism paradigm as an explanation for montane draconid lizard distributions in Sumatra (specifically for the three genera tested).

Pleistocene Highland Forest Refugia—We suggest that a more likely explanation for contemporary agamid lizard distributions is in situ diversification, driven by fluctuations in montane forest habitat across western Java and the Barisan Range of Sumatra. Hall et al. (2009) provide reconstructions of hypothesized forest habitat during several historical time periods. Parts of Hall's hypotheses are consistent with what we see in highland agamids; however, we suggest a more complex model for highland refugia during the Pleistocene. Based on point endemic species distributions with divergence points dated between 9.77 and 19.83 mya (depending upon which pairwise comparison is looked at) we hypothesize that several other isolated areas of forest remained above water during the Pleistocene, allowing for additional pockets of in situ diversification that are not depicted in Hall's reconstructions. There are simply too many point endemics to be explained by Hall's reconstructions of 2–3 land masses. To the contrary, we see almost only allopatric point endemic distributions, with the exception of two divergent species of *Pseudocalotes* that are distributed in southern Sumatra. This sympatric distribution can be explained by higher continuously shared strips (higher topographic prominence) of montane forest, where the valley floor between mountains is higher than other regions of Sumatra. These higher valleys between mountains would have facilitated dispersal during glacial maxima when montane forests retreated downward and higher valleys would have allowed interconnectivity between what are isolated strips in contemporary times. Furthermore, although we only define the breaks in point endemic distributions between the four main clades of *Dendragama*, there will likely be additional species that are described from within those main clades as future analyses identify distinguishing characters. This would only further support our hypotheses here.

Genetic Diversity around the Toba Blast Site—Dendragama schneideri is endemic to the Karo highlands, the location of the Toba blast 71.6 ka. *Dendragama schneideri* is also the only described species from these highlands, even after a considerable amount of sampling effort across several different mountains across the plateau. Based on these distributional patterns, there is currently no evidence for dispersal events by central or north Sumatran *Dendragama* populations to the Karo highlands before or after the Toba blast occurred. Genetic subdivision among *D. schneideri* populations across the the Karo highlands suggests that a considerable amount of diversity remained intact following the Toba blast and that the *D. schneideri* colonized the Karo highlands and become isolated long before the Toba blast. This provides evidence for the survival of some highland agamid lizard diversity near the Toba blast site despite the widespread impacts the blast is hypothesized to have had on several different species (Inger and Voris 2001, Meijaard 2004, De Bruyn et al. 2014).

Conclusions

Many of the taxa included here have not been previously included in a phylogenetic evaluation and only recently have several single locus analyses been published on almost all of the new *Pseudocalotes*, *Dendragama* and *Lophocalotes* species (Harvey et al. 2014, 2015, 2016, Shaney et al. in review). Our whole mitochondrial genome analyses show similar results to single locus mitochondrial and nuclear gene analyses. Highland draconid lizards show consistent distributional patterns among and within genera, in which they are distributed in point endemic arrangements. These patterns in combination with deep genetic divergence and relatively old divergence date estimates, suggest these species likely evolved under in situ diversification. Under the assumption that montane draconids inhabited similar forest habitat to what they inhabit today, we infer that contemporary distributional patterns yield insight into the extent of montane forest habitat during the Pleistocene. Wherever breaks (deep genetic divergence and isolation) occur in montane agamid distribution, we suggest montane forests remained isolated between those locations for at least as much time as is estimated in divergence estimates. Thus, we can hypothesize more accurately where montane forest refugia occurred during the Pleistocene, where and when those forests retreated during glacial maxima, and potentially where forests may have become connected for intermittent periods of time. We also hypothesize patterns of *Dendragama* distribution and genetic divergence suggest that the Toba blast did not cause Karo highland *Dendragama* to go extinct, providing information about historical evolutionary and ecological impacts of the Toba blast on some highland taxa. Additionally, patterns of point endemic agamid lizard diversity may also be projected for other taxonomic groups that inhabit the montane forest islands of Sumatra. Thus, high priority locations for new species discovery may be predicted based on the distributional patterns discussed here.

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Tables

Table 1. Pairwise genetic distances of *D. schneideri* surrounding the Toba blast site. Sample numbers correspond to numbers on Fig. 3 to highlight intact genetic diversity that predates the Toba blast. NA refers to *D. boulengeri* which is not included in Fig. 3.

	Sample Number	**1**	**2**	**3**	**4**	**5**	**6**	**NA**
Sample Number	**ID**	ENS 15615	ENS 16762	ENS 16774	ENS 15639	ENS 16846	ENS 16849	*D. boulengeri*
1	ENS 15615							
2	ENS 16762	0.003						
3	ENS 16774	0.003	0.000					
4	ENS 15639	0.000	0.003	0.003				
5	ENS 16846	0.007	0.007	0.007	0.007			
6	ENS 16849	0.008	0.008	0.008	0.008	0.005		
NA	*D. boulengeri*	0.078	0.076	0.076	0.078	0.081	0.080	

Figures

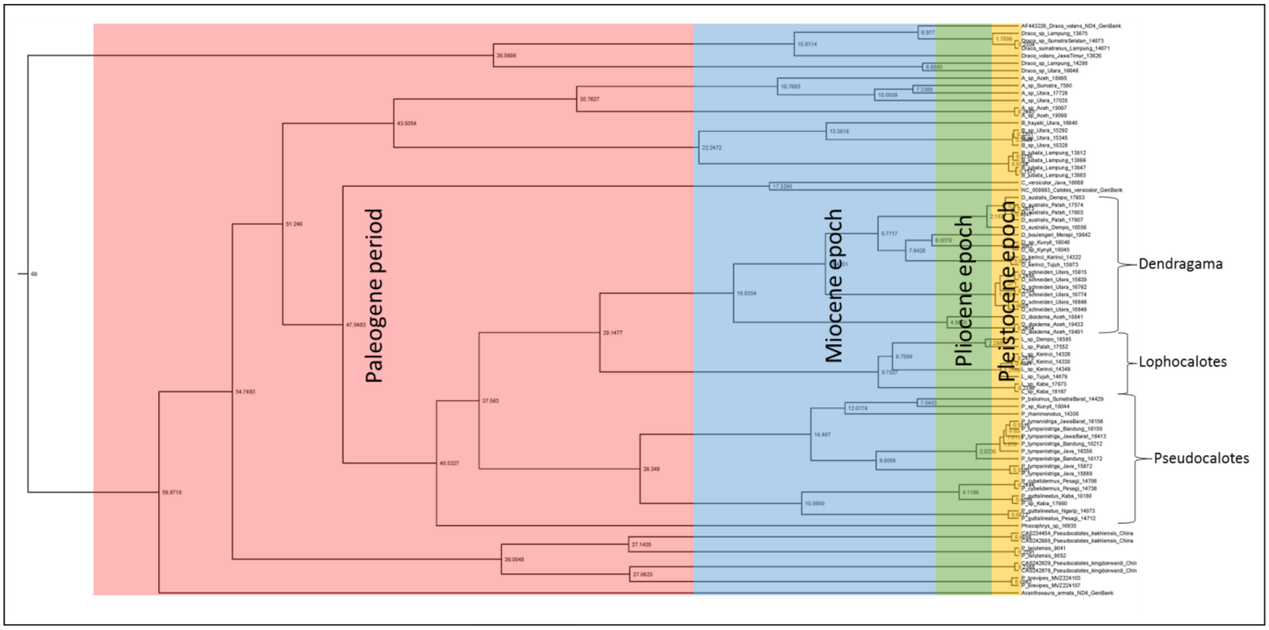

Fig. 1 Divergence time estimates with key genera and time periods highlighted.

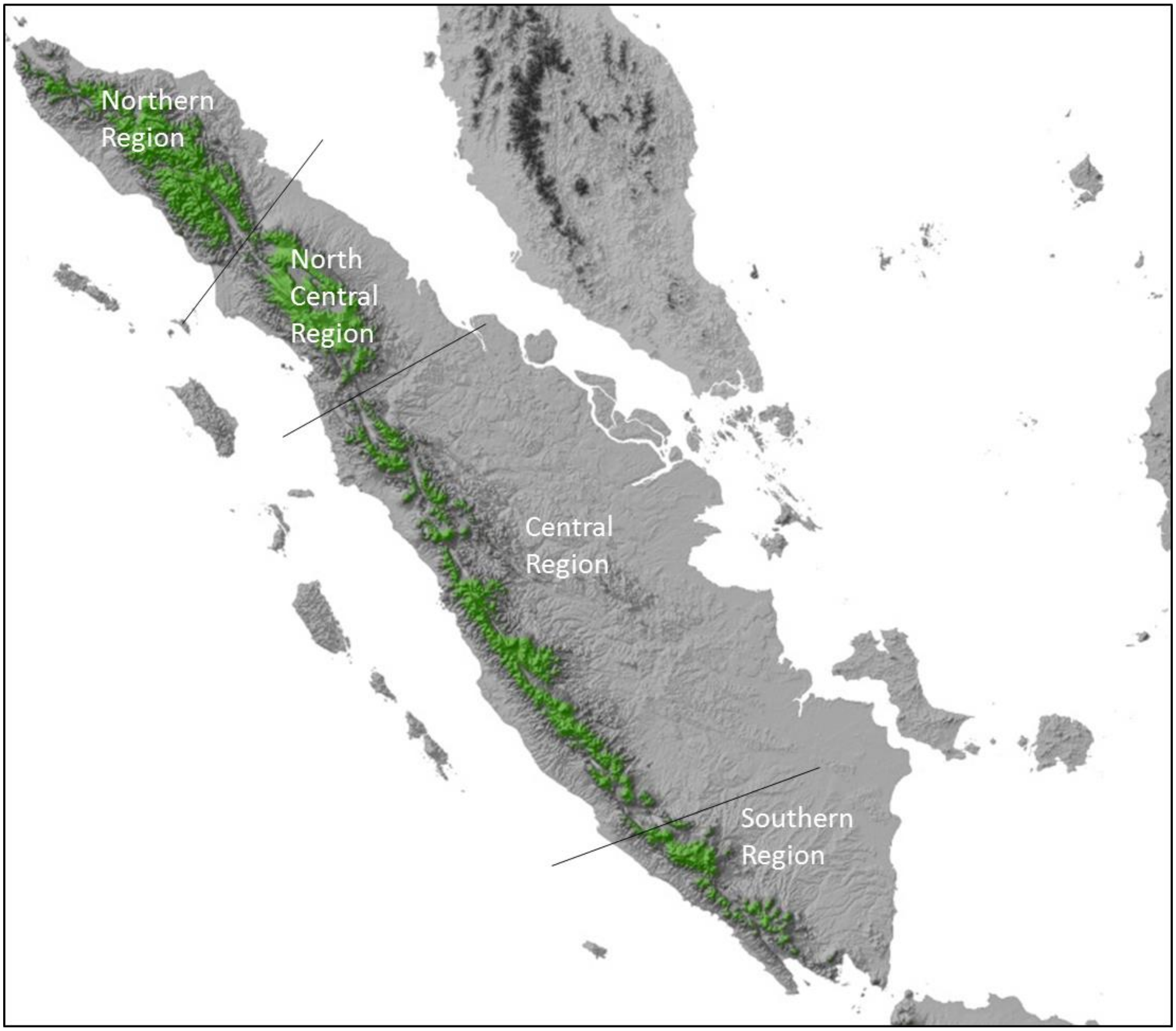

Fig. 2 Hypothesized forest limitations. Montane forest above a 1000 m. elevational line is highlighted in green, which exposes where major breaks in forest extent are expected to have occurred during the Pleistocene as well. Subsequently, those same breaks are where major breaks in montane agamid distribution occur.

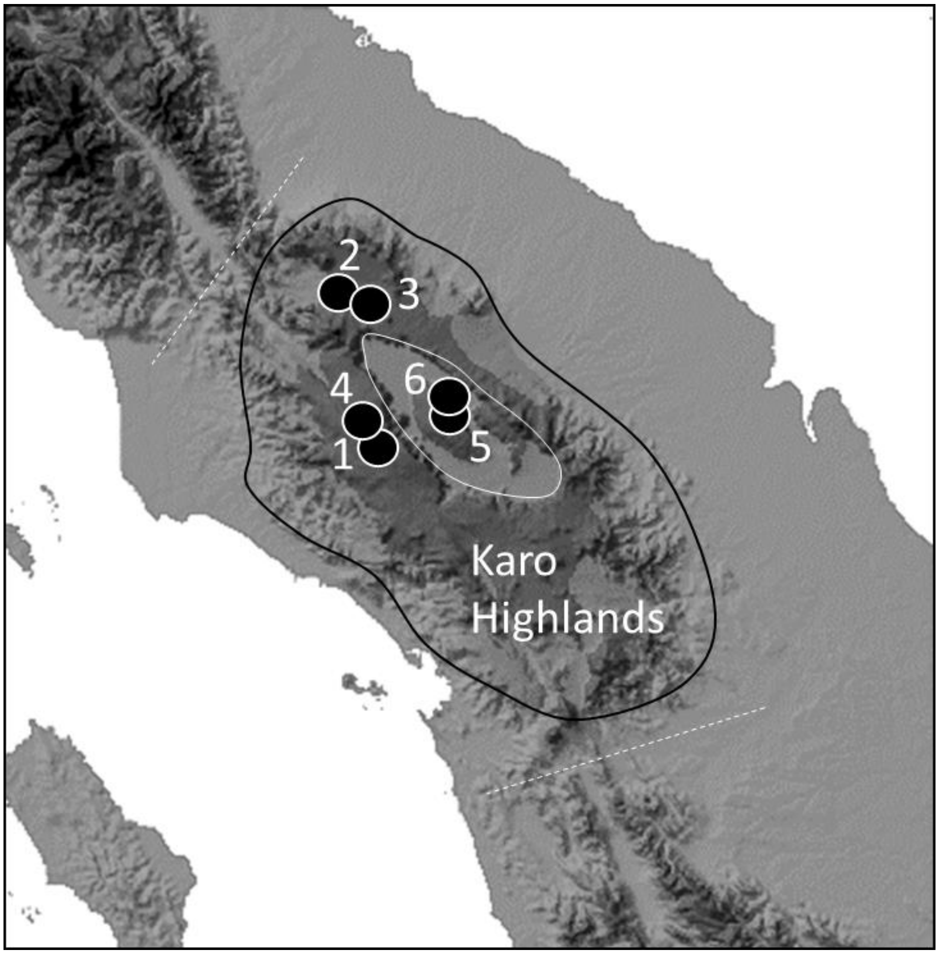

Fig. 3 *Dendragama schneideri* genetic diversity around Lake Toba. Lake Toba is circled in solid white, the Karo Highlands are circled in solid black, and the topographic breaks of the Karo highlands (extent of hypothesized *D. schneideri* distribution) are marked by dotted white lines. *Dendragama schneideri* sampling localities are marked by black circles with numbers that correspond to pairwise genetic diversity of each sample in Table 1.

Chapter 4

Revalidation of *Dendragama Schneideri* with the First Phylogeny of the genus *Dendragama*

Abstract

Lizards of the genus *Dendragama* are endemic to the highland cloud forests of Sumatra's Barisan Mountain Range in western Indonesia, and recent studies have uncovered widespread cryptic diversity within the genus. Here, we used a suite of morphological characters and mitochondrial DNA to compare three geographically isolated populations of *D. boulengeri* from (1) Mount Kerinci in Jambi province, (2) Mount Marapi of West Sumatra, and (3) the Karo Highlands of North Sumatra. We revalidate the Karo population as *D. schneideri* (previously *Acanthosaura schneideri*, Ahl 1926), from the synonomy of *D. boulengeri*. *Dendragama schneideri* is endemic to highland cloud forests above 1,200 meters in the Karo Highlands surrounding Lake Toba in Sumatera Utara province. *Dendragama schneideri* is most easily distguishable from other *Dendragma* species by low midbody scale counts, few ventral scales, and the presence of multiple, randomly disributed enlarged tubercles along the flanks of the body. We also describe distinct sexual dicromatism in this species. Mitochondrial DNA confirms our morphological diagnosis; pairwise genetic divergences of 6–11% separate *D. schneideri*) from congeners. Interestingly, we also identified two distinct clades of *D. boulengeri* from Mount Kerinci and Mount Marapi. These clades are 5.0% genetically divergent from one another. We do not describe the Kerinci clade as a new species here, but note this genetic differentiation between geographically isolated populations. However, the Kerinci population should be considered an evolutionary signicant unit for conservation initiatives. Collectively, these comparisons among *Dendragama* populations further elucidate the complex biogeographic history of Sumatra's montane forest species.

Introduction

Uncovering tropical diversity remains essential for conservation initiatives and understanding complex ecological and evolutionary processes. However, many regions and taxonomic groups across the globe remain largely unstudied. Montane agamid lizards of western Indonesia are no exception. Species of the genus *Dendragama* are endemic to Sumatra and are distributed across the Barisan Mountain Range, a volcanically active strip of the Pacific “Ring of Fire” which runs along the edge of Sumatra’s west coast.

There has been considerable uncertainty regarding the taxonomic status of *Dendragama boulengeri* [1], which until only recently was considered a monotypic genus [2 – 5]. Early studies reported *D. boulengeri* from isolated montane forests of Jambi, West Sumatra (Sumatera Barat) and North Sumatra (Sumatera Utara) provinces [4]. However, Harvey et al. [5] recently described two new species, *D. australis* from South Sumatra and *D. dioidema* from Aceh Province. They also provide a thorough redescription of *D. boulengeri*. In their paper, *D. boulengeri* is redescribed as a species distributed thoughout much of Central Sumatra, including the type locality (Mount Singgalang in Sumatera Barat) and nearby Mount Marapi.

Previously, *Acanthosaura schneideri* [6] was mentioned infrequently in the literature, but was also considered a distinct species from Sumatera Utara Province. In an unpublished dissertation, Moody [3] conducted a thorough family-wide review of the Agamidae and split the genus *Calotes* into four genera; *Bronchocela*, *Calotes*, *Dendragama* and *Pseudocalotes*. However, there is no mention of *A. schneideri* in his work. Only later did Manthey and Grossman [4] transfer *A. schneideri* to the synonomy of *D. boulengeri* [5].

We examined a series of *Dendragama* collected by M.B. Harvey and E.N. Smith from their herpetofaunal inventory conducted between 2012 and 2014 throughout the Barisan Mountain Range of Sumatra. These samples include specimens from various isolated mountain peaks across much of central, northern, and southern Sumatra. Using multiple morphological characters and phylogenetic techniques we compared *Dendragama* specimens to all currently recognized species and identify the individuals from North Sumatra Province as *A. schneideri.* We also discuss additional cryptic diversity yet to be described.

Materials and Methods

Biological Inventory

A thorough herpetofaunal survey was conducted across the highland forests of Sumatra's Barisan Mountain Range between 2013 and 2014. An international team of collaborators systematically targeted mountains based on geographic isolation from one another. We predominantly collected specimens at night, although some were collected during the day. We collected GPS coordinates and ecological data on site, or as soon as possible following collection. Animals were euthenized following appropriate IACUC protocols, then photographs and DNA samples were taken for future identification.

Counts and Measurements

We scored 32 different morphological characters (Table 1) for each specimen from the focal populations. To avoid systematic errors introduced by separate observers, K. Shaney collected all mensural and meristic characters. Sex was determined by examining the gonads. We examined 19 *D. boulengeri* collected from Mount Marapi, West Sumatra (Marapi population), nine specimens from Mount Kerinci and Mount Tujuh, Jambi (Kerinci population), and 10 specimens from various mountains across the Karo Highlands of North Sumatra (Karo population; Fig 1).

Because measurements and scores are often done differently depending upon the study, some of the morphological characters used here require further comment. We consider the last supralabial to be lower and more elongate than the supralabials in front of it, and the last infralabial is postitioned directly below the center of the last supralabial [7]. Gular counts began immediately after the mental (or the first pair of infralabials when in contact) and were taken to the crease where the gulars meet the pectoral region. From the crease we started ventral scale counts and counted to the last scale on the anterior edge of the cloaca. We counted nasal–rostral scales as the number of scales between the nasal and rostral. We counted postrostral scales as the number of scales contacting the rostral. We counted canthals as the number of scales between the nasal scale and the first supraocular scale. We counted the number of scales between the supralabials and the first canthal touching the nasal scale as the "scales between first canthal and supralabial". We count the circumorbital scales, including a canthal and a postciliary modified scale. We counted the number of postmentals (or chinshields) contacting the infralabials. We counted the number of midbody scales around the body, including the ventral and dorsal crest. We counted lamellae on the fourth digit of the hands and feet, starting from the interdigital skin at the base of the digit and ending to the claw (i.e., including the elongate ungual scale). Nuchal crest scales were counted from the first projecting scale to the last enlarged scale before the pectoral gap. We only counted the projecting scales and excluded small flat vertebrals and paravertebrals that interupt the crest.

To the nearest 0.1 mm with digital calipers, we measured snout-vent length (SVL) from the tip of the snout to the anterior lip of the cloaca, tail length by straighting the tail along the edge of the ruler and measureing from the posterior edge of the cloaca to the tip of the tail, head length from the posterior edge of the mandible to the tip of the snout, flank length as the distance from the axilla to the groin, hand and foot length from the proximal margin of the sole to the tip of the claw on toe IV, eye–nostril distance from the anterior corner of the eye to the tip of the snout, brachiam as the length of the entire humerus and the antibrachium as the length of the ulna, ending at the base of the palm, internarial distance as the distance between the upper edge of each nostril, orbit and tympanum width from the anterior to the posterior edge of each. Additional specimens examined from sister taxa and outgroups are provided in Supplementary Material S1.

Statistical Analyses

Using our mensural and meristic data we compared the Karo, Kerinci, and Marapi populations. For meristic characters, we compared means between the three populations using Tukey's test after confirming assumptions of normality (using the Shapiro-Wilk test) and homoscedasticity (using Levene's test). Some characters are best analyzed by comparing proportions of two discrete character states. We first generated proportions for scales between the rostral and nasal, scales between the nasal and supralabial, scales between first canthal and supralabials, and nasal-supralabial scales and canthals, then conducted hypothesis tests comparing proportions between populations [8].

When making comparisons among populations, we analyzed males only for head width and head length, because we found these traits to be sexually dimorphic in a preliminary study of our large series from Marapi. To investigate sexual dimorphism and to compare mensural characters among populations, we used analysis of covariance treating SVL as a covariate. To avoid inflation of the type I error rate in our morphometric comparisons, we performed three additional calculations. First, we made Bonferroni corrections to the probability scores (*P*multiplied by three) for the tests among populations. Second, having identified several apparent morphometric differences in the Kerinci population, we then verified the difference by rerunning the analysis using a different measurement as covariate in each apparently different trait: eye-nostril distance as a covariate for comparisons among thigh lengths, length of brachium for comparisons among foot length, length of shank for comparisons among hand lengths. Third, as a final validation of these results, M. B. Harvey measured SVL and tail length of a separate sample of nine *Dendragama* from Kerinci housed in the MZB and compared them to his own measurements for specimens from the type locality and Marapi [5].

DNA Extraction and Amplification

We digested tissue in 100 μl of lysis buffer, then added 5 μl of proteinase K and incubated at 55° for 1–6 hours. After incubation, we added 1.8 μl of serapure beads [9] for every 1 μl of digested sample. DNA extraction was carried out following the same methods that are used in PCR cleaning protocols described in AMPure magnetic beads literature (Agencourt, Bioscience, Beverly, MA, USA).

Phylogenetic Analyses—We extracted genomic DNA from 23 specimens of Sumatran *Dendragama*. We then combined new sequences from these specimens with sequences already published by Shaney et al. [11]) and Harvey et al. [5] on GenBank [10]. The published sequences include the outgroup taxa *Bronchocela cristatella* (Kuhl), *Lophocalotes ludekingi* (Bleeker), and *Pseudocalotes tympanistriga* (Gray, Supplementary Material S2).

We sequenced a fragment of the NADH dehydrogenase subunit 4 (ND4) gene using the forward primer “ND4” (CACCTATGACTACCAAAAGCTCATGTAGAAGC) and reverse primer “LEU” (CATTACTTTTACTTGGATTTGCACCA). The ND4 thermal cycle profile consisted of an initial denaturation at 94° C for three minutes, followed by 30 cycles of denaturation at 94° C for 30 seconds, a 50° C annealing phase for 45 seconds and a 72° C extension for one minute, followed by a 72° C extension for seven minutes, then a holding phase at 4° C. We cleaned the products of amplification using Sera-Mag Speedbeads (Fisher Scientific, Pittsburgh, PA, USA), following the procedure outlined by Rohland & Reich [9].

We aligned all sequences using the Geneious aligner implemented within Geneious v. 6.1.8 [12]. ND4 sequences range in length from 616 to 934 bp. We selected the most likely model of evolution for each codon position using Bayesian information criteria implemented in PartitionFinder [13]. We partitioned codon positions using GTR+ Γ. We conducted maximum likelihood analyses using raxmlGUI [14]. We utilized the thorough bootstrapping setting, sampling over 10 runs of 10,000 repetitions. We carried out Bayesian phylogenetic analysis using MrBayes v3.2.1 [15]. We used four independent runs (nruns = 4) and four chains (three heated chains and one cold chain) for 10 million generations, sampling every 100 generations. We discarded the first 25% of samples as burn-in. We confirmed adequate mixing and assessed the appropriate amount of burn-in and convergence by inspecting the trace files in the program TRACER v1.6 [16]. We conducted UPGMA analyses and calculated uncorrected pairwise distances using Mega 5.1 [17].

Results

Phylogentic Results

Both our Maximum Liklihood and Bayesian analyes revealed similar relationships within *Dendragama*, and recovered three clades witin *D. boulengeri* for the Marapi, Karo, and Kerinci populations (Fig 2). Within *Dendragama* five clades have strong nodal support (posterior probabilites and bootstrap values between 98 and 100): *D. autralis*, *D. dioidema*, and each of the three populations of *D. boulengeri*. *Dendragama dioidema* also has within species structure on the phylogenetic tree with the (1) Berni Terlong and (2) Takengon population forming distinct clades.

Both analyses found *Lophocalotes* to be sister to *Dendragama*, followed by insular *Pseudocalotes.* As in an earlier study, we did not find a close relationship between mainland and insular *Pseudocalotes* [5].

Genetic distances

The ND4 gene has diverged by 5.0–12.1% (Table 3) between species and the three populations of *Dendragama boulengeri*. At the lower extreme, 5.0% divergence separates the Marapi and Kerinci populations of *D. boulengeri*.. *Dendragama dioidema* is the most divergent from other populations. Its ND4 gene has diverged by 10.7–11.7% from *D. australis,* and 10.7–12.1% from populations of *D. boulengeri*. In contrast, ND4 sequences of *D. australis* (south Sumatra) have diverged 6.0–6.4% from populations of *D. boulengeri.*

The Karo population of *Dendragama boulengeri* has diverged by 6.0–8.0% from the Marapi and Kerinci populations and by 6.0–11.9% from *D. australis* and *D. dioidema*.

Morphology

A suite of meristic characters distinguishes the Karo population of *D. boulengeri* from the other two populations. Specimens from Karo have fewer scales around midbody, fewer ventral scales, and large heterogeneous scales along the flanks (Fig 3). The Marapi population of *D. boulengeri* has more scales between the nuchal and dorsal crest and subdigital lamellae than the other two populations. Finally, *D. boulengeri* specimens from Kerinci have fewer circumorbitals (11–13) than specimens from Marapi and Karo (usually 15) (Tables 1–2). We did not find interpopulation differences for the other meristic characters ($P > 0.05$).

Male *Dendragama boulengeri* from Marapi have wider ($F_{1,16} = 9.08$, $P = 0.008$) heads than females and width of their heads increases faster during ontongeny ($F_{\text{equal slopes}} = 6.50$, $P = 0.022$, Fig 3). Although just not significant if 0.05 is chosen as the type I error rate, male *D. boulengeri* from Marapi also have longer heads ($P = 0.072$) than females. With small samples sizes from Karo and Kerinci, we lacked sufficient statistical power to confirm sexual dimorphism in head size ($P > 0.2$). Nonetheless, males from Karo appear to follow the same growth trajectory

(Fig 3). We did not demonstrate sexual dimorphism in our meristic characters or in tail length, eye–nostril length, pectoral width, or length of the body ($P > 0.26$).

Dendrama boulengeri specimens from Kerinci have relatively shorter tails, hands, and feet than specimens from the other two *D. boulengeri* populations. They also have shorter thighs than specimens from Karo and a smaller orbit than specimens from Marapi. Small specimens from Karo have a relatively smaller orbit than small specimens from Marapi; however, orbits are about the same size for larger specimens from the two populations. Our limited data suggests a different growth trajectory for the orbit at Karo vis-à-vis Marapi, but having violated the assumption of parallel regression lines, we do not report a probability for this comparison between Karo and Marapi. As detailed in the methods, we confirmed each of these morphometric differences by treating other measurements as covariates. Moreover, a separate sample of nine *Dendragama* from Kerinci had relatively shorter tails ($F_{1,27} = 7.75$, $P = 0.010$) than the sample of *D. boulengeri* from both Marapi and the type locality described by Harvey et al. [5]. We did not find differences among populations for eye–nostril distance, pectoral width, length of body, length of shank, length of brachium, length of antebrachium, or internarial distance ($P > 0.12$). Tables 1 and 2 provide statistics for the three populations compared.

In addition to the quantitative differences, we also note two additional qualitative differences. *Dendragama* from the Marapi and Kerinci populations have a bright yellow buccal epithelium and tongue, whereas lizards from the Karo population have a pink to red buccal epithelium and tongue. Along their lower flanks, lizards from Karo have numerous distinctly enlarged tubercular scales. In contrast, specimens from the other populaitons lack these scales.

Species Delineation

Our analysis revealed numerous differences between the Karo population on the one hand and the Marapi and Kerinci populations on the other. Numerous different means and high genetic divergence is evidence of an interruption in gene flow among these populations, but is of only limited diagnostic value. However, we also identified four fixed characters that distinguish the Karo population from the other two. Unlike these populations (characters in parentheses), the Karo specimens have pink to red buccal epithelia (yellow, Fig 4), numerous enlarged tubercles on lower flank (scales of lower flanks homogenous or with few slightly enlarged scales), 59–68 scales around midbody (77–89), and 13–19 dorsals pointing upward and backward at midbody (20–25). Restricted to highland areas above 1,200 meters, inhospitable lowlands isolate the Karo population from all other populations and species of *Dendragama*. Direct comparison of Ahl' [6] type of *Acanthosaura schneideri* to the Karo specimens reveals that they are the same species. Accordingly, we remove *A. schneideri* from the synonymy of *D. boulengeri* and hereafter recognize the Karo populaton as a distinct species *Dendragama schneideri* (Ahl).

Description of *Dendragama schneideri*

Acanthosaura schneideri Ahl 1926: 186, Simbolon, Battaker Hochebene, Sumatra. *Dendragama boulengeri*: De Rooij 1915 [in part, 2]: 119, Manthey & Grossmen 1997 (in part, [4]): 166 – 167, Manthey: (in part, [18]): 100 – 101.

Holotype

An adult Male (ZMB 15664, Fig 5) from high elevation montane forest, Simbolon, Sumatera Utara Province, Indonesia.

Referred Material

All specimens were collected in Sumatera Utara near the type locality. Four specimens (UTA 62872, 2.91032N, 98.4516E; UTA 62873, 2.91329N, 98.46091E; UTA 62874, 2.9121N, 98.46222E; MZB 14126, 2.91189N, 98.46538E) from Mount Sibuatan, 1595–1883 m. Two specimens (UTA 62863, 3.2143N, 98.49955E; MZB 14127, 3.2143N, 98.49955E) from Sibayak, 1550 m. Two specimens (UTA 62865, 3.22576N, 98.51974E; UTA 62866, 3.20637N, 98.51974E) from the vicinity of Peceran, 1530–1727 m. One specimen (UTA 62870, 2.5911N, 99.93921E) from Mount Pangulubao, 1258 m. One specimen (UTA 62871, 2.1706N, 98.63612E) from an unnamed road near Onan Ganjang, 1231 m. One specimen (MZB 12098, 2.56103N, 98.59106E) from the vicinity of Tele, 1768 m.

Diagnosis

A species reaching at least 201.35 mm in total length (SVL) and distinguished from congeners by the following characters: (1) Midbody scale count 58–67; (2) dorsal scales heterogeneous across the flanks (Fig 6); (3) stongly keeled white/yellow scales randomly distributed along the flanks (more numerous and distinct in females); (4) ventral scales number 48–59; (5) banding pattern along flanks often muddled, but typically vertical when present; (6) mouth and tongue pink to red in life; (7) narrow, vertical black stripes across dorsal crest, limbs, digits and most of the tail; (8) female color in life dark brown, yellow and black with amber coloration on underside, while males green and lacking amber coloration along the ventral surface; (9) dorsal and nuchal crest clearly seperated by 5–9 dorsal scales; (10) dorsal crest serrate, extending to the base of the tail and numbering between 23–31; (11) a series of 3–4 enlarged tubercles present along the chin of males and females; (12) A series of 12–18 strongly keeled, white/yellow femoral spines present (combined count on both sides).

Description and variation

The description is based on the 19 referred specimens. Where appropriate we provide character state frequencies or means ± standard deviation in parentheses. When available and not subject to interobserver biases, we also provide data gathered by M.B. Harvey for the holotype in brackets.

Flank/pectoral width 2.41 – 3.41 (3.03 ± 0.32); thigh/shank length 1.26 – 1.70 (1.53 ± 0.12); brachium/antibrachium length 0.93 – 1.21 (1.10 ± 0.08); SVL/tail length 2.02 – 2.46 (2.24 ± 0.11); head length/head width 1.26 – 1.83 (1.62 ± 0.18); snout–vent length 61.35–79.2 (68.82 ± 5.59) [74 mm, tail length 145 mm].

Supralabials smooth nine (91%) or 10 (9%); infralabials smooth eight (45%) or nine (55%); supraocular scales five (82%) or six (18%); postrostrals small, five (91%) or six (9%) [5]; scales between nasal and rostral one (100%); nasal separated from supralabials by small lorilabials (75%) or contacting first supralabial (25%); canthals from nasal to supraocular five (45%), six (45%), or seven (9%) [5]; loreal scales six (73%) or seven (27%), scales between first canthal and supralabials two (37%) or three (63%); circumorbitals 13–15, usually 11 (73%); post mentals contacting infralabials one (9%) or two (91%); first pair of postmentals in medial contact (66%) or separated by one gular (34%) [1].

Nuchal crest clearly separated from dorsal crest and gap between crests ranges between 5–9 scales; dorsal crest serrate, continuous down to tail; scales on dorsum, large and heterogeneous, with series of enlarged strongly keeled, yellow/white scales in row below dorsal crest; all other scales along dorsum and flank smooth to feebly keeled; scales along flank consistent with dorsum, with more enlarged strongly keeled scales running vertically along sides; midbody scale counts 58–67 (61.36 ± 2.8) [61], gulars smooth 32–44 (36.81 ± 3.51) [30]; ventral scales 48–59 (52.45 ± 3.14) [52], ventrals keeled from chest to lower abdomen before transitioning to smooth scales near precloacal area; precloacal scale width small 0.75–1.4 (1.02 ± 0.22); scales along limbs strongly keeled, with continuation of keeled scales down to fingers on both hands and feet; subdigital lamellae on finger IV 22–26 (24.27 ± 1.19) [23]; subdigital lamellae on toe IV 25–32 (28.09 ± 2.02) [27];; dorsal crest scales 23–31 (26.63 ± 2.69) [28]; tail bands 14–18 (12.2 ± 0.83).

Coloration in life

There is distinct sexual dichromatism in this species and it is important to note that coloration changes in all *Dendragama* in response to rough handling. Females of *Dendragama schneideri* are typically shades of dark brown, green and black with vertical black and yellow bands running along the extent of the dorsal crest. Bands extend almost to the end of the tail, and enlarged green, yellow or white, strongly keeled scales are present intermittently along the flanks. Black and yellow/green bands also extend along all limbs, hands and feet. A black spot is present under the base of the nuchal crest as in other *Dendragama* species. The throat has amber and brown coloration, which may or may not be broken up by small lateral brown lines. Brown and amber coloration extends along the lower flanks and all the way to the end of the tail. Yellow and black lines radiate around the eyes and across much of the face. Yellow, green or white enlarged tubercles are present below the eye and ear, and the mouth is pink to red.

Males may also be brown, but are typically much lighter in coloration. They are often bright green and yellow with intermittent vertical stripes of black scales, which zig-zag vertically along the flanks. Black bands extend along the length of the dorsal crest and throughout the extent of the tail. Bands also cross the arms, legs, hands, and feet. A black spot is present under the base of the nuchal crest, but may be less pronounced in some specimens. The venter is much lighter than in females, with a white or cream gular region, with some brown shading along the ventral side. Darker individuals may have some brown shading along the gular region as well. Green or yellow and black stripes radiate out from the eyes and, as with females, the mouth is pink to red.

Coloration in Ethanol

Specimens of *Dendragama schneideri* lose their bright coloration and typically appear dark black and brown when preserved. Green coloration tends to be various shades of blue.

Etymology

The name *"schneideri"* comes from Johann Gottlab Schneider, a German zoologist (1750–1822).

Standard English Name

Schneider's Tree Dragons

Distribution and Natural History

Dendragama schneideri occurs in high elevation, montane forest in north Sumatra's Bukit Barisan Mountain Range (Figs. 1, 7). The latitudinal limits of this species are currently unknown; however, our sampling encompasses Lake Toba and the surrounding mountains. The referred specimens were found sleeping in low vegetation between 1200–2800 m.

Key to the species of *Dendragama*

We present a key to the species of *Dendragama* based on morphology and color pattern. Fig 8 shows photos of all four species. High supratemporal ridges enclosing a depressed parietal region, a row of white to yellow sublabial tubercles, and a visible tympanum immediately distinguish species of *Dendragama* from all other Sumatran agamids.

1. A. Gular scales *large,* 15–30, ventrals smooth to feebly keeled …………………...........……..2

B. Gular scales, *small,* 32–42 ……………………..……………………………………………3

2. A. *Small* midbody scales, 61–94; mouth/tongue orange to yellow; short white sublabial stripe extending from below the eye to below (or just behind) the ear; brown band on neck, but large black prescapular blotch absent; proximal half of tail with 8–13 dark brown or green bands ……………………..…………………………………………………….....….*D. australis*

B. Midbody scales *moderate* in size, between 57–77; mouth/tongue pink to red; no distinctive prescapular blotch present; proximal half of tail with 6–10 dark brown or green bands; *no* white sublabial stripe, however one or two white or pale yellow spots *present* …………..…*D. dioidema*

3. A. *Large* midbody scales, 59–68, paravertebral 13–19 of them directed upward and backward; mouth/tongue pink to red; enlarged tubercles present on lower flanks..............……*D. schneideri*

B. *Small* Midbody, 74–88, paravertebral 20–25 of them directed upward and backward; mouth/tongue yellow; few weakly keeled scales along lower flanks, enlarged tubercles absent …...……………………………………………………………………………………*D. boulengeri*

Discussion

Our morphological and molecular data presented here show the clear distinction between *D. boulengeri* and *D. schneideri*. *Dendragama schneideri* is also clearly geographically isolated from other species, occurring in high elevation cloud forest allopatric from *D. australis*, *D. boulengeri,* and *D. dioidema*. Based on the lack of biological inventory in other parts of the Barisan Range, it is likely that other cryptic *Dendragama* species may also occur across the region. Mountain peaks throughout Aceh and northern West Sumatra provinces may be particularly interesting if *Dendragama* specimens are collected, considering their distance from the type localities of *D. boulengeri* and *D. schneideri*.

Our phylogenetic analysis also uncovered two distinct clades of *D. boulengeri*. The first clade from Mount Kerinci and the second clade from near the type locality (Mount Marapi). These two clades are 5.0% pairwise genetically divergent, which in many cases would constitute distinct species designations, if accompanied by readily identifiable morphological variation between populations. Our morphological comparisons also uncovered differences between Mount Kerinci and Mount Marapi populations of *D. boulengeri*. However, many of these differences overlap in character ranges and thus, the Kerinci population requires further study to determine if it is a species distinct from *D. boulengeri.* Currently, our sample size from Mount Kerinci is relatively low (n = 9). Collection of additional specimens would increase statistical power for comparisons.

A comparative biogeographic analysis between *Dendragama* and other agamid lizard groups would be a fascinating and informative study for which to better understand Sumatra's complex geologic history. Frequent connections between the greater Sunda islands and Peninsular Malaysia have occurred at multiple times over the last two hundred thousand years [20 – 22] and the series of faunal dispersal events which may have occurred during that time period are not yet estimated for highland agamid lizards [23 – 24]. Furthermore, genetic splits between agamid lizard species seem quite old, and divergence dating of Sumatran agamid phylogenies may corroborate estimated geologic events from before the Pleistocene, which contributed to rapid speciation. Interestingly, our phylogenetic analyses uncovered point endemics across isolated mountain ranges and an absence of sympatry between any *Dendragama* species, which may also be informative for historical biogeography of Sumatra's montane forests.

The conservation status of *Dendragama* lizards has not yet been assessed [25], particularly because of the lack of population data. The information from this paper contributes a significant amount of data on populations of *D. boulengeri* and *D. schneideri*, which we believe have small distributions. The exact latitudinal and longitudinal limits of *D. boulengeri* and *D. schneideri* are not yet known, but breaks in montane forest habitat below 1,000 meters are likely boundaries for these species. These data may be used towards conducting IUCN Red List status assessments in the future. Regardless of their current conservation status, it is clear that rapidly increasing anthropogenic pressures throughout Sumatra are likely to have a significant impact on all *Dendragama* species' persistence [26]. Shaney et al. [10] provide examples of how cryptic Indonesian lineages may be lost before being described and cryptic species may be overharvested due to poor taxonomic evaluation. Thus, continuation of biological inventory will be quite important in agamid lizard discovery and conservation of Sumatra's montane forest diversity in the near future. Given the rapid discovery of herpetofaunal diversity across Sumatra's highlands [27], [7] it is likely that an array of new agamid lizard species remain undiscovered throughout the region.

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Tables

Table 1. Uncorrected pairwise genetic distances (ranges) for ND4 sequences between populations of *Dendragama* (including species described by Harvey et al. [5], *Lophocalotes ludekingi* and *Pseudocalotes tympanistriga*. For *Dendragama*, M=Marapi population, K=Kerinci population, Ka=Karo population.

Species	*D. boulengeri* (M)	*D. boulengeri* (K)	*D. schneideri* (Ka)	*D. australis*	*D. dioidema*	*L. ludekingi*	*P. tympanistriga*
D. boulengeri (M)							
D. boulengeri (K)	5%						
D. schneideri (Ka)	6.0–7.0%	7.0–8.0%					
D. australis	6.0–6.4%	6.0–6.4%	7.0–8.0%				
D. dioidema	10.7–12.1%	9.0–10.1%	9.0–10.1%	10.7–11.7%			
L. ludekingi	16–17%	16–17%	16–17%	16–17%	16–17%		
P. tympanistriga	19–20%	19–20%	19–20%	19–20%	19–20%	19–20%	

Table 2. Measurements of *D. schneideri* and D. boulengeri populations. Ranges are followed by average ± standard deviation in parentheses.

Measurement	***D. boulengeri* (Marapi population, n = 19)**	***D. boulengeri* (Kerinci population, n = 9)**	***D. schneideri* (Karo population, n = 15)**
Flank/Pectoral Width	2.58–4.21% (3.54 ± 0.43)	2.57–4.99% (3.20 ± 0.92)	2.41–3.41% (3.03 ± 0.32)
Thigh/Shank Length	1.02–1.55% (1.31 ± 0.15)	1.46–1.67% (1.55 ± 0.08)	1.26–1.70% (1.53 ± 0.12)
Brachium/Antibrachium Length	0.90–1.29% (1.11 ± 0.08)	0.96–1.40% (1.13 ± 0.14)	0.93–1.21% (1.10 ± 0.08)
Snout Vent/Tail Length	2.05–4.15% (3.14 ± 0.64)	2.0–2.18% (2.06 ± 0.06)	2.02–2.46% (2.24 ± 0.11)
Head Length/Head Width	1.47–2.45% (2.0 ± 0.29)	1.29–1.66% (1.48 ± 0.14)	1.26–1.83% (1.62 ± 0.18)
Maximum Snout–Vent Length	78.13 mm	80.56 mm	79.2 mm
Nasal to Rostral Scales	1–2, 1 (95%), 2 (5%)	1 (100%)	1 (100%)
Nasal to Supralabial Scales	0–2, 0 (58%), 1 (37%), 2 (5%)	0 (100%)	0 (75%), 1 (25%)
Post Rostral Scales	5 (100%)	5 (100%)	5–6, 5 (91%), 6 (9%)
Canthals (Nasal to Supraoculars)	5–7, 5 (74%), 6 (21%), 5%)	5 –6, 5 (83%), (17%)	5–7, 5 (45%), 6 (45%), 7 (9%)
Loreal Scales	5–6, 5 (89%), 6 (11%)	6–7, 6 (50%), 7 (50%)	6–7, 6 (73%), 7 (27%)
Scales between first canthal and Supralabials	2–4, 2 (5%), 3 (90%), 4 (5%)	2–3, 2 (17%), 3 (83%)	2–3, 2(37%), 9 (63%)
Circumorbital Scales	13–16, 13 (37%), 14 (53%), 15 (5%), 16 (5%)	11–13, 11 (17%), 12 (66%), 13 (17%)	13–15, 13 (73%), 14 (18%), 15 (9%)
Scales Between Nuchal and Dorsal Crest	8–10, 8 (47%), 9 (21%), 10 (26%), 11 (5%)	6–9, 6 (17%), 7 (33%), 8 (33%), 9 (17%)	5–9, 5 (9%), 6 (9%), 7 (36%), 8 (18%), 9 (27%)
Scales Pointing up at Midbody	20 –24 (21.21 ± 1.27)	20–25 (23.66 ± 1.9)	13– 19 (16 ± 1.95)
Midbody Scales	77–84 (79.57 ± 1.89)	75–89 (84.16 ± 4.99)	59–68 (62.36 ± 2.8)
Gular Scales	35–43 (38.95 ± 2.01)	34–42 (37.89 ± 2.97)	32–44 (36.81 ± 3.51)
Ventral Scales	52–63 (57.89 ± 3.71)	56–68 (62.16 ± 3.97)	48–59 (52.45 ± 3.14)
Subdigital Lamellae of Toe IV	27–36 (30.42 ± 2.38)	25–31 (28.5 ± 2.58)	25–32 (28.09 ± 2.02)
Subdigital Lamellae of Finger IV	24–31 (27.42 ± 1.95)	22–24 (23.16 ± .75)	22–26 (24.27 ± 1.19)
Supralabials	9–10, 9 (58%), 10 (42%)	8–10, 8 (50%), 9 (33%), 10 (17%)	9–10, 9 (91%), 10 (9%)
Infralabials	8–11, 8 (21%), 9 (53%), 10 (21%), 11 (5%)	8–9, 8 (67%), 9 (33%)	8–9, 8 (45%), 9 (55%)

Table 3. Results of statistical comparisons for meristic (upper half of table) and morphometric (lower half) differences among three populations of *Dendragama*. (NS = not significant): Marapi based on data from 19 specimens, Karo based on 15 specimens, and Kerinci based on 9 specimens.

Character	**Tukey's *Q*, Probability**	
	Marapi	**Kerinci**
Circumorbitals		
Karo	NS	5.00, 0.003
Kerinci	8.21, 0.000	
Scales Between Nuchal and Dorsal		
Karo	4.16, 0.015	NS
Kerinci	4.92, 0.004	
Dorsals Pointing Upward		
Karo	10.89, 0.000	13.44, 0.000
Kerinci	NS	
Scales Around Midbody		
Karo	21.3, 0.000	20.8, 0.000
Kerinci	NS	
Ventral Scales		
Karo	4.40, 0.010	6.04, 0.000
Kerinci	NS	
Lamellae Under Toe 4		
Karo	3.89, 0.024	NS
Kerinci	3.82, 0.027	
Lamellae Under Finger 4		
Karo	7.81, 0.000	NS
Kerinci	10.2, 0.000	

	ANCOVA *F*, Bonferroni corrected probability	
	Marapi	**Kerinci**
Tail Length		
Karo	NS	15.57, 0.002
Kerinci	6.77, 0.046	
Hand Length		
Karo	NS	11.25, 0.009
Kerinci	11.61, 0.007	
Foot Length		
Karo	NS	10.51, 0.012
Kerinci	17.8, 0.001	
Orbit		
Karo	Nonparallel (18.94, $P <$ 0.001)	NS
Kerinci	8.67, 0.021	
Thigh Length		
Karo	NS	7.91, 0.031

Kerinci	NS

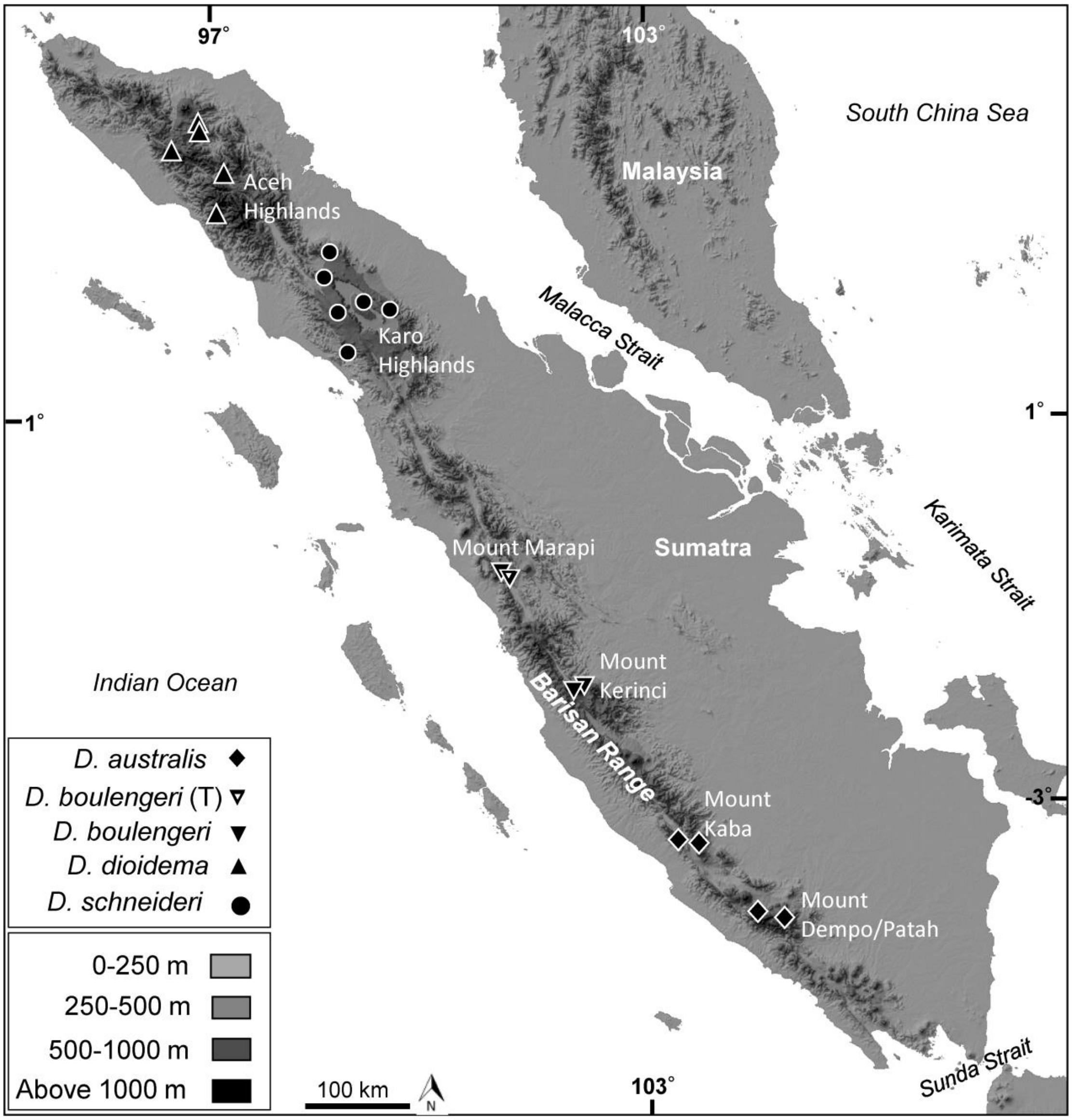

Figure 1. *Dendragama* specimen collection localities used for comparisons in this study. (T) designates type locality.

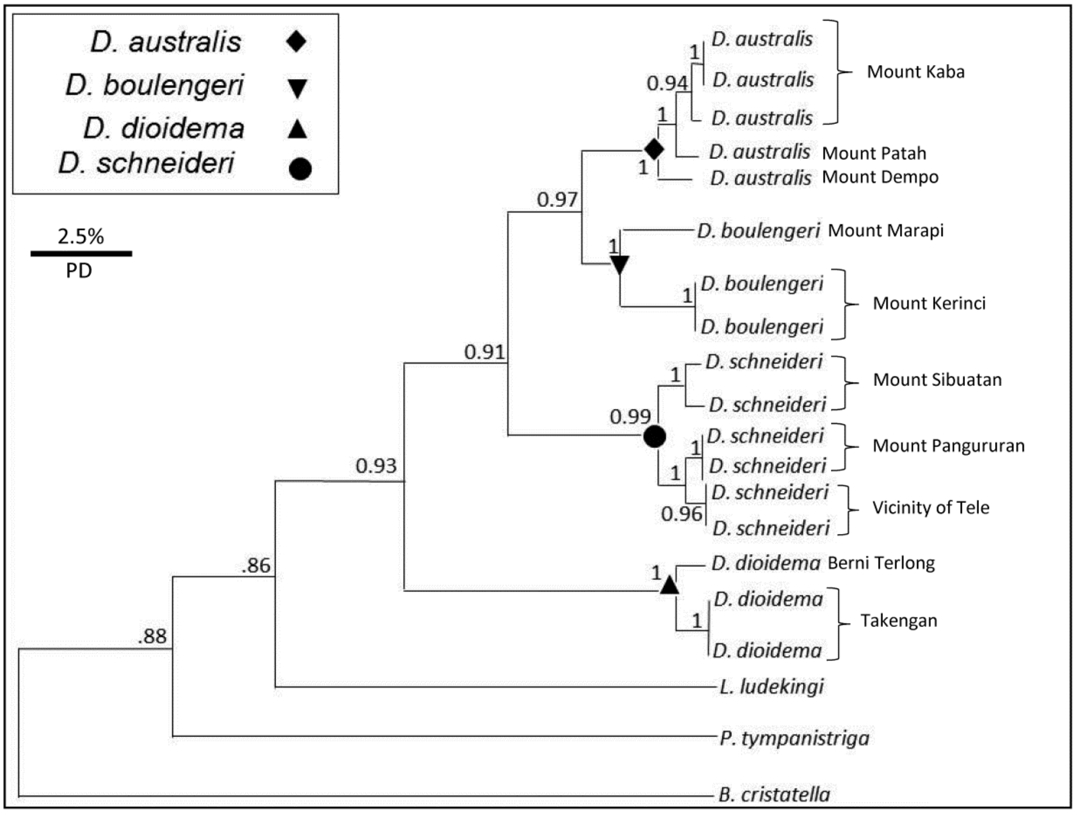

Figure 2. Bayesian tree of *Dendragama* and other agamid taxa included in our analyses. PD = Pairwise Distance. Mountains associated with *Dendragama* population sampling are noted.

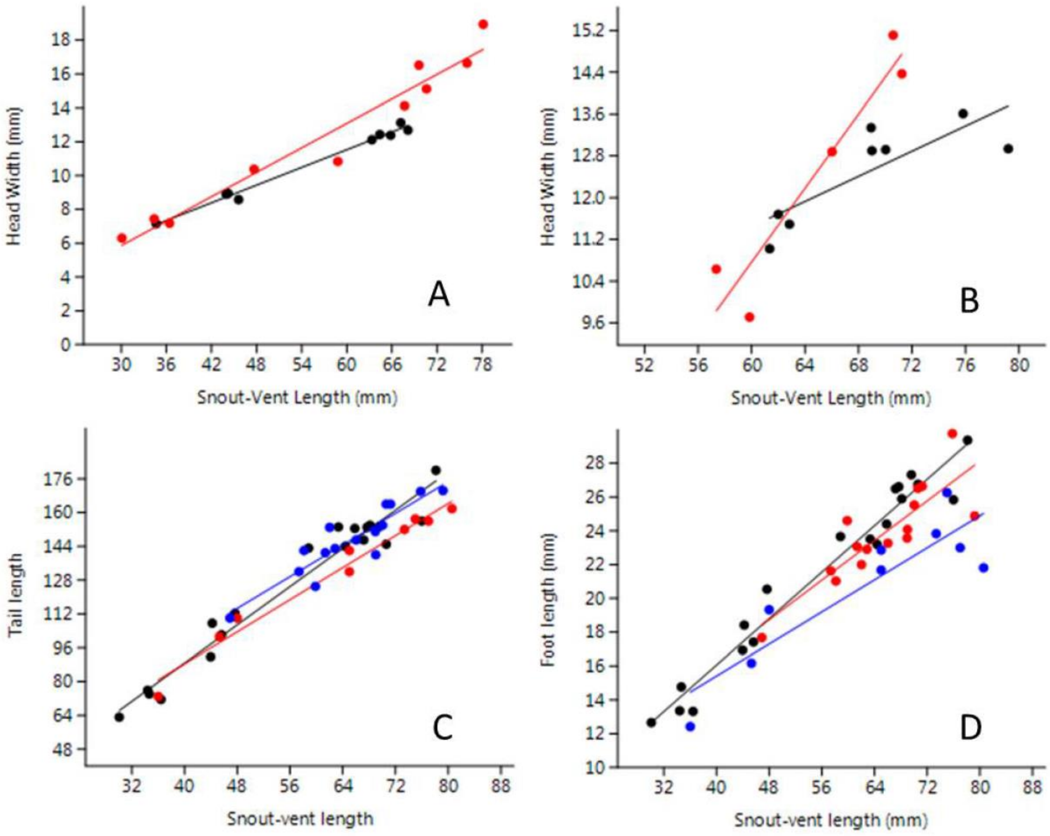

Figure 3. A and B show sexual dimorphism in *D. boulengeri* and *D. schneideri,* whereas C and D show variation between all populations in tail length and foot length.

Figure 4. The bright orange mouth of *Dendragama boulengeri* is shown in plate A, whereas the pink mouth of *D. schneideri* is shown in plate B (Photos by E.N. Smith).

Figure 5. Plates A and C show the holotype of *D. schneideri* from two different angles (Photos by M.B. Harvey), whereas plates B and D show a referred specimen (MZB 12098) from the same angles (Photos by E.N. Smith).

Figure 6. Plate A shows the flank of a male of *Dendragama boulengeri* (MZB 9825) and its thin, horizontal banding patterns, thick vertical bands along dorsal crest, small homogenous scales and lack of enlarged, keeled scales. Plate B shows the flank of a male of *D. schneideri* (UTA 62868) and its lack of horizontal banding along the flanks, thin vertical bands along dorsal crest, large heterogeneous scales and enlarged, strongly keeled scales dispersed across the flanks (Photos by E.N. Smith).

Figure 7. A and B show highland cloud forest habitat where *Dendragama schneideri* occur (Photos by E.N. Smith). Photos taken at Mount Kerinci, Sumatera Barat Province.

Figure 8. Male representatives of all four currently recognized *Dendragama*. A is *D. boulengeri* (ENS 19656), B is *D. australis* (ENS 18556), C is *D. dioidema* (ENS 19433), D is *D. schneideri* (UTA 62868) (photos by E.N. Smith). Figure 1 provides locality information for each species.

Chapter 5

Impacts of anthropogenic pressures on the contemporary biogeography of threatened crocodilians in Indonesia

Abstract—The Greater Sunda Region of southeast Asia supports a rich diversity of economically and ecologically important species. However, human pressures are rapidly reshaping contemporary biogeography across the region. Megafaunal distributional patterns have been particularly impacted because of deforestation, poaching and human-wildlife conflict. Crocodilians are at the epicenter of these conflicts in Indonesia and yet remain poorly studied across much of the archipelago. We conducted crocodile population surveys in Sumatra on Saltwater Crocodiles (*C. porosus*) and False Gharials (*T. schlegelii*) and examined whether crocodile abundance and distribution are correlated with variation in human disturbance, fishing pressure, and habitat type. We then used these data to model *T. schlegelii*'s remaining suitable habitat across southeast Asia. We find that *T. schlegelii* and *C. porosus* abundance is correlated with distance from human settlements and fish trapping pressure. Our data also expand the known range of *T. schlegelii* as we have documented this species in a new river system. We also find that *T. schlegelii*'s predicted remaining suitable habitat in Indonesia is largely limited to areas of low human activity. From these empirical and modeling approaches, we propose several key conservation priorities: (1) Eliminate the use of fish traps in remaining patches of *T. schlegelii* habitat, (2) Prioritize crocodile population surveys in remaining suitable habitat, particularly in remote areas, (3) Consider *T. schlegelii* as potentially, locally "Endangered" in Sumatra, (4) Expand existing reserves around the Lower Kampar River and Berbak National Park/Sembilang National Park areas in Sumatra.

Introduction

Sodhi et al. (2004) state that agricultural practices across the Greater Sunda Region (GSR; i.e. Borneo, Java, Peninsular Malaysia, and Sumatra) are driving one of the world's highest rates of deforestation. Indonesia is at the forefront of contemporary global change, where habitat alteration and hunting pressure are drastically reshaping species' distributions. In turn, vertebrate populations are increasingly being forced into remote, refugial habitat. Conversion of forest to oil palm, rubber, tea and coffee plantations, in conjunction with a lack of wildlife management resources (e.g. revenue and staff), has led to unregulated over-harvesting of natural resources (Margono et al. 2012, Miettinen et al. 2014). Unregulated hunting pressure for meat, skin and pet trade in Indonesia has also drastically effected vertebrate populations across the GSR (Brooks et al. 1997, Brodie et al. 2015). Although the impacts of human pressures on vertebrates in the GSR have been addressed to some extent, impacts on reptilian groups are largely unquantified.

Indonesia's crocodilians are an excellent model system for understanding the impacts of human pressures on contemporary biogeography. Furthermore, crocodilians present an interesting system for developing long-term carnivore conservation schemes, in light of human-carnivore conflicts across the globe. Saltwater Crocodiles (*C. porosus*, Schneider 1801) are distributed across southeast Asia and considered a significant threat to humans (http://www.crocodile-attack.info/). A large proportion of *C. porosus* attacks occur in the country of Indonesia, many of which occur in the GSR. *Crocodylus porosus* are also listed as a CITES appendix II species and harvest of wild adults within Indonesia is only legal from the eastern province of Papua, while the collection of eggs and juveniles from Kalimantan and Sumatra has recently been legalized (http://www.iucncsg.org/365_docs/attachments/protarea/Indo-24da7cd0.pdf). *Crocodylus porosus* is listed as "Least Concern" on the IUCN Red List, but their population status across most of Indonesia is unknown (Webb et al. 2010).

The False Gharial (*Tomistoma schlegelii*, Müller 1838) also inhabits the GSR and is considered one of the least understood crocodilians in the world (Bezuijen et al. 1995, 1997, 2001, Auliya et al. 2006, Stuebing et al. 2006, Simpson 2014). They primarily inhabit black water, peat swamp forest, although most lowland swamp forest in the GSR has been lost due to deforestation (Sodhi et al. 2004, Miettinen et al. 2014). *Tomistoma schlegelii* are a CITES Appendix I species and were listed as "Endangered" on the IUCN

Red list until an update in 2014 changed the status to "Vulnerable" (http://www.iucnredlist.org/details/21981/0). Despite the recent status update, data on *T. schlegelii's* population status is sparse across much of the species' range and Sumatra has been particularly underrepresented in recent years. Although Cox et al. (Unpublished report) and Bezuijen et al. (1995, 1997, 2001) conducted significant work on *T. schlegelii*, only approximately 100 confirmed *T. schlegelii* sightings have been recorded in Sumatra (Stuebing et al. 2006) and to the best of our knowledge, no crocodilian surveys have been conducted in the last 13 years in Sumatra.

We gathered population data on *C. porosus and T. schlegelii* in Sumatra in areas that have and have not been previously assessed for crocodilian abundance. We examined whether crocodilian abundance is negatively impacted by proximity to humans and whether crocodiles are capable of persisting in areas of high human disturbance. We also examined whether fish trapping activity is associated with declines in crocodilian abundance. We predicted that increased fish trapping activity and proximity to humans will be associated with declines in the abundances of crocodiles. We used species distribution modelling techniques to elucidate potential remaining suitable *T. schlegelii* habitat across its range and suggest key areas for conservation priority.

Material and Methods

Study Areas—Crocodylus porosus are distributed across North Australia and southeast Asia, while *T. schlegelii* are restricted to the GSR. Our work focused on these two species in four study areas on the island of Sumatra (Fig. 1A – D): The Air Hitam Laut River system (AHLR) in Berbak National Park (AHLR, A, previously surveyed), Lower Kampar River system (LKR, B, not previously surveyed), Simpang Kanan River system (SKR, C, not previously surveyed), and Lalan River System (LR, D, previously surveyed). Surveys on these rivers were conducted during two field seasons in 2014 and 2015, between June and August. The LR and SKR were surveyed in 2014, the AHLR was surveyed during 2015, and the LKR was surveyed during both field seasons.

BNP falls within Jambi Province and was previously surveyed by Cox et al. (1990) and Bezuijen et al. (1997, 2002). BNP is located along the southeastern edge of Jambi Province (Fig. 1A) and includes one of the largest remaining tracts of peat swamp forest habitat in Sumatra. Two distinct seasons, wet and dry, affect water levels in the peat swamp forests (lowland acidic swamp) of the region. In Sumatra, the wet season typically lasts from October until late February, in which large sections of the forest become flooded. During the dry season, from March through September, the forests progressively dry up. By mid-August, only the main tributaries, billabongs and lakes still hold water. The park is intersected by the AHLR System (surveyed here) and encompasses branches of the Batanghari River in the North (Air Hitam Dalam Tributary, not surveyed here) and Benu River in the South (not surveyed here). Logging and hunting activity is illegal within the park boundaries; however, illegal activity has penetrated the perimeter of the park in multiple locations.

The lower Kampar River (LKR) encompasses some of the last remaining patches of primary peat swamp forest in Riau Province (Fig. 1B) and has not been previously surveyed for crocodilian activity. Multiple black water tributaries originate in the surrounding forests and enter the river in various locations, immediately East and West of Teluk Meranti Village (Shaney et al. 2015). Major tributaries in the area include the Kerumutan River, Kutup River, Serkap River, and Turip River. Two small reserves are located along the Serkap River (Tasik Metas and Tasik Serkap Reserves) and a larger reserve along the Kerumutan River (Kerumutan Reserve). Reserves in the area are rarely monitored by wildlife officials and illegal logging, fishing and hunting activity continue to occur in multiple portions of these reserves. We also surveyed the SKR which originates within the peat swamp forest adjacent to the Kerumutan Reserve; however, the river drains directly in to the ocean rather than into the LKR (Fig. 1C). The SKR had not been previously surveyed prior to our study.

Our final survey area included the LR, with a particular focus on the Merang River. The headwaters of the Merang River originate near the BNP study area; however the Merang River drains to the South, entering the LR System in South Sumatra Province (Fig. 1D). Amongst Sumatran rivers, the Merang River has received the most survey attention for *T. schlegelii* activity in the past and the majority of historical *T. schlegelii* sightings in Sumatra have been recorded in the Merang River (Stuebing et al. 2006). Bezuijen et al. (1995, 1997, 2001) and Shaney et al. (2015) provide thorough information on the study area.

Survey Method— Surveys followed techniques from Bayliss (1987) and Bezuijen et al. (1997, 2001). Nighttime spotlight surveys were conducted along four tributaries of the LKR system, including:

Kerumutan River (22 km surveyed), Kutup River (2 km surveyed), Serkap River (41.2 km surveyed), Turip River (11.2 km surveyed) and sections of the main Kampar river (54.8 km surveyed). We also surveyed tributaries along the AHLR system, including: Simpang Kubu (4.6 km surveyed), Simpang Melakka (11.4 km surveyed), Simpang T (8.7 km surveyed) and sections of the main AHLR river (27.3 km surveyed) and Kumpe River nearby (16.1 km surveyed). We surveyed 40.8 km of the Merang River (Lalan River System), 25 km of the main Lalan River and 45 km of the SKR (Fig. 1A – D). Start and end points of transects were recorded in decimal degrees with a Garmen, Etrex 30, Geographic Positioning System (GPS). Transect lengths were recorded and used to determine the number of crocodiles sighted per kilometer of river surveyed to determine relative abundance. Repeat surveys were only conducted in three locations and we subtracted potential repeat sightings from total crocodilian counts and densities. A total of 326.2 km of river were surveyed; 60 km were paddled and 266.2 km were travelled with the aid of small motors. A total of 26 survey nights and 40 days were spent in the study areas. Of the survey nights, 12 survey nights were spent on the AHLR System, 12 nights were spent on the LKR System, 1 night on the SKR and 1 night on the Lower Merang River.

We used a five meter wooden boat, with a 25 hp motor on larger rivers and four meter canoes on small tributaries. We traversed transects during the day to record ecological and dependent variables for statistical analyses. Surveys were typically initiated 30 minutes to one hour after night fall (18:30 to 19:30). In tidally influenced areas we altered survey start times around tide. In upper tributaries unaffected by tide, water levels were quite low and did not extend into fringing vegetation. We recorded pH levels at the beginning and end of each transect and when a crocodile was located, we noted the pH measurement recorded closest to the sighting. Crocodile eye shines were recorded using 10,000 lumen headlamps. We approached crocodiles after each sighting and when possible recorded a confirmed species identification and species size range. We defined crocodiles by the following age classes: hatchlings (young of the year, ~0.3 – 0.6 m), juveniles (not yet sexually mature, ~0.6 – 2.1 m), or adults (sexually mature, >2.1 m). When crocodiles submerged before further identification could be made, we recorded the location as an “eye shine” or “probable” species Identification. “Probable” species ID was given when there was high confidence in the species identification, but only a short glimpse of the animal occurred.

Statistical Analysis—Survey results from the four major river systems detailed above and nine of their tributaries were included in analyses. The dependent variables associated with our crocodile data include: (1) confirmed crocodile species identification counts, (2) probable species identification counts (3) confirmed species identification counts and daytime sign (description of daytime data below) and (4) probable species identification counts and daytime sign. We also tested for varying effects on each age class and combined species counts because of low sample size. Poisson loglinear regressions were used to test the factors that are associated with variation in crocodile abundance using SPSS v.21. We tested whether crocodiles were more likely to be found in remote areas, using distance from human inhabitance as a quantifiable measure. We measured Euclidian and river distance between villages and sightings. We identified villages holding >500 residents as a cutoff point following Stoner et al. (2014). Next, we tested whether fish trapping pressure is negatively correlated with crocodile abundance. To accomplish this goal, we counted fish traps along transects and used fish traps per km as a predictor variable. We also identified habitat preferences based on each species sighting and partitioned sightings into four distinct habitat categories: (1) primary forest (forest that appears unaltered), (2) secondary forest (regrowth after logging), (3) mangrove forest, (4) no forest. We identified habitat types along the edges of waterways where crocodiles were sighted and confirmed habitat types using landcover data in ArcMap 10.3. Last, we used a two tailed T-Test to test for interspecific habitat partitioning, using pH levels associated with sightings (N=42 for *C. porosus* and N=15 for *T. schlegelii* for nighttime sightings only, N=43 for *C. porosus* and N=21 for *T. schlegelii* for night and daytime data combined). The daytime data includes each unique locality where animals were seen during the day, or where we collected bones, eggshells, or saw slide marks (Fig. 2 shows night and daytime data examples). Analyzing data with or without daytime data was done independently to use datasets with larger sample sizes and more assumptions, or lower sample sizes and fewer assumptions. We tested for possible multicollinearity between variables using collinearity statistics in SPSS.

Species Distribution Modelling—We used the program Maxent 3.3.3k to model suitable *T. schlegelii* habitat across the GSR. We focused only on *T. schlegelii* for this analysis because they are currently listed as Vulnerable across their range. We created four separate species distribution models

(SDM's) to compare and contrast variable effects on potential distribution: (1) climate layers (19 bioclim layers, worldclim.com), (2) climate layers + landcover, (3) climate layers + human population density, (4) climate layers + landcover + human population density. Population density and landcover layers acquired from (www.diva-gis.org) (all layers 929 m pixel resolution). We used all confirmed *T. schlegelii* records found in Stuebing et al. (2006), Auliya et al. (2006), Bonke et al. (2008), data from Staniewicz (unpublished data in East Kalimantan), and our own data described here. Collinearity is not considered problematic when using Maxent, therefore we did not exclude any variables after model testing (Elith et al. 2011); however, we did conduct jackknife tests to determine which variables were most predictive of *T. schlegelii* distribution. We used the "Auto Features" settings provided, changed iterations to 5,000, replicated run type to "subsample" and set random test percentage to "25". We assessed the area under the curve data plot (AUC) for each model which is used to measure model performance using the presence localities provided. AUC models are only produced in Maxent runs when test values are provided. AUC values closer to 1.0 indicate higher performance of the predictive suitability models. Next, we extracted areas from the SDM models that intersected with rivers and inland water bodies (www.diva-gis.org), because *T. schlegelii* is aquatic. We quantified the amount of suitable aquatic habitat across their range with a probability of occurrence greater than 0.2 to be conservative. We also distinguish other break points at 0.4, 0.6, and 0.8 for context. Although, *T. schlegelii* have been located in disturbed habitat, the majority of sightings have occurred in unfragmented primary lowland forest. Therefore, we also extracted suitable habitat from within remaining primary lowland forest areas and quantified those areas separately. We restricted final quantifications with a polygon mask, which excludes biogeographic areas beyond the species' range. We repeated these steps explicitly for Sumatra.

Results

Survey Data—A total of 57 crocodiles (*C. porosus* and *T. schlegelii* combined, eyeshine's only included) were counted during nighttime surveys and eight signs of crocodile presence were found during the day (Table 1). 42 sightings were recorded on the AHLR and 15 in the LKR. No crocodilian sightings were recorded in the LR or SKR. In total, eight sightings were confirmed *T. schlegelii*, 15 were probable *T. schlegelii* and seven forms of daytime *T. schlegelii* sign were recorded, significantly increasing previous *T.*

schlegelii documentations in Sumatra. The Simpang T tributary of the AHLR has not been mentioned in previously published data and is also the tributary where we located 12 of the 14 *T. schlegelii* sighted on the AHLR. Interestingly, we recovered a single, deceased juvenile *T. schlegelii* in Kerumutan Village along the Kerumutan River. This is the first confirmed documentation of *T. schlegelii* from the Kerumutan River and from the LKR System in general. All sighting localities are found in a report that can be obtained from the IUCN crocodile specialist group (Shaney et al. 2017). We also compared species densities in our study to previous studies conducted on the AHLR and LR systems (Table 2).

Poisson regressions—Measures of collinearity indicated that 'fish trapping activity' and 'remoteness' (i.e., distance to human settlements) were in fact independent measures (collinearity statistics: Tolerance value=.998, VIF value=1.002). We observed significant ($p < 0.05$) effects of remoteness and fish trapping activity on crocodile abundance (Table 3). Fish trap density was a significant predictor of crocodile counts for six out of eight estimates of crocodile abundance and remoteness was a significant predictor of crocodile counts in all analyses (Table 3). For all significant trends, *T. schlegelii* and *C. porosus* counts were positively correlated with increasing distance from human inhabitance (high remoteness increases likelihood of seeing crocodiles) and negatively correlated with increasing fish trap density.

Age-class results—We evaluated the effects of human activities and fishing pressure on age classes separately. Hatchlings and adults were significantly more likely to be found in remote areas, and hatchlings were more likely to be found in areas with low fish trapping activity (Table 3). We could not test if fish trapping activity had an effect on juveniles or adults because there was no variation in those data (e.g. zero fish traps along transects where adults and juveniles were found).

Habitat preferences and Habitat Partitioning—*Crocodylus porosus* were more likely to be found in secondary forest, while *T. schlegelii* were more likely to be found in primary forest (Table 4). We also identified habitat partitioning between crocodile species (p-value < .01). Figure 3 shows that the presence/absence of these species abruptly shifts with changes in pH on the AHLR. pH shifts from 6.5 to 4.5 along the junctions of black water tributaries and saline environments. *Tomistoma schlegelii* were significantly more likely to be found in low pH water (ranging between 4.5 and 4.8 pH) and *C. porosus* were significantly more likely to be found in high pH water (ranging between 5.0 and 6.5).

Habitat Suitability—All four *T. schlegelli* SDM models largely identified the same suitable areas and returned similar AUC values (training data AUC's 0.95 – 0.96, test data AUC's 0.88 – 0.89). Therefore, we assess the most conservative model here (Model 4), which modelled the largest amount of suitable habitat and includes all habitat variables (climate + landcover + human population density). Model 4 identified 22,396.07 km^2 suitable habitat across the species range (>0.2 probability of occurrence), of which 3,772.6 km^2 fall within remaining primary lowland forest (Fig. 4). Of this suitable habitat, 17, 820.06 km^2 fall within Indonesia (3,356.31 km^2), 3,862.74 km^2 within Malaysia (196.99 km^2), and 713.27 km^2 in Brunei (219.3 km^2) (primary lowland forest habitat in parentheses). From these data, we determined that approximately 10,558 km^2 suitable habitat remain in Sumatra, of which only 1,548.98 km^2 fall within remaining primary lowland forest. All values only reflect where suitable habitat and waterways overlap. Our model returned four key areas for *T. schlegelii* conservation in Sumatra and five areas in Borneo.

Discussion

Given the critical need for crocodilian conservation efforts in Indonesia, we consider these data valuable to the conservation of *T. schlegelii* and *C. porosus,* and also broadly to the conservation and management of vertebrates regarding shifting contemporary biogeography in southeast Asia. The Balai Konservasi Sumber Daya Alam (Natural Resources Conservation Agency, BKSDA) currently regulates animal harvest quotas in Indonesia and is in the process of considering new harvest regulations for *C. porosus* across the archipelago. Thus, we suggest several key conservation priorities for crocodilians in the GSR.

Habitat Partitioning—We identified clear habitat partitioning between crocodile species, which confirms the findings of others (Bezuijen et al. 2001; Auliya et al. 2006). *Crocodylus porosus* was found along the coastline and in brackish environments, while *T. schlegelii* was restricted to freshwater, in black water tributaries. We find that these species coincide along a transitional pH zone (interspecific sightings only 2 km apart) on the AHLR. The location where species composition changes along the river is precisely where saltwater *Nypa* palms transition into freshwater *Pandanus* palms and pH changes drastically (Fig. 3). In many parts of its range, *C. porosus* is found far upriver in freshwater environment. Conversely, *T. schlegelii* is not believed to inhabit saline environments. Further investigation of the relationship between *C. porosus* and *T. schlegelii* may yield interesting information regarding competition between these two large crocodilian species. For example, how does the relationship between these two crocodile species change seasonally (e.g. such as the wet season when *C. porosus* often travels far up freshwater systems in other parts of its range)? Also, do these species commonly engage in intraguild predation? Answering these questions may also impact future management schemes as well.

Human Disturbance—C. porosus and *T. schlegelii* abundance is negatively correlated with proximity to humans (although *C. porosus* were found in disturbed habitat). We also found that common fish trapping methods throughout the region are negatively associated with crocodile abundance. It is important to consider that the correlations we identified do not necessarily indicate causations. There are other factors that could potentially impact crocodilian abundance that are cross correlated with the independent variables we tested. Thus we interpret our results with this in mind. We suggest future surveys target remote locations and management officials consider eliminating fish trapping from areas holding remaining core crocodile habitat. Despite being difficult to implement, BNP has already successfully eliminated trapping from one section of the park. Park officials stated to us that this change was made approximately five years ago along the Simpang T tributary of the AHLR (Fig. 1A). Based on further conversations and personal experience in the area, it is apparent that these regulations have been successful and little illegal fishing activity is currently occurring on Simpang T. Because fish trapping yields important resources for many local communities, regulations requiring woven box or funnel traps (rather than netting) with access to air for crocodile bi-catch could be implemented, rather than complete elimination of fish trapping in key areas.

Crocodilian Population Assessments and Suitable Habitat—Crocodylus porosus population densities were quite low across our study areas. Additionally, *C. porosus* densities in the AHLR were mostly made up of hatchlings, many of which were in close proximity to each other. This suggests that many individuals were of the same clutches and given the low hatchling survival rate, the true *C. porosus* density is probably much lower, and more representative of a few adults that had separate clutches along the river. Moving forward, we recommend continued *C. porosus* population surveys be conducted across other parts of Sumatra. This is particularly important given recent changes to *C. porosus* management in Indonesia that will allow the take of eggs and juveniles from Sumatra (Brien et al. 2015). Sembilang

National Park has never been surveyed for crocodilian abundance, but encompasses large swaths of intact mangrove forest along the East coast of Sumatra and could potentially hold large *C. porosus* populations. Multiple *C. porosus* were encountered in the LKR, particularly in the mouths of blackwater tributaries and in sections of mangrove near the coast. Thus, we suggest surveys targeted on the far eastern portion of the LKR may yield high densities of *C. porosus* and may be important areas for long-term *C. porosus* viability. Other regions, such as the Bangka Islands and Riau province coastline seem to hold relatively high *C. porosus* populations based on attack numbers, but still require scientific study for population density estimates. We suggest repeat surveys be conducted as often as possible on the AHLR and LKR as we well.

Tomistoma schlegelii populations seem severally fragmented in Sumatra, occurring in potentially less than five locations. Only three locations in Sumatra currently hold confirmed extant *T. schlegelii* subpopulations, which are all isolated by distance and terrain (currently AHLR, LR and LKR). Although we recorded the first documentation of *T. schlegelii* in the Kerumutan River, we only confirmed the presence of a single individual. This suggests that *T. schlegelii* densities may be quite low in the LKR. We suggest focusing future survey efforts in the LKR on the upper reaches of the Kerumutan River, including a tributary which was suggested by local villagers, known as the Eka River (Fig. 3). The Eka River has never been previously surveyed, but may hold higher numbers of *T. schlegelii* than other sections of the lower Kerumutan River. We also suggest the upper reaches of the Serkap River, near Tasik Metas Reserve and the upper reaches of the Kutup River be surveyed (Fig. 3). Given the logistical challenges of reaching those sections of river and time limitations we could not survey the far upper reaches of those tributaries, which could hold *T. schlegelii* populations (based on remoteness and habitat characteristics). The AHLR still has a relatively high density of *T. schlegelii* and should be considered critical to *T. schlegelii* survival in Sumatra. The upper AHLR, particularly "Simpang T" had the highest *T. schlegelii* densities of anywhere in the park and those remote tributaries require continued protection. Overall, *T. schlegelii* densities are similar to previous surveys conducted by Bezuijen et al. (1995, 1997, 2001, 2002) on the main AHLR river and lower on Simpang Melaka Creek. Simpang T's *T. schlegelii* densities in this study were considerably higher than any other densities on other AHLR tributaries in the past.

Because we were only able to spend a single day and night on both the LR and SKR, we suggest those areas still be targeted for future surveys. Although no crocodilian activity was recorded, the LR and Merang River in particular, have had high *T. schlegelii* population densities in the past (Bezuijen 1995, 1997, 2001, 2002). Although this study marks the first to survey the SKR, its proximity to the LKR and habitat characteristics suggest it may be an important river for both *C. porosus* and *T. schlegelii* populations, and other neighboring rivers and sections of mangrove forest may important areas for future survey efforts as well (See Shaney et al. 2017).

Our models identified a maximum of 22,396.07 km^2 of remaining suitable habitat and minimum of 3,772 km^2 within remaining primary forest areas across the range of *T. schlegelii* (10,558 km^2 suitable habitat remain in Sumatra, 1,548.98 km^2 within primary forest). Although *T. schlegelii* have been found in disturbed habitat (Bezuijen et al. 2001, Stuebing et al. 2006), we only found *T. schlegelii* in primary forest habitat during our study (Table 4). Therefore, we believe our maximum model estimates could be an over-estimation of remaining suitable habitat in the GSR (particularly in Sumatra). Furthermore, our quantification included all modelled habitat with probability of occurrence greater than 0.2 percent, which is a conservative estimation. Regardless, based on severely fragmented populations, low local population density when present, and severe habitat fragmentation, we believe that *T. schlegelii* may potentially be "locally endangered" in Sumatra. We cannot yet assess extent and area of occurrence or make a range wide assessment without continued work on the island of Borneo and we acknowledge that *T. schlegelii* may inhabit some areas that were not modelled in our analyses. Future SDM models would benefit from additional movement ecology data on *T. schlegelii*. Whether or not *T. schlegelii* are commonly inhabiting other kinds of habitat or capable of making ocean crossings between freshwater systems requires further investigation. Such studies may also continue to fine tune habitat suitability models. However, our SDM approach revealed specific areas in Borneo and Sumatra for which to consider concentrating future population surveys and show limited remaining suitable habitat across the species' range (Fig. 4).

Rödder et al. (2010) conducted a similar modelling approach with *T. schlegelii* and identified similar key areas for *T. schlegelii* population viability. This suggests that many of those same locations remain important for *T. schlegelii* conservation today. Based on our models, some key areas that may be important for *T. schlegelii* populations in Sumatra, include: the Air Hitam Laut River System and Merang River System (Jambi and South Sumatra respectively), Lower Kampar River System and areas surrounding the Simpang Kanan River System (Riau), areas surrounding the Bukit Batu and Giam Siak Kecil reserves (Riau), and areas surrounding the Rokan River (Riau); and in Borneo some key areas, include: the lower and upper Kapuas River (West Kalimantan), Tanjung Puting and Sebangua National Parks (Central Kalimantan), Lake Mesangat (East Kalimantan), and the Labi Forest Reserve area along the Brunei-Sarawak border, including tributaries such as the Belait River (Fig. 4). In Borneo, areas such as the Kapuas River, Tanjung Putting National Park, and Lake Mesangat, have yielded small to high *T. schlegelii* densities in the past (Bezuijen 2004, Auliya 2006, Bonke 2008, Stuebing 2015) and Lake Mesangat is one of the only known locations in Borneo to also hold Critically Endangered *C. siamensis* populations (Stuebing et al. 2015).

Reserve Expansion—Because there is still intact habitat surrounding the LKR and BNP study areas, we suggest expanding reserves to protect the remaining lowland habitat around those areas. There are large areas of primary and secondary forest between BNP and Sembilang National Park, as well as between several reserves on the north bank of the LKR. We acknowledge that this may be quite difficult to accomplish. However, if attempts are not made to initiate reserve or national park expansion, remaining habitat will be lost to continued habitat alteration across Sumatra’s lowlands. We present maps for potential reserve expansion (Fig. 5). Proposals to the BKSDA and Indonesian Institute of Science (LIPI) are likely required first steps for park expansion and involvement from stakeholders such as the various IUCN specialist groups could aid significantly in this process. Rödder et al. (2010) also suggested other important areas for reserve expansion, particularly in the lowlands of West Kalimantan, which should still be considered for reserve expansion today, which include most of the areas mentioned in our modelling results above. Given rapid forest conversion and degradation across the GSR reserve expansion in suitable *T. schlegelii* habitat would also benefit other threatened species, including Sumatran Rhinos, Elephants, Tigers, Clouded Leopards, and myriad other species.

As evidenced by the majority of our crocodilian survey data, BNP is currently a standout example of the importance of the protected areas in Sumatra’s lowlands. BNP currently protects some of the last lowland swamp forest in Sumatra, as well as some of the only remaining populations of Sumatra Tigers, False Gharials and Tapirs that the island has. The BKSDA and BNP staff has done an outstanding job managing the park to date and if reserve expansions modelled BNP's approach there may be a chance to protect much more of Sumatra's lowland biodiversity. That being said, limited management resources are still a challenge for BNP, while illegal logging activity penetrates the peripheral edges of the park. BNP is in a constant battle to protect the remaining biodiversity within its boundaries and continued support from the Indonesian government, NGO's, and the public is critical to the future of the park.

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Tables

Table 1. Crocodile counts and densities (confirmed and probable combined). The * indicates river found adjacent to main river system. Berbak National Park (BNP), Lower Kampar River (LKR), Simpang Kanan River (SKR), Lalan River (LR).

	Transect (km)	***T. schlegelii***	***C. porosus***	***T.* density**	***C.* density**	**Eyeshines**
LKR System						
Serkap River	41.2	0	8	0	0.19	1
Main Kampar River	54.8	0	2	0	0.037	0
Kerumutan River	22	0	1	0	0.046	0
Turip River	11.2	0	3	0	0.27	0
Kutup River	2	0	0	0	0	0
Total	**131.2**	**0**	**14**	**NA**	**NA**	**1**
AHLR System						
Main AHLR	27.3	3	26	0.11	0.95	0
Simpang Melakka	11.4	0	1	0	0.09	0
Simpang Kubu	4.6	0	0	0	0	0
Simpang T	8.7	12	0	1.38	0	0
Kumpe River*	16.1	0	0	0	0	0
Total	**68.1**	**15**	**27**	**NA**	**NA**	**0**
SKR System						
Main SKR	45	0	0	0	0	0
Ocean Mangroves	16.1	0	0	0	0	0
Total	**61.1**	**0**	**0**	**0**	**0**	**0**
LR System						
Main LR	25	0	0	0	0	0

Merang River	40.8	0	0	0	0	0
Total	**65.8**	**0**	**0**	**0**	**0**	**0**
Grand Total	**326.2**	**15**	**41**	**NA**	**NA**	**1**

Table 2. All crocodilian sightings separated by species, study area, age class. Relative densities are listed with eye shine information (W ES) and without eye shine information (WO ES) because of the possibility that eye shines can be *C. porosus* or *T. schlegelii*. Areas covered in our study are in bold. Age classes taken from Bezuijen et al. (1995, 1997, 2001, 2002) are adapted to age class from foot class data. Bezuijen et al. (1995, 1997) foot classes of >6 feet are included as adults in this table. HD = Heading Downstream.

Air Hitam Laut River System	**Km Sections Surveyed**	**Hat.**	**Juv.**	**Ad.**	**ES**	**Tot.**	**Den. W ES**	**Den. WO ES**	**Source**
Air Hitam Laut River									
1990	0 - 20.5	7 False Gharials seen, no size given				7	0.34	0.34	Cox (unpublished data)
1996	0 - 25	0	1	1	2	4	0.16	0.08	Bezuijen et al. (1997)
2001	0 - 31	1	0	0	3	4	0.13	0.03	Bezuijen et al. (2001)
2002	0 -32	-	1	0	3	4	0.13	0.03	Bezuijen et al. (2002)
2015	**0 - 27.3**	**1**	**1**	**1**	**0**	**3**	**0.11**	**0.11**	**This study**
Simpang Melaka Creek									

	1996	0 - 2	0	1	0	2	3	1.5	0.5	Bezuijen et al. (1997)
	2001	0 - 7.2	2	1	0	2	5	0.69	0.4	Bezuijen et al. (2001)
	2002	0 - 7.2	0	0	0	1	1	0.14	0	Bezuijen et al. (2002)
	2015	**0 - 11.4**	**0**	**0**	**0**	**1**	**1**	**0.09**	**0**	**This study**
Simpang Kubu										
	2015	**0 - 4.6**	**0**	**0**	**0**	**0**	**0**	**NA**	**NA**	**This study**
Simpang T										
	2015	**Headwaters - 8.7 (HD)**	**3**	**5**	**4**	**0**	**12**	**1.379**	**1.379**	**This study**
Lalan River System										
Lalan River										
	1990	0 - 150	2 TS seen, no size given (100 - 160 km)			2	4	0.03	0.01	Cox (unpublished data)
	1995	0 - 160	0	0	0	0	0	0	0	Bezuijen et al. (1995)
	2014	**80 - 140**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**This study**
Kepahyang										
		0 - 16.5	0	0	0	0	0	0	0	Bezuijen et al. (1995)
Medak River										

	1990	0 - 8	0	0	0	0	0	0	0	Cox (unpublished data)
	1995	0 - 53	0	0	2	0	2	0.03	0.03	Bezuijen et al. (1995)
Medak River Upper Tributaries										
		See Bezuijen et al. 1995	0	0	0	0	0	0	0	Bezuijen et al. (1995)
Merang River										
	1990	0 - 45	1 TS seen, no size given				1	0.04	0.07	Cox (unpublished data)
	1995	0 - 45	0	4	0	3	7	0.16	0.09	Bezuijen et al. (1995)
	1996	0 - 45	0	1	0	1	2	0.04	0.02	Bezuijen et al. (1997)
	2001	0 - 45	0	4	0	0	4	0.09	0.09	Bezuijen et al. (2001)
	2002	0 - 45	0	1	0	0	1	0.04	0.02	Bezuijen et al. (2002)
	2014	**0 - 45**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**This study**
Merang River										
	1995	45 - 67	0	2	0	5	7	0.34	0.09	Bezuijen et al. 1995

1996	45 - 67	0	4	1	5	10	0.49	0.23	Bezuijen et al. 1997
2001	45 - 67	1	12	0	1	14	0.64	0.6	Bezuijen et al. (2001)
2002	45 - 67	0	0	0	2	2	0.16	0	Bezuijen et al. (2002)

Table 3. Poison regressions; W/D refers to partitioned data with daytime sign included in counts. Groups with no data are blank. All significant p-values are highlighted.

Model Data	**(N)**	**Remoteness, P Values**	**Fish Trap Density, P Values**
Confirmed *T. schlegelii*	8	**<.01**	**<.01**
Probable *T. schlegelii*	15	**0.01**	**0.01**
Confirmed *T. schlegelii* W/D	20	**0.01**	**0.01**
Probable *T. schlegelii* W/D	22	**<.01**	**<.01**
Confirmed *C. porosus*	32	**0.01**	0.1
Probable *C. porosus*	41	**<.01**	**0.03**
Confirmed *C. porosus* W/D	33	**0.01**	0.112
Probable *C. porosus* W/D	42	**<.01**	**0.04**
Hatchling crocodiles (species combined)	38	**0.02**	**0.05**
Juvenile crocodiles (species combined)	18	0.695	**………**
Adult crocodiles (species combined)	10	**0.02**	**……..**

Table 4. Species habitat preference across all study areas, with bold numbers showing *C. porosus* preference for secondary forest and *T. schlegelii* preference for primary forest.

Species	**Primary Forest (N)**	**Secondary Forest (N)**	**Mangrove Forest (N)**	**No Forest (N)**
C. porosus confirmed	5	**23**	1	0
C. porosus probable	9	**32**	1	0
C. porosus confirmed W/D	5	**24**	1	0
C. porosus probable W/D	9	**33**	1	0
T. schlegelii confirmed	**10**	0	0	0
T. schlegelii probable	**14**	0	0	0
T. schlegelii confirmed W/D	**13**	0	0	0
T. schlegelii probable W/D	**21**	0	0	0

Figures

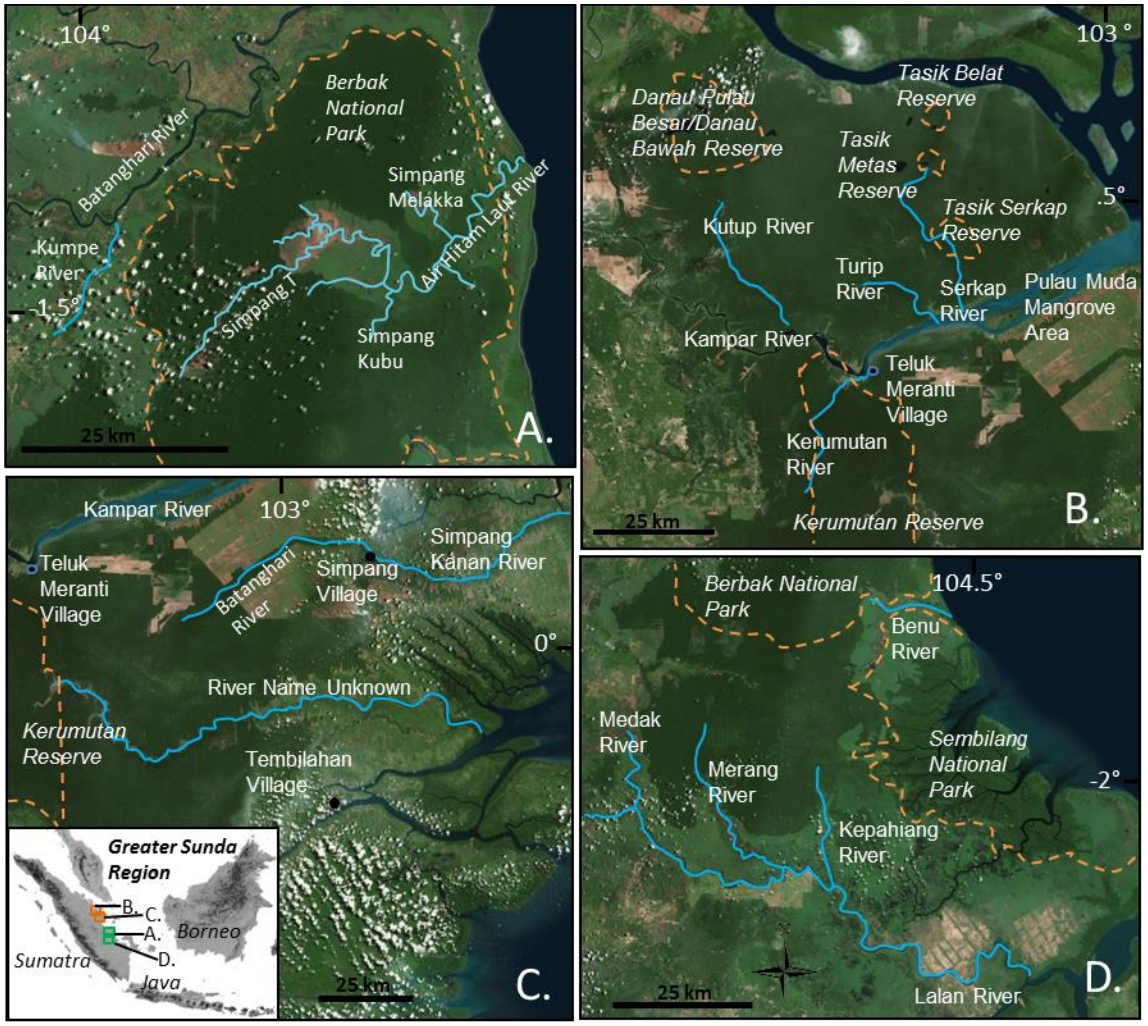

Fig. 1. Study areas: A) Berbak National Park (BNP), B) Lower Kampar River (LKR), C) Simpang Kanan River (SKR), D) Lalan River (LR). In the GSR sub-map, orange boxes indicate areas not previously surveyed, green boxes indicate previously surveyed areas.

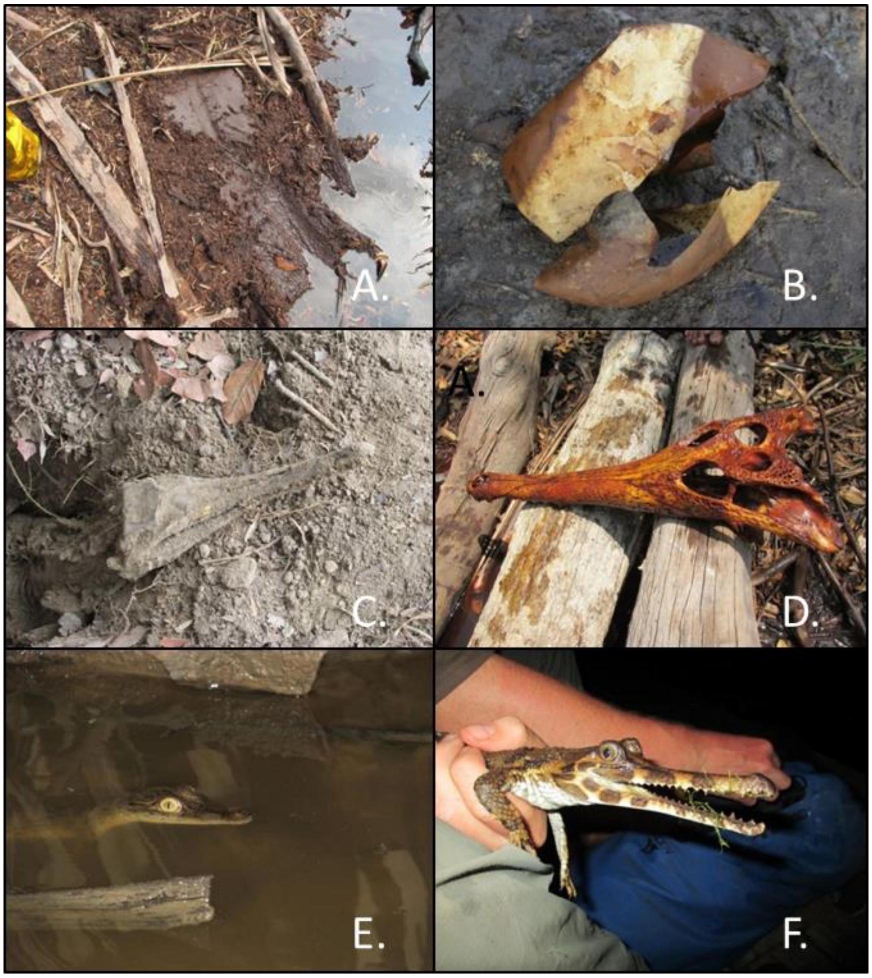

Fig. 2. Examples of crocodile sightings or crocodile sign. A) Daytime slide mark in the mud, B) *T. schlegelii* eggshell (measurements confirm this), C) deceased *T. schlegelii*, D) *T. schlegelii* skull, E) hatchling *C. porosus*, F) hatchling *T. schlegelii*.

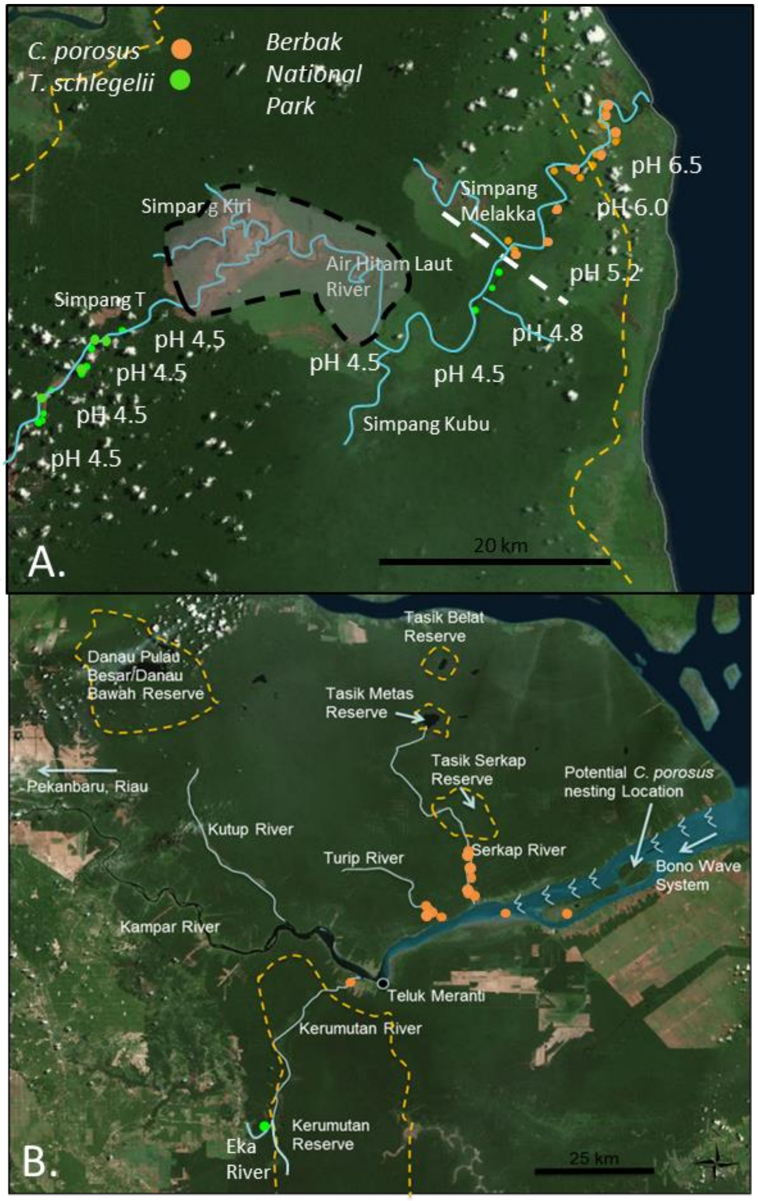

Fig. 3. A) is the Air Hitam Laut study area within Berbak National Park (BNP) and B) is the Lower Kampar River study area (LKR). Saltwater crocodile sightings are marked by orange dots and False Gharial sightings are marked by green dots. All parks and reserves are marked by dotted orange lines and important waterways are marked by blue solid lines. Evidence of habitat partitioning is marked along a pH gradient in Fig. B, where a white dotted line shows the distinct shift from Saltwater Crocodile to False Gharial sightings. The area encompassed in a black dotted line marks a section of river which could not be surveyed because of low water levels and thick vegetation.

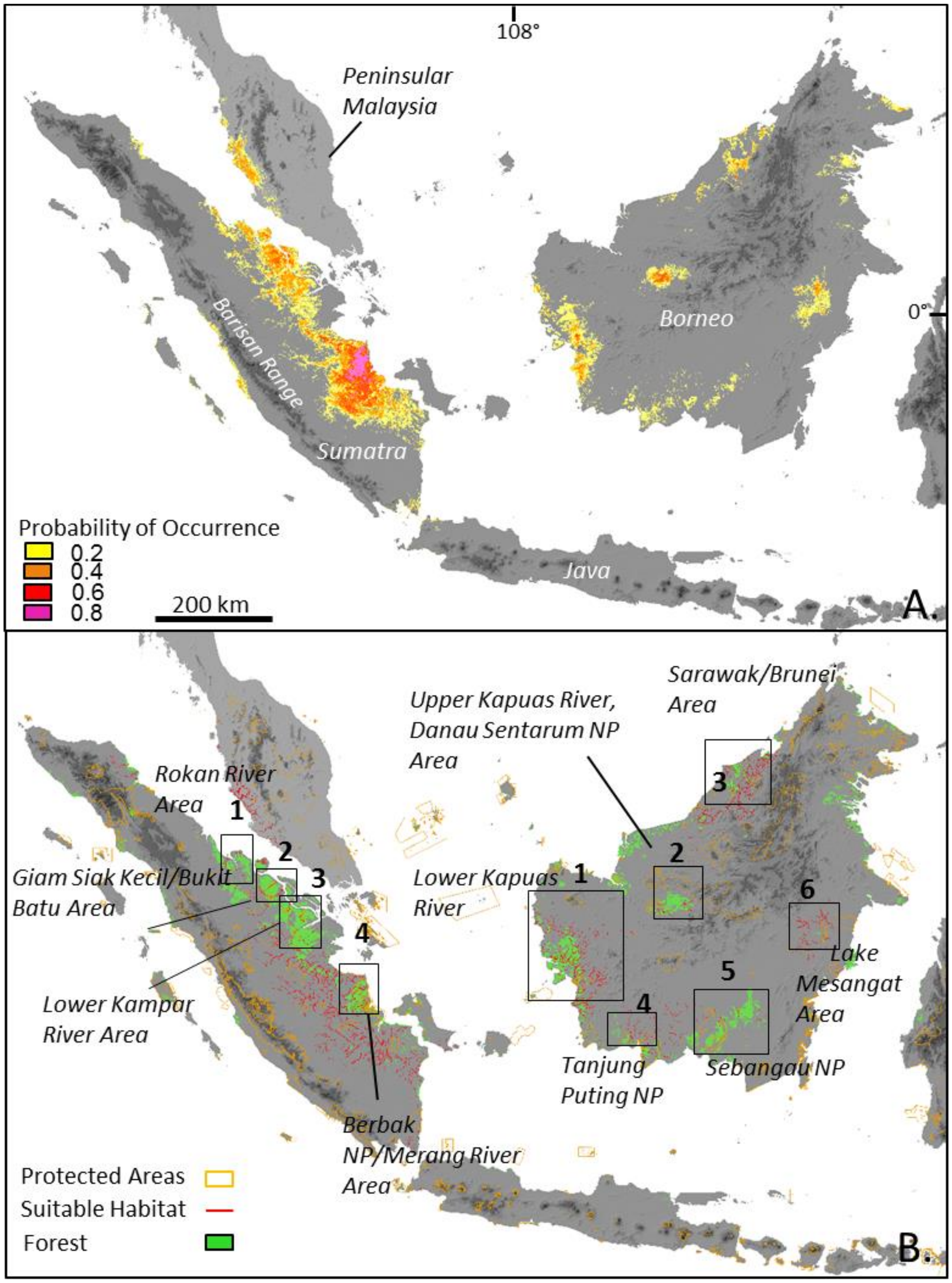

Fig. 4. Habitat suitability maps. A) Suitable habitat (Model 4), B) Suitable habitat clipped by water networks (red), protected areas (orange) and remaining lowland primary forest (green).

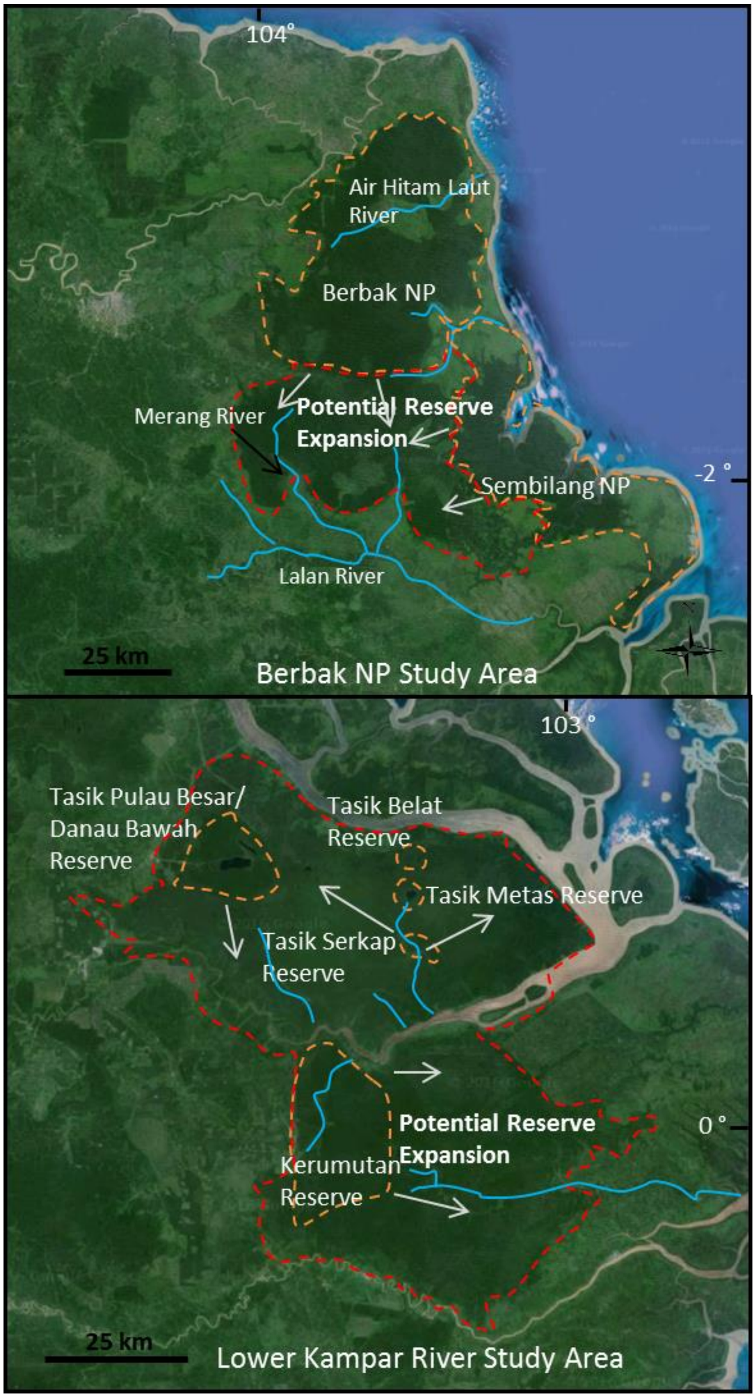

Fig. 5. Orange dotted lines indicate national parks and reserves in our study areas. Red dotted lines indicate remaining primary forest for reserve expansion. Grey arrows indicate expansion potential.

Chapter 6

Conclusions

Conservation and wildlife management are inherently reliant upon understanding floral and faunal distributional patterns, both historically and contemporarily. In order to conserve biodiversity across the Indonesian archipelago, and throughout the world for the matter, it is imperitive to develop a deeper understanding of floral and faunal distrubutional patterns and taxonomic relationships. Some of the most basic survey work will likely be the most important for the preservation of natural resources across the globe's tropical regions. For speciose groups, such as the agamid lizards of the Greater Sunda Region, there are probably dozens of new species that remain undescribed, many of which are endemic to single islands, or mountain tops throughout the region. Aside from lizards, there are undoubtedly more diverse taxonomic groups such as insects, or plants for which biologists have only scratched the surface in much of western Indonesia. Continuation of thorough biological inventory will become increasingly important for conservation and management of this untapped diversity over the next several decades and will allow biologists from myriad of disciplines to answer complex hypothesis driven questions.

Similarly, continuation of population surveys for keystone megafaunal species such as crocodilians should be done regularly in order to properly manage each individual species accordingly. There is a complex dichotomy at the heart of carnivore management and conservation, particularly for species like crocodilians. That is, the people throughout much of the Indonesian archipelago use crocodilians as a natural resource for food, leather products, and sometimes traditional medicinal uses. However, some species of crocodilians are responsible for a high number of attacks on people and livestock. The dangers that select crocodilians pose to people sometimes make it justifiable for local communities to kill crocodiles out of fear. Thus, it is a complex relationship where people are reliant upon species that they often times try to eliminate from their region. Further complicating the issue of exploitation of these megafuanal species is the unknown ramifications which may occur after removing large links from the trophic cascade.

Considering the importance of both, multispecies (agamid lizards) and single species (crocodiles) conservation research projects, and the role of biogeography in natural resource management, this work may serve to make up a piece of both facets for western Indonesia.

Appendices

Appendix A. List of species currently believed to be found in Java and Sumatra and current status. Ordered by "Order" column, then by "Status". Occurrence column refers to certainty of occurrence: 1 = Believed to Occur, ? = Questionable, INT = Believed it may be introduced.

Order	Family	Species	Status	Occurrence
Crocodylia	Crocodylidae	*Crocodylus siamensis*	CE	?
Crocodylia	Crocodylidae	*Tomistoma schlegelii*	V	1
Crocodylia	Crocodylidae	*Crocodylus porosus*	LC	1
Sauria	Agamidae	*Gonocephalus lacunosus*	DD	1
Sauria	Agamidae	*Harpesaurus modigliani*	DD	1
Sauria	Agamidae	*Pseudocophotis sumatrana*	DD	1
Sauria	Gekkonidae	*Ptychozoon horsfieldii*	DD	1
Sauria	Scincidae	*Larutia sumatrensis*	DD	1
Sauria	Agamidae	*Aphaniotis fusca*	LC	1
Sauria	Agamidae	*Bronchocela jubata*	LC	1
Sauria	Agamidae	*Draco cornutus*	LC	1
Sauria	Agamidae	*Draco haematopogon*	LC	1
Sauria	Agamidae	*Gonocephalus grandis*	LC	1
Sauria	Gekkonidae	*Gekko smithii*	LC	1
Sauria	Gekkonidae	*Hemidactylus frenatus*	LC	1
Sauria	Lacertidae	*Takydromus sexlineatus*	LC	1
Sauria	Scincidae	*Dasia olivacea*	LC	1
Sauria	Varanidae	*Varanus bengalensis*	LC	?
Sauria	Varanidae	*Varanus salvator*	LC	1
Sauria	Agamidae	*Acanthosaura armata*	NE	1

Sauria	Agamidae	*Aphaniotis acutirostris*	NE	1
Sauria	Agamidae	*Bronchocela cristatella*	NE	1
Sauria	Agamidae	*Bronchocela hayeki*	NE	1
Sauria	Agamidae	*Calotes versicolor*	NE	1
Sauria	Agamidae	*Dendragama boulengeri*	NE	1
Sauria	Agamidae	*Draco fimbriatus*	NE	1
Sauria	Agamidae	*Draco lineatus*	NE	1
Sauria	Agamidae	*Draco maximus*	NE	1
Sauria	Agamidae	*Draco melanopogon*	NE	1
Sauria	Agamidae	*Draco modiglianii*	NE	1
Sauria	Agamidae	*Draco obscurus*	NE	1
Sauria	Agamidae	*Draco quinquefasciatus*	NE	1
Sauria	Agamidae	*Draco spilopterus*	NE	1
Sauria	Agamidae	*Draco sumatranus*	NE	1
Sauria	Agamidae	*Draco volans*	NE	1
Sauria	Agamidae	*Gonocephalus beyschlagi*	NE	1
Sauria	Agamidae	*Gonocephalus chamaeleontinus*	NE	1
Sauria	Agamidae	*Gonocephalus klossi*	NE	1
Sauria	Agamidae	*Gonocephalus kuhlii*	NE	1
Sauria	Agamidae	*Gonocephalus liogaster*	NE	1
Sauria	Agamidae	*Gonocephalus megalepis*	NE	1
Sauria	Agamidae	*Harpesaurus beccarii*	NE	1
Sauria	Agamidae	*Harpesaurus ensicauda*	NE	1
Sauria	Agamidae	*Harpesaurus tricinctus*	NE	1
Sauria	Agamidae	*Leiolepis belliana*	NE	1

Sauria	Agamidae	*Lophocalotes ludekingii*	NE	1
Sauria	Agamidae	*Phoxophrys tuberculata*	NE	1
Sauria	Agamidae	*Pseudocalotes cybelidermus*	NE	1
Sauria	Agamidae	*Pseudocalotes guttalineatus*	NE	1
Sauria	Agamidae	*Pseudocalotes rhammanotus*	NE	1
Sauria	Agamidae	*Pseudocalotes tympanistriga*	NE	1
Sauria	Dibamidae	*Dibamus leucurus*	NE	1
Sauria	Eublepharidae	*Aeluroscalabotes felinus*	NE	1
Sauria	Gekkonidae	*Cnemaspis dezwaani*	NE	1
Sauria	Gekkonidae	*Cyrtodactylus fumosus*	NE	1
Sauria	Gekkonidae	*Cyrtodactylus lateralis*	NE	1
Sauria	Gekkonidae	*Cyrtodactylus marmoratus*	NE	1
Sauria	Gekkonidae	*Gehyra mutilata*	NE	1
Sauria	Gekkonidae	*Gekko gecko*	NE	1
Sauria	Gekkonidae	*Gekko monarchus*	NE	1
Sauria	Gekkonidae	*Gekko vittatus*	NE	?
Sauria	Gekkonidae	*Hemidactylus craspedotus*	NE	1
Sauria	Gekkonidae	*Hemidactylus garnotii*	NE	1
Sauria	Gekkonidae	*Hemidactylus platyurus*	NE	1
Sauria	Gekkonidae	*Hemiphyllodactylus margarethae*	NE	1
Sauria	Gekkonidae	*Hemiphyllodactylus typus*	NE	1
Sauria	Gekkonidae	*Lepidodactylus lugubris*	NE	1
Sauria	Gekkonidae	*Ptychozoon kuhli*	NE	1
Sauria	Scincidae	*Carlia nigrauris*	NE	1
Sauria	Scincidae	*Cryptoblepharus virgatus*	NE	INT

Sauria	Scincidae	*Dasia grisea*	NE	1
Sauria	Scincidae	*Emoia atrocostata*	NE	1
Sauria	Scincidae	*Eutropis macrophthalma*	NE	1
Sauria	Scincidae	*Eutropis multifasciata*	NE	1
Sauria	Scincidae	*Eutropis rudis*	NE	1
Sauria	Scincidae	*Eutropis rugifera*	NE	1
Sauria	Scincidae	*Lamprolepis leucosticta*	NE	1
Sauria	Scincidae	*Lipinia relicta*	NE	1
Sauria	Scincidae	*Lipinia vittigera*	NE	?
Sauria	Scincidae	*Lygosoma bowringii*	NE	1
Sauria	Scincidae	*Lygosoma quadrupes*	NE	1
Sauria	Scincidae	*Sphenomorphus malayanum*	NE	1
Sauria	Scincidae	*Sphenomorphus modigliani*	NE	1
Sauria	Scincidae	*Sphenomorphus necopinatus*	NE	1
Sauria	Scincidae	*Sphenomorphus puncticentralis*	NE	1
Sauria	Scincidae	*Sphenomorphus sanctus*	NE	1
Sauria	Scincidae	*Sphenomorphus scotophilus*	NE	1
Sauria	Scincidae	*Sphenomorphus temmincki*	NE	1
Sauria	Scincidae	*Sphenomorphus tenuiculus*	NE	1
Sauria	Scincidae	*Sphenomorphus vanheurni*	NE	1
Sauria	Varanidae	*Varanus dumerilii*	NE	1
Sauria	Varanidae	*Varanus rudicollis*	NE	1
Sauria	Scincidae	*Sphenomorphus cyanolaemus*	NT	1
Serpentes	Anomochilidae	*Anomochilus weberi*	DD	1
Serpentes	Colubridae	*Amphiesma kerinciense*	DD	1

Serpentes	Colubridae	*Anoplohydrus aemulans*	DD	1
Serpentes	Colubridae	*Boiga bengkuluensis*	DD	1
Serpentes	Colubridae	*Calamaria abstrusa*	DD	1
Serpentes	Colubridae	*Calamaria alidae*	DD	1
Serpentes	Colubridae	*Calamaria crassa*	DD	1
Serpentes	Colubridae	*Calamaria doederleini*	DD	1
Serpentes	Colubridae	*Calamaria eiselti*	DD	1
Serpentes	Colubridae	*Calamaria forcarti*	DD	1
Serpentes	Colubridae	*Calamaria javanica*	DD	1
Serpentes	Colubridae	*Calamaria lateralis*	DD	1
Serpentes	Colubridae	*Calamaria margaritophora*	DD	1
Serpentes	Colubridae	*Calamaria ulmeri*	DD	1
Serpentes	Colubridae	*Dendrelaphis underwoodi*	DD	1
Serpentes	Colubridae	*Etheridgeum pulchrum*	DD	1
Serpentes	Colubridae	*Rhabdophis chrysargoides*	DD	1
Serpentes	Elapidae	*Calliophis gracilis*	DD	1
Serpentes	Gerrhopilidae	*Gerrhopilus bisubocularis*	DD	1
Serpentes	Homolapsidae	*Enhydris albomaculata*	DD	1
Serpentes	Homolapsidae	*Enhydris alternans*	DD	1
Serpentes	Homolapsidae	*Enhydris bennettii*	DD	1
Serpentes	Homolapsidae	*Enhydris punctata*	DD	1
Serpentes	Viperidae	*Trimeresurus toba*	DD	1
Serpentes	Achrochordidae	*Acrochordus granulatus*	LC	1
Serpentes	Achrochordidae	*Acrochordus javanicus*	LC	1
Serpentes	Colubridae	*Ahaetulla mycterizans*	LC	1

Serpentes	Colubridae	*Ahaetulla prasina*	LC	1
Serpentes	Colubridae	*Amphiesma inas*	LC	1
Serpentes	Colubridae	*Amphiesma petersii*	LC	1
Serpentes	Colubridae	*Boiga cynodon*	LC	1
Serpentes	Colubridae	*Boiga drapiezii*	LC	1
Serpentes	Colubridae	*Boiga jaspidea*	LC	1
Serpentes	Colubridae	*Boiga nigriceps*	LC	1
Serpentes	Colubridae	*Calamaria albiventer*	LC	1
Serpentes	Colubridae	*Calamaria bicolor*	LC	1
Serpentes	Colubridae	*Calamaria leucogaster*	LC	1
Serpentes	Colubridae	*Calamaria linnaei*	LC	1
Serpentes	Colubridae	*Calamaria lovii*	LC	1
Serpentes	Colubridae	*Calamaria lumbricoidea*	LC	1
Serpentes	Colubridae	*Calamaria modesta*	LC	1
Serpentes	Colubridae	*Calamaria schlegeli*	LC	1
Serpentes	Colubridae	*Calamaria sumatrana*	LC	1
Serpentes	Colubridae	*Calamaria virgulata*	LC	1
Serpentes	Colubridae	*Chrysopelea pelias*	LC	1
Serpentes	Colubridae	*Coelognathus flavolineatus*	LC	1
Serpentes	Colubridae	*Dendrelaphis formosus*	LC	1
Serpentes	Colubridae	*Dendrelaphis haasi*	LC	1
Serpentes	Colubridae	*Dendrelaphis kopsteini*	LC	1
Serpentes	Colubridae	*Dendrelaphis striatus*	LC	1
Serpentes	Colubridae	*Dendrelaphis subocularis*	LC	1
Serpentes	Colubridae	*Dryocalamus subannulatus*	LC	1

Serpentes	Colubridae	*Dryophiops rubescens*	LC	1
Serpentes	Colubridae	*Elapoidis fusca*	LC	1
Serpentes	Colubridae	*Gongylosoma baliodeirus*	LC	1
Serpentes	Colubridae	*Gongylosoma longicauda*	LC	1
Serpentes	Colubridae	*Gonyosoma oxycephalum*	LC	1
Serpentes	Colubridae	*Lepturophis albofuscus*	LC	1
Serpentes	Colubridae	*Liopeltis tricolor*	LC	1
Serpentes	Colubridae	*Lycodon capucinus*	LC	1
Serpentes	Colubridae	*Lycodon effraenis*	LC	1
Serpentes	Colubridae	*Lycodon subcinctus*	LC	1
Serpentes	Colubridae	*Macropisthodon flaviceps*	LC	1
Serpentes	Colubridae	*Macropisthodon rhodomelas*	LC	1
Serpentes	Colubridae	*Oligodon bitorquatus*	LC	1
Serpentes	Colubridae	*Oligodon octolineatus*	LC	1
Serpentes	Colubridae	*Oligodon purpurascens*	LC	1
Serpentes	Colubridae	*Oligodon signatus*	LC	1
Serpentes	Colubridae	*Pseudorabdion longiceps*	LC	1
Serpentes	Colubridae	*Pseudoxenodon inornatus*	LC	1
Serpentes	Colubridae	*Ptyas carinata*	LC	1
Serpentes	Colubridae	*Ptyas fusca*	LC	1
Serpentes	Colubridae	*Rhabdophis chrysargos*	LC	1
Serpentes	Colubridae	*Rhabdophis conspicillatus*	LC	1
Serpentes	Colubridae	*Rhabdophis subminiatus*	LC	1
Serpentes	Colubridae	*Sibynophis geminatus*	LC	1
Serpentes	Colubridae	*Sibynophis melanocephalus*	LC	1

Serpentes	Colubridae	*Xenelaphis ellipsifer*	LC	1
Serpentes	Colubridae	*Xenelaphis hexagonotus*	LC	1
Serpentes	Colubridae	*Xenochrophis maculatus*	LC	1
Serpentes	Colubridae	*Xenochrophis melanzostus*	LC	1
Serpentes	Colubridae	*Xenochrophis trianguligerus*	LC	1
Serpentes	Colubridae	*Xenochrophis vittatus*	LC	1
Serpentes	Cylindrophiidae	*Cylindrophis ruffus*	LC	1
Serpentes	Elapidae	*Bungarus candidus*	LC	1
Serpentes	Elapidae	*Bungarus fasciatus*	LC	1
Serpentes	Elapidae	*Bungarus flaviceps*	LC	1
Serpentes	Elapidae	*Calliophis bivirgata*	LC	1
Serpentes	Elapidae	*Calliophis intestinalis*	LC	1
Serpentes	Elapidae	*Naja sputatrix*	LC	1
Serpentes	Elapidae	*Naja sumatrana*	LC	1
Serpentes	Homolapsidae	*Cantoria violacea*	LC	1
Serpentes	Homolapsidae	*Cerberus rynchops*	LC	1
Serpentes	Homolapsidae	*Enhydris enhydris*	LC	1
Serpentes	Homolapsidae	*Enhydris plumbea*	LC	1
Serpentes	Homolapsidae	*Fordonia leucobalia*	LC	?
Serpentes	Homolapsidae	*Gerarda prevostiana*	LC	?
Serpentes	Homolapsidae	*Homalopsis buccata*	LC	1
Serpentes	Pareatidae	*Aplopeltura boa*	LC	1
Serpentes	Pareatidae	*Asthenodipsas laevis*	LC	1
Serpentes	Pareatidae	*Asthenodipsas malaccanus*	LC	1
Serpentes	Pareatidae	*Asthenodipsas vertebralis*	LC	1

Serpentes	Pareatidae	*Pareas carinatus*	LC	1
Serpentes	Pythonidae	*Python brongersmai*	LC	1
Serpentes	Typhlopidae	*Ramphotyphlops lineatus*	LC	1
Serpentes	Typhlopidae	*Typhlops diardii*	LC	1
Serpentes	Typhlopidae	*Typhlops fuscus*	LC	1
Serpentes	Typhlopidae	*Typhlops muelleri*	LC	1
Serpentes	Viperidae	*Calloselasma rhodostoma*	LC	1
Serpentes	Viperidae	*Daboia siamensis*	LC	1
Serpentes	Viperidae	*Ovophis monticola*	LC	1
Serpentes	Viperidae	*Trimeresurus albolabris*	LC	1
Serpentes	Viperidae	*Trimeresurus andalasensis*	LC	1
Serpentes	Viperidae	*Trimeresurus barati*	LC	1
Serpentes	Viperidae	*Trimeresurus hageni*	LC	1
Serpentes	Viperidae	*Trimeresurus insularis*	LC	1
Serpentes	Viperidae	*Trimeresurus puniceus*	LC	1
Serpentes	Viperidae	*Trimeresurus sumatranus*	LC	1
Serpentes	Viperidae	*Tropidolaemus wagleri*	LC	1
Serpentes	Xenodermatidae	*Xenodermus javanicus*	LC	1
Serpentes	Colubridae	*Boiga dendrophila*	NE	1
Serpentes	Colubridae	*Boiga multomaculata*	NE	1
Serpentes	Colubridae	*Calamaria mecheli*	NE	1
Serpentes	Colubridae	*Chrysopelea paradisi*	NE	1
Serpentes	Colubridae	*Coelognathus radiatus*	NE	1
Serpentes	Colubridae	*Dendrelaphis caudolineatus*	NE	1
Serpentes	Colubridae	*Dendrelaphis pictus*	NE	1

Serpentes	Colubridae	*Oligodon wagneri*	NE	1
Serpentes	Colubridae	*Oreocryptophis porphyraceus*	NE	1
Serpentes	Colubridae	*Orthriophis taeniurus*	NE	1
Serpentes	Colubridae	*Ptyas korros*	NE	1
Serpentes	Colubridae	*Ptyas mucosa*	NE	1
Serpentes	Colubridae	*Xenochrophis piscator*	NE	1
Serpentes	Gerrhopilidae	*Gerrhopilus ater*	NE	1
Serpentes	Homalopsidae	*Karnsophis siantaris*	NE	1
Serpentes	Lamprophiidae	*Psammodynastes pictus*	NE	1
Serpentes	Lamprophiidae	*Psammodynastes pulverulentus*	NE	1
Serpentes	Pareatidae	*Asthenodipsas tropidonotus*	NE	1
Serpentes	Pythonidae	*Broghammerus reticulatus*	NE	1
Serpentes	Pythonidae	*Python curtus*	NE	1
Serpentes	Typhlopidae	*Ramphotyphlops braminus*	NE	1
Serpentes	Viperidae	*Trimeresurus purpureomaculatus*	NE	1
Serpentes	Colubridae	*Tetralepis fruhstorferi*	V	1
Serpentes	Elapidae	*Ophiophagus hannah*	V	1
Serpentes	Pythonidae	*Python bivittatus*	V	1
Testudines	Bataguridae	*Batagur baska*	CE	1
Testudines	Bataguridae	*Batagur borneoensis*	CE	1
Testudines	Trionychidae	*Chitra chitra*	CE	1
Testudines	Bataguridae	*Geoemyda spengleri*	E	1
Testudines	Bataguridae	*Heosemys spinosa*	E	1
Testudines	Bataguridae	*Orlitia borneensis*	E	1
Testudines	Testudinidae	*Manouria emys*	E	1

Testudines	Trionychidae	*Pelochelys cantorii*	E	1
Testudines	Trionychidae	*Dogania subplana*	LC	1
Testudines	Bataguridae	*Batagur affinis*	NE	1
Testudines	Bataguridae	*Cyclemys enigmatica*	NE	1
Testudines	Bataguridae	*Cyclemys oldhami*	NE	1
Testudines	Bataguridae	*Malayemys subtrijuga*	NE	INT
Testudines	Bataguridae	*Cyclemys dentata*	NT	1
Testudines	Bataguridae	*Cuora amboinensis*	V	1
Testudines	Bataguridae	*Notochelys platynota*	V	1
Testudines	Bataguridae	*Siebenrockiella crassicollis*	V	1
Testudines	Trionychidae	*Amyda cartilaginea*	V	1

Appendix B. List of individuals used in taxonomic evaluation and their corresponding GenBank accession numbers. See phylogenetic tree for comparisons. Province, Latitude and Longitude listed respectively. PA refers to previous authors entry to GenBank.

Species	**Province**	**Coordinates**	**Museum ID Numbers**	**GenBank Accession**
B. cristatella	Lampung	-5.36079, 104.63215	UTA R 62895	KT180148
B. jubata	Lampung	-5.54653, 105.04678	UTA R 62896	KT180152
B. jubata	Lampung	-5.5525, 105.18384	UTA R 62897	KT180151
B. jubata	Lampung	-5.57861, 105.22708	UTA R 62898	KT180150
B. jubata	Lampung	-5.57861, 105.22708	UTA R 62899	KT180146
C. versicolor	Jawa Barat	-6.49597, 106.85198	UTA R 62861	KT180149
C. versicolor	GenBank (PA)	NA	NA	NC009683.1
G. species	Lampung	-5.2787, 104.56198	UTA R 60571	KT180144
P. cybelidermus	Sumatra Selatan	-4.90149, 104.13401	UTA R 60551	KT180139
P. cybelidermus	Sumatra Selatan	-4.90711, 104.1348	UTA R 60549	KT180140
P. guttalineatus	Lampung	-5.28105, 104.56183	UTA R 60540	KT180141
P. guttalineatus	Sumatra Selatan	-4.90681, 104.13457	UTA R 60501	KT180142
P. rhammanotus	Lampung	-4.9394, 103.85292	MZB 10804	KT180147
P. species 4	Sumatra Barat	-2.04294, 101.31129	MZB 13295	KT211019
P. tympanistriga	Jawa Barat	-6.74181, 107.0061	UTA R 60544	KT180143
P. tympanistriga	Jawa Barat	-6.74181, 107.0061	UTA R 60547	KT180145
P. vitticeps	GenBank (PA)	NA	NA	AB166795.1

Appendix C: Dryad entries for mitochondrial genomes

ENS Number	**Species (Tentative)**	**Dryad Accession**
7580	*Aphaniotis sp.*	Pending
7655	*Lophocalotes sp.*	Pending
13521	*Gonocephalus sp.*	Pending
13717	*Bronchocela sp.*	Pending
13812	*Bronchocela sp.*	Pending
13847	*Bronchocela sp.*	Pending
13883	*Bronchocela sp.*	Pending
14022	*Bronchocela cristatella*	Pending
14073	*Pseudocalotes guttalineatus*	Pending
14078	*Gonocephalus sp.*	Pending
14300	*Pseudocalotes rhammanotus*	Pending
14310	*Draco sp.*	Pending
14317	*Bronchocela cristatella*	Pending
14322	*Dendragama sp.*	Pending
14326	*Lophocalotes sp.*	Pending
14330	*Lophocalotes sp.*	Pending
14349	*Lophocalotes sp.*	Pending
14429	*Pseudocalotes baliomus*	Pending
14709	*Gonocephalus sp.*	Pending
14710	*Gonocephalus sp.*	Pending
14712	*Pseudocalotes guttalineatus*	Pending
14713	*Gonocephalus sp.*	Pending
14736	*Pseudocalotes cybelidermus*	Pending
14790	*Pseudocalotes cybelidermus*	Pending
14810	*Pseudocalotes cybelidermus*	Pending
14836	*Gonocephalus sp.*	Pending
14858	*Gonocephalus sp.*	Pending
14879	*Lophocalotes sp.*	Pending
14978	*Aphaniotis sp.*	Pending
14993	*Bronchocela cristatella*	Pending
15866	*Gonocephalus sp.*	Pending
15889	*P. tympanistriga clade 1*	Pending
15974	*Lophocalotes sp.*	Pending
16046	*Dendragama sp.*	Pending
16068	*Calotes versicolor*	Pending
15292	*Bronchocela sp.*	Pending
15345	*Bronchocela sp.*	Pending
15615	*Dendragama schneideri*	Pending
15663	*Bronchocela sp.*	Pending

16156	*Pseudocalotes clade 2*	Pending
16171	*Pseudocalotes clade 2*	Pending
16173	*Pseudocalotes clade 2*	Pending
16408	*Pseudocalotes clade 2*	Pending
16409	*Pseudocalotes clade 2*	Pending
16411	*Pseudocalotes clade 2*	Pending
16935	*Phoxophrys sp.*	Pending
16992	*Aphaniotis sp.*	Pending
17035	*Aphaniotis sp.*	Pending
CAS242676	*Pseudocalotes sp.*	Pending
16846	*Dendragama schneideri*	Pending
16849	*Dendragama schneideri*	Pending
16149	*Pseudocalotes clade 2*	Pending
16172	*Pseudocalotes clade 2*	Pending
16150	*Pseudocalotes clade 2*	Pending
16212	*Pseudocalotes clade 2*	Pending

Appendix D: Additional Genbank Accessions for Draconids

ENS Number	**Species**	**Gene**	**GenBank Accession**
15615	*Dendragama schneideri*	BDNF	Pending
15639	*Dendragama schneideri*	BDNF	Pending
16045	*Dendragama sp.*	BDNF	Pending
16646	*Draco sp.*	BDNF	Pending
16762	*Dendragama schneideri*	BDNF	Pending
17552	*Lophocalotes sp.*	BDNF	Pending
17603	*Dendragama australis*	BDNF	Pending
17607	*Dendragama australis*	BDNF	Pending
17653	*Dendragama australis*	BDNF	Pending
18556	*Dendragama australis*	BDNF	Pending
18841	*Dendragama dioidema*	BDNF	Pending
18995	*Aphaniotis sp.*	BDNF	Pending
19099	*Aphaniotis sp.*	BDNF	Pending
19481	*Dendragama dioidema*	BDNF	Pending
19642	*Dendragma boulengeri*	BDNF	Pending
MVZ224103	*Pseudocalotes brevipes*	BDNF	Pending
MVZ224107	*Pseudocalotes brevipes*	BDNF	Pending
7655	*Lophocalotes sp.*	BDNF	Pending
13717	*Bronchocela jubata*	BDNF	Pending
14317	*Bronchocela jubata*	BDNF	Pending
14330	*Lophocalotes ludekingi*	BDNF	Pending
14349	*Lophocalotes ludekingi*	BDNF	Pending
14710	*Gonocephalus sp.*	BDNF	Pending
14712	*Pseudocalotes guttalineatus*	BDNF	Pending
14736	*Pseudocalotes cybelidermus*	BDNF	Pending
14858	*Gonocephalus sp.*	BDNF	Pending
14993	*Bronchocela cristatella*	BDNF	Pending
15866	*Gonocephalus sp.*	BDNF	Pending
16046	*Dendragama sp.*	BDNF	Pending

Appnedix E: Additional specimens examined for *Dendragama* Description

Dendragama australis (38): **INDONESIA**. SUMATERA SELATAN. An adult male (MZB 13786, Holotype) from trail up Gunung Dempo above Kampung Empat, Kabupaten Pagaralam, Provinsi Sumatera Selatan, Indonesia, 4.03744°S, 103.14526°E, 1953 m, Seven males (MZB 13776, 13778, 13782, 13783; UTA 63420, 63421, 63423), four females (MZB 13777, 13779, 13781, UTA 63424), and four unsexed specimens (MZB 13780, UTA 63418, 63419, 63422) from Gunung Patah near Desa Segamit, Kabupaten Muara Enim, Provinsi Sumatera Selatan, Indonesia, 4.21–4.23°S, 103.41–103.42°E, 1742–2142 m, three males (MZB 13784, UTA 63427, 63428), two females (MZB 13785, 13787), and six unsexed specimens (MZB 13788, UTA 63425, 63426, 63429–63431) from Gunung Dempo above Kampung Empat, Kabupaten Pagaralam, Provinsi Sumatera Selatan, Indonesia, 4.04°S, 103.14– 103.17°E, 1764–2111 m. **INDONESIA**. BENGKULU. Three males (MZB 13789, 13790, UTA 63433) and one unsexed specimen (UTA 63432) from Bukit Daun, above desa Air Nipas, Rimbo Pengadang, Kabupaten Rejang Lebong, 3.36°S, 102.38° E, 1646–1728 m, five males (MZB 13791–13793; UTA 63434, 63435), one female (UTA 63436), and one unsexed specimen (UTA 63437) from Air Duku, Selupu Rejang, trail up Gunung Kambing from police academy near road to Gunung Kaba, Kabupaten Rejang Lebong, 3.39–3.40°S, 102.63–102.64°E, 1516– 1748 m.

Dendragama boulengeri (27): **INDONESIA**. SUMATERA BARAT: One male (MSNG 29936, Lectotype) from “monte Singalang (Sumatra occidentale) ad un’ altezza di metri circa 2800” [traced to Gunung Singgalang, Kabupaten Agam, 0.38°S, 100.36°E], five paralectotypes, including nine males (BMNH 1946.8.13.15; ZMB 10155, 54503, MZB 13822, 13824, 43 13825; UTA 63463, 63466, 63469) and 10 females (MNHN 1889- 27; ZMB 54502, MZB 13819– 13821, 13823, 13826; UTA 63465, 63467) from the type locality (above desa Beringin) 0.3752–0.3753°S, 100.363°E, 1376–1473 m, and seven unsexed specimens (MZB 13817, 13818, 13824; UTA 63461, 63462, 63464, 63468) from Aie Angek, Sepuluh Koto, Gunung Marapi, Kabupaten Tanah Datar, 0.395°S, 100.425°E, 1526–1553 m, nine specimens (UTA

62852–62870) from Gunung Kerinci, Jambi Province, 1.710°S, 101.253°E, 1400–1800 m.

Dendragama dioidema (43): **INDONESIA**. ACEH. An adult male (MZB 13814, Holotype) from Bukit Sama, Kampung Telege Atu, Kebayakan, Kabupaten Aceh Tengah, 4.66512° N, 96.80937° E, 1567 m, Three males (MZB 13794; UTA 63448, 63449), six females (MZB 13804, 13805; UTA 63438, 63440, 63441, 63446), and 15 unsexed specimens (MZB 13795–13803; UTA 63439, 63442–63445, 63447) from Kute Baru, Linge, along road from Takengon to Isaq, Kabupaten Aceh Tengah, 4.52875° N, 96.85316° E, 1827 m, one 63 unsexed specimen (UTA 63450) from foot of Berni Terlong, near Desa Rambune, Kabupaten Bener Meriah, 4.7648° N, 96.80196° E, 1471 m, four male (MZB 13807, 13808, 13810; UTA 63452) and two unsexed specimens (MZB 13809; UTA 63453) from Beutong Ule, high point on Meulaboh-Takengon road, Kabupaten Nagan Raya, 4.38367° N, 96.51633° E, 1950 m, one male (MZB 13811), three females (UTA 63456–63458), and three unsexed specimens (MZB 13812, 13813; UTA 63455) from Bukit Sama, Kampung Telege Atu, Kebayakan, Kabupaten Aceh Tengah, 4.66512– 4.66583° N, 96.80627– 96.80937° E, one male (UTA 63460), one female (MZB 13815), and two unsexed specimens (MZB 13816; UTA 63459) from Hutan Timang Gajah, Gunung Burni Telong, Kabupaten Bener Meriah, 4.77122–4.77142° N, 96.80907– 96.81017° E, 1875–1957 m

Pseudocalotes brevipes (10): **LAO PDR**. XE KONG; Kaleum District, Xe Sap National Biodiversity Conservation Area, near 16° 0410N, 106° 5845"E, 1200–1300 m (FMNH 258703). **VIETNAM**. VINH PHU; Tam Dao, Vinh Yen District (MVZ 224103–224106; 226486, 226487, 226489, 226490, 226494).

Pseudocalotes cybelidermus (15): **INDONESIA.** LAMPUNG: Montane forest above Ngarip, Lampung, Sumatra, Indonesia, 5.28°S, 104.56° E, 1376–1521 m (MZB 9766, 9769, 9800, UTA 60537–60539, 60552–6055 paratypes). SUMATERA SELATAN: Montane forest at Maura Dua, Remanan Jaya, Gunung Pesagi (locally known as Masagi), 4.91°S, 104.13°E, 1474–1643 m (MZB 9767 holotype; MZB 9650, 9760, 9799, UTA 60549–60551 paratypes).

Pseudocalotes dringi: **MALAYSIA.** PAHANG: “Gunung Tahan, 6500–7200 ft (1981–2194 m) elevation” (BMNH 1906.2.28.10 holotype). TERENGGANU: “Summit Ridge, 4000 ft (1219 m) elevation, Gunung Lawit, Terengganu, W-Malaysia” (BMNH 1974.4929 paratype).

Pseudocalotes flavigula (1): **MALAYSIA.** PAHANG; Gunnong Brinchang, Cameron Highlands, 1524–1829 m (FMNH 143903); “Cameron Highlands between 5,000 and 6,000 feet” (BMNH 1946.8.11.14 holotype).

Pseudocalotes floweri (2): **CAMBODIA.** KOH KONG; Cardamom Highlands Plateau. 0349359 Easting, 1325813 Northing, 1200 m (FMNH 270127). **THAILAND.** No other data (FMNH 114514), “Chantaboon” = Chantaburin (BMNH 1946.8.11.25 lectotype).

Pseudocalotes guttalineatus (16): **INDONESIA**. LAMPUNG: Montane forest above Ngarip, 5.28°S, 104.56° E, 1341–1521 m (MZB 9796 holotype; MZB 9652, 9765, 9792–9795, 9801, UTA 60536, 60540–60543, 60554 paratypes). SUMATERA SELATAN: Maura Dua, Remanan Jaya, Gunung Pesagi (localy known as Masagi), 4.91°S, 104.13°E, 1574–1643 m (UTA 60500–60501, paratypes).

Pseudocalotes kakhienensis (6): **CHINA.** YUNAN; Nujiang Prefecture, small village S of Gongshan, 27° 42' 13.7016" N, 98° 42' 10.1982" E, ca 1451 m (CAS 214907, 214940, 214949), Fugong County, Shiwuli, 27° 09’ 22.5” N, 98° 47’ 57.4” E (CAS 234454–234455), Gongshan County, vicinity of village S of Gongshan, 27° 42’ 13.1” N, 98° 42’ 10.6” E, 1437 m (CAS 242105).

Pseudocalotes kingdonwardi (11): **BURMA.** “Adung Valley, 7000ft, Burma-Tibet border” (BMNH 1946.8.11.17 holotype). **CHINA.** YUNAN; Nujiang Prefecture, Gongshan County; road between Kongdang and Bapo in Dulong Valley, 27° 49’ 33.9” N, 98° 19’ 31.7” E, 1478 m (CAS

241965), ca 5 km N (by Dulong River) of Kongdang (CAS 241992, 241994, 241997), Dulong Valley, E of Kongdang (CAS 242015), Dulong Valley, 2 km N of Kongdang, W side of Dulong River (CAS 242020), Dulong Valley, road from Bapo N toward Kongdang, 27° 45’ 29.9” N, 98° 20’ 52.8” E, 1357 m (CAS 242628), Dulong Valley, Kongdang, 27° 50’ 28.4” N, 98° 19’ 45.4” E, 1450 m (CAS 242653), Dulong Valley, Kongdang, 27° 52’ 07.7” N, 98° 20’ 09.4” E, 1451 m (CAS 242674), Dulong Valley, Kongdang, 27° 51’ 44.0” N, 98° 20’ 04.3” E (CAS 242675), Dulong Valley, Kongdang, 27° 52’ 07.2” N, 98° 20’ 09.8” E, 1450 m (CAS 242676).

Pseudocalotes microlepis (2): **LAO PDR.** Phong Saly (FMNH 14499). **VIETNAM.** BAC THAI; Ba Be Lake National Park, cave area, ca. 1.5 km E of guest house, 22° 24’ 1” N, 105° 37’ 54” E. **THAILAND.** “Plapoo Tenasserim” (BMNH 1946.8.11.21).

Pseudocalotes poilani (2): **LAO PDR.** CHAMPASAK; Pakxong District, Dong Hua Sao National Biodiversity Conservation Area, near Ban Nongluang Village, near 15° 0470N, 106° 1203”E, 1100 m (FMNH 258704), Pakxong District, Dong Hua Sao National Biodiversity Conservation Area, Bolaven Plateau, near 15° 0355N, 106° 1303”E, 1200 m (FMNH 258710).

Pseudocalotes rhammanotus (1). **INDONESIA.** LAMPUNG: montane forest along the ridge of a mountain south of Danau Ranau (= Lake Ranau), 4.9394° S, 103.85292° E, 1237 m (MZB 10804, holotype).

Pseudocalotes tympanistriga (16): **INDONESIA.** JAWA BARAT. Cibodas Botanical Garden, 6.74181° S, 107.0061° E (UTA 60544–60548); Gunung Tilu, 7.15601° S, 107.52309° E, 1389–1647 m (UTA 63094–63096); road from S coast of Java to Gunung Patuha, 7.24716° S, 107.35696° E, 1156 m (UTA R 63097); road from S coast of Java to Gunung Patuha, 7.24711° S, 107.35722° E, 1183 m (UTA R 63098–63099); Gunung Puntang. Gibbon Research Center, 7.11828° S, 107.60493° E, 1393–1468 m (UTA 63100–63101); Gunung Waringin, 7.15603° S, 107.49647° E, 1583–1607 m (UTA 63102–63103).

NO OTHER DATA: “Java” (ZMB 689 holotype).

Appendix F: Specimens included in phylogenetic assessment and GenBank accession numbers

Species	**Museum number**	**Locality**	**GenBank Accessions**
B. cristatella	UTA 62895	Gunung Patah, Sumatera Selatan	KT180148
D. australis	MZB 13781	Gunung Patah, Sumatera Selatan	KY576737
D. australis	UTA 63424	Gunung Patah, Sumatera Selatan	KY576738
D. australis	MZB 13783	Gunung Patah, Sumatera Selatan	KY576739
D. australis	MZB 13784	Gunung Dempo, Sumatera Selatan	KY576740
D. australis	UTA 63432	Bukit Daun, Bengkulu	KY576741
D. boulengeri	MZB 13818	Gunung Marapi, Sumatera Barat	KY576742
D. dioidema	UTA 63442	Kute Baru, Aceh	KY576743
D. dioidema	MZB 13811	Bukit Sama, Aceh	KY576744
D. dioidema	MZB 13815	Hutan Timang, Aceh	KY576745
D. schneideri	UTA 62872	Gunung Sibuatan, Sumatera Utara	Pending Acceptance
D. schneideri	UTA 62874	Gunung Sibuatan, Sumatera Utara	Pending Acceptance
D. schneideri	MZB 12098	Vicinity of Tele, Sumatera Utara	Pending Acceptance
D. schneideri	MZB 12103	Above Pangururan, Sumatera Utara	Pending Acceptance
D. schneideri	MZB 14128	Above Pangururan, Sumatera Utara	Pending Acceptance
L. ludekingi	MZB 14129	Gunung Kerinci, Jambi	Pending Acceptance
P. tympanistriga	UTA 60544	near Bogor, Jawa Barat	KT180143

Appendix G: Crocodile sighting localities

Year	Tributary	lat	lon	Day or Night	Status	Species
2014	Serkap	0.301231	102.7123	Night	Confirmed	*C. porosus*
2014	Serkap	0.29051	102.7227	Night	Confirmed	*C. porosus*
2014	Serkap	0.290473	102.7225	Night	Confirmed	*C. porosus*
2014	Serkap	0.330561	102.7123	Night	Probable	*C. porosus*
2014	Serkap	0.28712	102.7221	Night	Probable	*C. porosus*
2014	Serkap	0.303892	102.7129	Night	Probable	*C. porosus*
2014	Serkap	0.286943	102.7217	Night	Unknown	Unknown
2014	Turip	0.258338	102.6723	Night	Confirmed	*C. porosus*
2014	Turip	0.263245	102.6713	Night	Confirmed	*C. porosus*
2014	Turip	0.26042	102.6681	Night	Probable	*C. porosus*
2015	Air Hitam Laut	-1.31704	104.4162	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.31742	104.4169	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.32149	104.4181	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.32315	104.4181	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.32705	104.4157	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.3292	104.4173	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.32933	104.4186	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.33264	104.423	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.33582	104.424	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.33759	104.4244	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.33831	104.4238	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.34184	104.4156	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.3425	104.4152	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.34355	104.4141	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.34529	104.413	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.35129	104.4113	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.35812	104.4043	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.35263	104.3979	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.3545	104.3899	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.3981	104.3679	Night	Confirmed	*C. porosus*
2015	Air Hitam Laut	-1.31793	104.4171	Night	Probable	*C. porosus*
2015	Air Hitam Laut	-1.32961	104.42	Night	Probable	*C. porosus*
2015	Air Hitam Laut	-1.33273	104.4228	Night	Probable	*C. porosus*
2015	Air Hitam Laut	-1.39582	104.3683	Night	Probable	*C. porosus*
2015	Air Hitam Laut	-1.37562	104.3924	Night	Probable	*C. porosus*
2015	Air Hitam Laut	-1.40553	104.3655	Night	Probable	*C. porosus*
2015	Air Hitam Laut	-1.31573	104.4185	Daytime/Sign	Other	*C. porosus*
2015	Air Hitam Laut	-1.43758	104.3476	Daytime/Sign	Other	*T. schlegelii*
2015	Air Hitam Laut	-1.43133	104.346	Night	Confirmed	*T. schlegelii*
2015	Air Hitam Laut	-1.43144	104.3461	Night	Confirmed	*T. schlegelii*

2015	Air Hitam Laut	-1.41049	104.3593	Night	Confirmed	*T. schlegelii*
2015	Kampar	0.225612	102.6482	Night	Confirmed	*C. porosus*
2015	Kerumutan	0.167048	102.5269	Night	Confirmed	*C. porosus*
2015	Kerumutan	-0.05236	102.4203	Daytime/Sign	Other	*T. schlegelii*
2015	Pulau Muda	0.281959	102.8926	Night	Confirmed	*C. porosus*
2015	Serkap	0.290873	102.7221	Night	Confirmed	*C. porosus*
2015	Serkap	0.288979	102.7237	Night	Probable	*C. porosus*
2015	Simpang Melakka	-1.39305	104.3644	Night	Confirmed	*C. porosus*
2015	Simpang T	-1.46395	104.1309	Daytime/Sign	Other	*T. schlegelii*
2015	Simpang T	-1.43752	104.1444	Daytime/Sign	Other	*T. schlegelii*
2015	Simpang T	-1.48573	104.1091	Daytime/Sign	Other	*T. schlegelii*
2015	Simpang T	-1.45369	104.1345	Daytime/Sign	Other	*T. schlegelii*
2015	Simpang T	-1.49323	104.1052	Night	Confirmed	*T. schlegelii*
2015	Simpang T	-1.49256	104.1065	Night	Confirmed	*T. schlegelii*
2015	Simpang T	-1.4527	104.134	Night	Confirmed	*T. schlegelii*
2015	Simpang T	-1.44712	104.136	Night	Confirmed	*T. schlegelii*
2015	Simpang T	-1.46276	104.1313	Night	Confirmed	*T. schlegelii*
2015	Simpang T	-1.46659	104.1286	Night	Confirmed	*T. schlegelii*
2015	Simpang T	-1.49358	104.1048	Night	Confirmed	*T. schlegelii*
2015	Simpang T	-1.4555	104.1347	Night	Probable	*T. schlegelii*
2015	Simpang T	-1.45125	104.1337	Night	Probable	*T. schlegelii*
2015	Simpang T	-1.45804	104.1346	Night	Probable	*T. schlegelii*
2015	Simpang T	-1.47587	104.1128	Night	Probable	*T. schlegelii*
2015	Simpang T	-1.49379	104.1044	Night	Probable	*T. schlegelii*
2015	Simpang T	-1.44684	104.3462	Daytime/Sign	Other	*T. schlegelii*

Biographical Information

Kyle J. Shaney was born in Reno, Nevada on January 3, 1989 to Debbie and J.J. Shaney and also has a younger sister, Brittany Shaney. He received a Bachelor's degree in Integrated Studies with a focus in three areas; Botany, Environmental Studies, and Zoology from Weber State University (WSU) in 2012. Kyle was mentored by Jonathon Marshall over the course of his time at WSU before starting graduate school at the University of Texas at Arlington (UTA), where he received his Ph.D. in Quantitative Biology in 2017. During his time in graduate school, Kyle published several peer reviewed papers in notable journals, presented at international scientific meetings, and gained a great deal of field experience working in remote regions of West Indonesia. He also received notable grants, including a Young Explorer's Grant from National Geographic and an IUCN research grant, which were used to study threatened crocodilians on the island of Sumatra. Kyle intends to continue in academia as a postdoctoral researcher with a focus on Biogeography, Conservation Biology, Ecology, and Wildlife Management.