Impacts of environmental change on large mammal distributions in Southeast Asia

Nonthiwat Taesuk
Department of Genetics, Evolution and Environment
University College London

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Declaration

I, Nonthiwat Taesuk, confirm that the work presented here in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Nonthiwat Taesuk
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Abstract

It is suggested climate change contributes considerably to global biodiversity loss. Southeast Asia, one of the world's richest biodiversity hotspots, is predicted to lose most of its species by 2100. Hence, it is important to identify the key impact of environmental changes in order to develop more appropriate and effective conservation plans to mitigate species extinction risks. In this thesis, Species Distribution Modelling (SDM) techniques were used to predict potential species distributions in relation to 6 climatic variables. The effects of climate changes on large mammal distributions were examined across three time intervals: past (the last interglacial ~120,000 – 140,000 years before present), present (AD 1945 - present) and future (2050); while rates of species range shifts between the time intervals were also determined. It is found that large mammals are particularly vulnerable to climate change. The species will have to move 33 – 105 times faster than they once did in the past in order to search out suitable habitat. There is also evidence of niche conservatism and niche shift among the taxa. However, species niche shifts likely result from anthropogenic factors. Limited availability of species occurrence data in many parts of the world leads to an increased use of species range maps in research on species responses to changing environments. Predictions based on SDMs suggest that relying on a single data source may skew the species' realistic threatened status and misguide conservation planning. The Zonation software was employed to evaluate the effectiveness of protected areas (PAs) in Thailand under future warming climate and identify high priority areas. Currently, nearly 60% of high priority areas fall within the PAs. In the future, the conservation values of the PAs are expected to remain relatively unchanged. However, it is suggested that enhancing PAs connectivity in the northern part of the country may yield a high return on conservation investment. A deliberate and consistent conservation effort will also be needed to maintain the effectiveness of the existing PAs.

Impact Statement

Climate change is a serious threat to global biodiversity. The recent rapid rate of change is predicted to negatively affect ecosystem functions and services, which in turn cause ripple effects on human well-being. Southeast Asia is renowned for its complexity of geology and biodiversity. The region, listed as one of the world's myriad biodiversity hotspots, houses a high level of species richness and endemism. Tropical rainforests of Southeast Asia also play an important role in carbon sequestration. Therefore, the predicted extensive loss of biodiversity by 2100 in this part of the word will be of global magnitude and significance.

The thesis is aimed at determining the impacts of climate change on the distributions of large mammal species in Southeast Asia where studies of tropical species are currently lacking generally due to limited availability of data. This study was potentially the first to amass large mammal records of Southeast Asia. Fossil records of the species were also compiled and used to investigate the species responses to environmental changes over a long geological timescale. Thus, the findings derived from this study have led to a wide spectrum of impact across several sectors and are likely to draw the attention of researchers, authorities, policy makers and the public in general. Having a direct bearing on macroecological research, this study adds to the knowledge of both ecological and evolutionary processes. Model predictions describe the dynamics of species ranges under changing environments over time, which help to enhance the current understanding of species adaptability and niche conservatism among large mammal species of Southeast Asia. The results also provide useful information on potential species responses to future climate change for policy makers and local authorities who are responsible for the planning of conservation actions. Furthermore, the study can serve to raise public awareness of the vulnerability of other species and key resources to tackle climate change. Ultimately, it is essential that we as a collective community embrace scientific recommendations and work together to address the challenges of climate change and mitigate adverse effects on biodiversity.

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List of Abbreviations

AUC	Area under the receiver operating characteristic curve
CMIP5	Coupled Model Intercomparison Project Phase 5
ENM	Ecological Niche Modelling
GBIF	Global Biodiversity Information Facility
GCM	General Circulation Model
IUCN	International Union for Conservation of Nature and Natural Resources
LGM	Last Glacial Maximum
LIG	Last interglacial
MaxSSS	Maximum sum of sensitivity and specificity
PAs	Protected areas
RCP	Representative Concentration Pathway
SDM	Species Distribution Modelling

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Chapter 1: General introduction

1.1 Introduction

Southeast Asia is a region that has drawn global concern over its biodiversity crisis. Many species are at risk of extinction or severely threatened by native habitat loss and habitat degradation, mainly as a result of deforestation (Sodhi et al., 2004). The annual deforestation rate in Southeast Asia ranks highest amongst all of the tropical regions in the world and has continued to rise over the last decade (Miettinen et al., 2011; Sodhi et al., 2010). Studies have revealed that insular Southeast Asia has lost 1.0% of its forest cover yearly to conversion to plantations and secondary vegetation (Miettinen et al., 2011). It is predicted that 13-85% of the biodiversity in the region is likely to disappear by 2100 (Sodhi et al., 2010). Climate change has recently become another contributing threat to the loss of global biodiversity (Trisurat et al., 2011). Even though the world has experienced many extreme climate change events in the past (Zachos et al., 2001) and many species have managed to survive periods of such changes (Huber, 2009), the current change is occurring at a much faster rate than those of the previous events (IPCC, 2013). These rapid environmental changes could cause tropical species to reach the limit of their adaptive and evolutionary abilities (Bickford et al., 2010). Hence, it is important to identify the key impacts of changes in environmental conditions on biodiversity in order to develop more appropriate and effective action plans and strategies to mitigate species extinction risk and maintain functioning ecosystems.

1.2 Geological history and biodiversity of Southeast Asia

Southeast Asia is home to the highest concentration of the world’s biodiversity hotspots, accommodating 20-25% of global plant and animal species (Sodhi et al., 2010; Woodruff, 2010). The region also contains the highest mean proportion of country-endemic species of birds (9%) and mammals (11%) among the tropical regions (Sodhi et al., 2010). This high species richness and endemism are partly due to the overlap of four bioregions: Indochina, Sundaic, Philippines and Wallacea (Figure 1.1) (Woodruff, 2010). In addition, collisions of tectonic plates and periodic sea-level fluctuations in the past allowed the migration of floral and faunal species between the mainland and the Sundaic archipelagic region, and facilitated speciation (Sodhi et al., 2010). Wallacea is separated from the other areas by deep-water channels and no land bridges have ever been formed between Wallacea and the other two adjacent regions. This unique geological history together with numerous insular biota have therefore encouraged speciation and led to the evolution of species highly endemic to the Wallacea region (Bird et al., 2005; Sodhi et al., 2004). Similarly, the Philippines represents approximately 7000 islands; two-thirds of the speciation events in this hotspot are related to dispersal to newly formed oceanic islands and this results in extremely high species richness and endemism, including 50-85% of endemic non-flying mammals (Steppan et al., 2003).

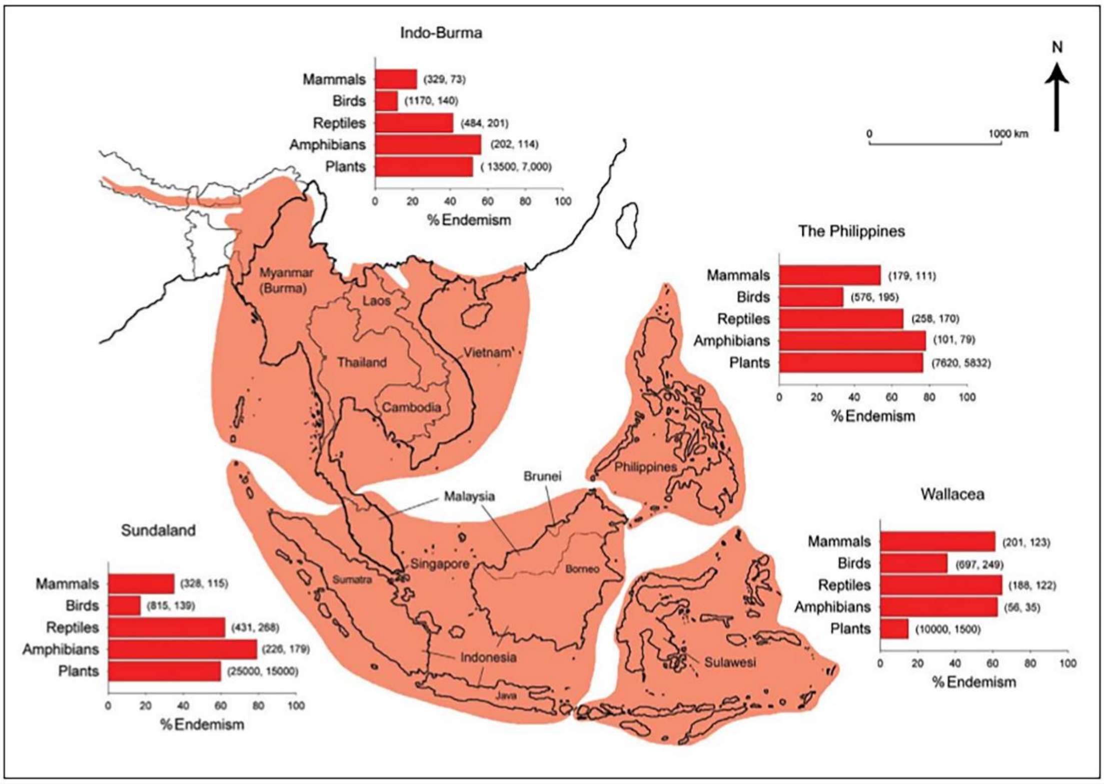


Figure 1.1. The overlap between four biodiversity hotspots, which has led to high species richness and endemism in Southeast Asia. Numbers in parentheses are total and endemic species known, respectively (Sodhi et al., 2004).

1.3 Environmental changes in Southeast Asia

Southeast Asia is a highly dynamic area where environmental change has occurred persistently across large temporal and spatial scales. This is because it is situated in a variety of complex terrains that can trigger large variations in the environment (IPCC, 2013).

1.3.1 Palaeobiogeography and palaeoenvironments

The biogeography of Southeast Asia has been a subject of considerable debate and yet it has only been partially understood because of the intense geological activity occurring in this highly insular region and the limited evidence currently available (Louys and Meijaard, 2010). However, many studies have attempted to provide an overview of the palaeobiogeography, palaeoecology and palaeoenvironments of the region (Bird et al., 2005; Gathorne-Hardy et al., 2002; Heaney, 1991; Hope et al., 2004; Louys and Meijaard, 2010; Slik et al., 2011). Southeast Asia has been largely covered by tropical rainforests believed to have been existed in the region for at least 65 million years (Heaney, 1991). The extent of these forests has been determined by variations in temperature, rainfall and sea level (Heaney, 1991).

During the Miocene, the rainforest cover extended as far north as Southern China and Japan, but it has contracted continuously since that time (Heaney, 1991). The major pressure on the region during the Pleistocene was the fluctuation in environmental conditions caused by glacial and interglacial cycles that subsequently affected the climate and vegetation of Southeast Asia (Bird et al., 2005). The expansion of continental glaciers during glaciations led to a reduction in the ocean volume (Heaney, 1991), thereby causing sea level and temperature during the Last Glacial Maximum (LGM) to be 120m and 2-6°C lower than those at present (Heaney, 1991; Voris, 2000). The Savannah-Corridor hypothesis suggests that the emergence of the savannah corridor in Sundaland while sea levels were lower during the last glacial period (LGP) had important implications for the dispersal of terrestrial species and caused the conversion of vegetation types throughout the Sundaic region. A decrease in rainfall during that period together with increased drought and seasonality resulted in the transition from rainforest to savannah (Gathorne-Hardy et al., 2002). Narrow land bridges were formed between the open vegetation lands north and south of the equator, which may have facilitated the rapid dispersal of early humans between 60 to 45 ka, but deterred the dispersal of other terrestrial species that favoured the rainforest habitat (Bird et al., 2005).

Evidence gathered from the investigation of exposed sea-bed soils, however, does not support the Savannah-Corridor hypothesis. It is suggested that when sea level dropped to a certain level, central Sundaland was likely to have been dominated by either heath or swamp forests, depending on the drainage capacity of the soil (Slik et al., 2011). The soil dispersal barrier could also have acted as a dispersal barrier for terrestrial species that disfavoured such soil conditions and vegetation types. Swamp and heath forests are likely to be inhospitable for humans since they are generally low in productivity and difficult to traverse (Slik et al., 2011). Slik et al. (2011) therefore suggest that early humans might have taken coastal routes along Sundaland to reach

Java and other parts of the archipelago. Although the controversy surrounding the palaeobiogeography and paleoenvironments of Southeast Asia remains unresolved, the majority of evidence converges on the sensitivity of vegetation to environmental changes. A decrease in temperature by 1-2°C significantly affects vegetation types in the region, which can in turn lead to changes in the composition, structure and functions of ecosystems (Heaney, 1991).

1.3.2 Current environmental conditions

The Holocene has been largely affected by the current interglacial period, resulting in expanses of evergreen forests dominating the Southeast Asian region (Louys, 2014). Climate change during this geological period has been less intense compared to the past (Hope et al., 2004). However, despite these relatively uniform and stable environmental conditions, a number of species have been put under threat of extinction due to strong anthropogenic pressures, especially from hunting, urbanisation and deforestation over the last 5-6 ka (Louys, 2014; Sodhi et al., 2004; Woodruff, 2010). Although the arrival of early humans in Southeast Asia was unlikely to have caused immediate environmental changes or species extinctions, humans with increasing intelligence, and the abilities to produce tools and make fire potentially posed a threat to biodiversity and the environment (Louys et al., 2007; Zhao and Zhang, 2013). Populations of many species have been found to dramatically decline and be extirpated from their historical ranges (Harrison et al., 2016). Humans, for example, are believed to have driven small populations of hyenas to extinction in Southeast Asia (Louys, 2014). Turvey et al. (2018) postulated that the extinction of *Junzi imperialis*, a species of gibbon existing 2,250 years ago, was the first example of a human-caused Asian ape extinction. A decrease in prey availability due to higher hunting pressure together with habitat loss from human activities also led to the local extinctions of tigers in Palawan (Piper et al., 2008). Moreover, humans have played an important role in land use changes. Paddy fields are estimated to have emerged in the region 4,500 years ago with developed water management systems. Over the last 1,500 years, there has been a rapid increase in deforestation due to urbanisation (Corlett, 2009).

Today, Southeast Asia has seen a continuous human population growth rate of 1.5% per annum during the last decade (Sodhi et al., 2010). As human populations increase, more resources are required to support them. Increased population density has led to a rapid loss of forest cover because of a growing demand in expanding agricultural land and urban areas (Sodhi et al., 2010). These socioeconomic factors and unsustainable use of resources have contributed greatly to the environmental degradation in the region, leaving it highly vulnerable to the effects of climate change (Yuen et al., 2009). Many Southeast Asian countries are now having to cope with more frequent and extreme climate-related hazards, including floods, droughts, landslides, fires and cyclones. The intensity of typhoons affecting East and Southeast Asia has been found to have increased by 12-15% over the past 37 years (Mei and Xie, 2016). For example, Typhoon Haiyun, with the maximum wind speed of 315 kph that struck the Philippines in 2013, was one of the strongest typhoons in recorded history; it claimed more than 6000 lives, injured nearly 30,000 more and caused huge damage to property (Lagmay et al., 2015).

1.3.3 Future climate changes

In 2008, many climate modelling groups worldwide come to an agreement to develop the new global climate models (GCMs) which aim to enhance an understanding of past and future climate changes and provide projections of future climate change for the analysis of possible consequences (Taylor et al., 2012). These developments are currently in the fifth phase of the Coupled Model Intercomparison Project (CMIP5). The four Representative Concentration Pathways (RCPs) of CMIP5 can be used to facilitate the assessment of potential climate change impacts and provide useful information for possible mitigation and adaptation strategies (Taylor et al., 2012; van Vuuren et al., 2011). RCPs were produced based on comprehensive data on climate change forcing agents such as future concentration and emission of greenhouse gases (GHG), and land cover, to represent a projected radiative forcing level of all major forcing components by the end of 2100 (van Vuuren et al., 2011). Radiative forcing is defined as “a measure of the influence a factor has in altering the balance of incoming and outgoing energy in the Earth-atmosphere system and is an index of the importance of the factor as a potential climate change mechanism” (Solomon et al., 2007). The commonly used four RCPs (RCP2.6, 4.5, 6.0 and 8.5) indicate varying forcing levels from very low to high. RCP2.6 can be considered a low emission scenario whereas RCP8.5 represents a very high scenario due to increased GHG emission from high fossil fuel/coal consumption to support rapid population growth. RCP4.5 and RCP6.0 are a representative of intermediate/medium mitigation scenarios (Table 1) (van Vuuren et al., 2011).

Table 1.1. Summary of each RCP characteristics (van Vuuren et al., 2011).

Scenario Component	**RCP2.6**	**RCP4.5**	**RCP6.0**	**RCP8.5**
Greenhouse gas emissions	Very low	Medium-low mitigation	Medium baseline; high mitigation	High baseline
Agricultural area	Medium for cropland and pasture	Very low for both cropland and pasture	Medium for cropland but very low for pasture (total low)	Medium for both cropland and pasture
Air pollution	Medium-low	Medium	Medium	Medium-high

Future climate change scenarios predict a continuous increase in both temperature and precipitation in Southeast Asia. While the region's temperature has risen at a rate of 0.14°C to 0.20°C per decade since the 1960s, there has been an increase by 22 mm per decade in annual wet-day rainfall totals (Caesar et al., 2011; Tangang et al., 2007). The climate of Southeast Asia is affected by many large-scale phenomena such as the El Nino-Southern Oscillation (ENSO), Maritime Continent monsoon, and Indian Ocean Dipole (IOD), causing variations in climate change projections across the region (Table 2). It is predicted that by the end of this century (2081-2100), the median increase in temperature in Southeast Asia will range from 0.8°C to 3.2°C and a moderate increase in precipitation of 1% to 8% is expected (IPCC, 2013).

Table 1.2. Annual temperature and precipitation projections in Southeast Asia by CMIP5 global models for the RCP4.5 scenario (adapted from IPCC, 2013).

		Temperature (°C)		**Precipitation (%)**	
Region	**Year**	**min**	**max**	**min**	**Max**
Southeast Asia (Land)	2035	0.3	1.2	-2	3
	2065	0.7	2.2	-1	7
	2100	0.8	2.7	-2	10
Southeast Asia (Sea)	2035	0.3	1.0	-4	3
	2065	0.6	1.9	-2	5
	2100	0.9	2.5	-3	6

In the future, the on-going emission of greenhouse gases will likely cause an increase in frequency, severity and magnitude of extreme climate-related events (IPCC, 2013), posing ever greater threats to the biodiversity in Southeast Asia. A slight increase in warming can have a significant impact on tropical species that have a narrow thermal-tolerance range than that of temperate species (Brodie et al., 2012). In Sundaland, 9-36% of lowland forest mammals are predicted to become extinct in the high emission scenario (Wilcove et al., 2013).

1.4 Impact of environmental changes on species distribution

Climate change has become an important threat to biodiversity. Evidence gathered from fossil records and a number of recent research studies have shown that changes in environmental conditions have both direct and indirect effects on species distributions and range sizes (Araújo et al., 2008; Bertin, 2008; Brodie et al., 2012; Ceballos, 2002; Dudei and Stigall, 2010; Fortelius et al., 2002; Thomas, 2010; Turvey et al., 2015). Direct impacts of climate changes include shifts in species geographic ranges, and the expansion and reduction of species range size, while indirect impacts on species distribution are, for example, phenological shifts, the introduction of non-native species into area, and the disruption of species interactions. Projections of future climate change are also expected to increase the vulnerability of species and continuously impact species distribution (Pearson and Dawson, 2003). Thus, an improved understanding of the possible consequences of such changes is key to alleviating adverse effects on biodiversity.

1.4.1 Geographic range shifts

Climate variables can act as range-limiting factors, determining species geographical range extent and spatial pattern (Hill and Preston, 2015). Meta-analyses of a wide range of floral and faunal species suggested that over the past decades, the majority of the species have shifted their distributions to track their desirable climate conditions in response to climate change (Hickling et al., 2006; Root et al., 2003; Thomas, 2010). In the face of recent warming, many taxonomic groups have moved to higher latitudes two to three times faster than previously documented (Chen et al., 2011). Bird species in the tropics were found to move up to higher elevations during the period that coincided with a period of climate change (Peh, 2007). However, such shifts in species distribution may also pose a threat to species persistence through range reduction or habitat fragmentation, leading to a decline in species population (Velásquez-Tibatá et al., 2013). Furthermore, new habitats, in which the species move into, may not be protected areas or there is a presence of competitor species (Araújo et al., 2011; Lovari et al., 2013). Endemic species are particularly sensitive to range reduction because their ranges are already small (Manne and Pimm, 2001). Hence, regions with high species endemism and severe habitat transformation, such as biodiversity hotspots, has been suggested to be especially vulnerable to climate change (Raxworthy et al., 2008).

1.4.2 Phenology

Phenology is the seasonal timing of key-life history events. It is a primary indicator of species response to climate change (Staudinger et al., 2019). Changes in climatic conditions have an important impact on ecological consequences, which are the advancements in the timing of seasonal activity or phenology of species, and the disruption of species interaction (Cohen et al., 2018; Yang and Rudolf, 2010). Phonological shifts can lead to species population reduction by altering the availability of resources and generating mismatches between species, e.g. plants and pollinators, plants and herbivores, and migrating birds and their preys (Cohen et al., 2018; Hegland et al., 2009; McKinney et al., 2012; McKinnon et al., 2012). Furthermore, the effect of climatic changes on environmental cues can determine species presence through processes such as migration and hatching (Yang and Rudolf, 2010). In seasonal environments, vertebrate species are found to time their reproduction to coincide with food availability in order to ensure the survival of offspring (McKinnon et al., 2012). Several bird species have expanded their breeding range and advanced their breeding dates in response to climate warming. Barnacle geese (*Branta leucopsis*) that migrate to their northern breeding sites, for example, have been found to make a shorter migration journey to breed in the south where it was previously used solely as a stop-over site (Both, 2010).

1.4.3 Extinction

Extreme climate events related to temperature and rainfall such as heat stress and droughts have affected mortality rates, which in turn result in changes in species distribution and the composition and structure of ecosystems (Allen et al., 2010). The expansion and establishment of non-native species in new habitats facilitated by climate change may have detrimental effects on native species and the community (Willis et al., 2010). The mountain pine beetle (*Dendroctonus ponderosae*), which is a native species to western North America, has increased pine tree mortality over extensive areas from Alaska to Northern Mexico, causing the forest to degrade and fail to serve as a carbon sink (Bentz et al., 2005; Mitton and Ferrenberg, 2012). Moreover, climate warming has led to local extinction of a widespread mountain plant (*Androsace septentrionalis*) in the Warming Meadow in the USA by reducing fecundity and survival across multiple life stages of the species (Panetta et al., 2018). Crucially, many animal species have been threatened by habitat loss and range contraction due to climate change. Species that fail to expand or are unable to expand to a new suitable habitat due to geographic barriers can be driven to extinction (Parmesan, 2006). Climate change has a significant impact on amphibian and reptile biodiversity because the distribution and ecology of these two animal groups are closely related to rainfall and temperature patterns (Bickford et al., 2010). The current change in climatic conditions has been found to occur at a faster pace than previous climate change events. These rapid changes are beyond the ability of species to adapt to or evolve to cope with (Bickford et al., 2010; IPCC, 2013). The geography of Southeast Asia, where a myriad of islands and mountains exist, may also prevent most herpetofauna from shifting to more favourable habitats. Therefore, biodiversity loss and extinction of these species from the region can be expected in the near future (Bickford et al., 2010).

1.5 Species distribution models (SDMs)

SDMS has become an increasingly common technique, having found applications in several studies that investigated the relationship between species occurrences and their environmental niches (Chatterjee et al., 2012; Klorvuttimontara et al., 2011; Kuemmerle et al., 2011; Thorn et al., 2009). SDMs can also be applied in many other ways to, for instance, predict the spread of invasive species (Thuiller et al., 2005), and distributions of unknown populations, facilitate the discovery of new species (Raxworthy et al., 2003), and investigate the mechanisms of speciation (Graham et al., 2004).

1.5.1 Concept of SDMs

The early work of species distribution modelling has started in the late 1970s, focusing on the development of methods to investigate the shape of species response to environmental gradients. However, rapid advancement in the field of SDMs has been made over the past two decades. SDMs have witnessed their applications in the examination of a broad set of conservation, ecological and evolutionary questions (Zimmermann et al., 2010). The model commonly estimates a relationship between environmental variables and known species occurrences to identify a set of environmental conditions in space, which can maintain species persistence (Pearson, 2010). The concept of SDMs has its foundations in ecological niche theory. In SDMs, the niche describes a species fitness in environmental space, a statistical method quantitatively describes environmental profile, and the resulting predicted map translates the environmental profile into some measure of suitability in a geographic space (Miller, 2010). Hutchinson (1957) defined the fundamental niche of a species as a suite of environmental conditions where species can survive and persist, while the realized niche is described as a subset of those conditions where species actually occupies as a result of biotic interactions (Miller, 2010). SDMs have been regarded to provide a spatial representation of the realised niche since they are based on an empirical relationship between observed species occurrences and environmental variables. SDMs correlate climatic variables with species presences, assuming that species current distributions represent the best indicator of species climatic requirements. However, observed species occurrences in reality are also limited by non-climatic variables such as dispersal and biotic interactions (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003).

1.5.2 Input data

SDMs requires two types of input data: biological data and environmental data. Biological data is the known species occurrences, while environmental data describes the landscape where species occur. Biological data can be either presence-only (e.g. records of localities where species have been observed) or presence/absence (e.g. records of species presences and absence at sampled localities). Many modelling approaches have been developed around these natures of species data (Pearson, 2010). However, the absence data on most species is usually unavailable, especially in tropical regions where species are often under-reported and poorly sampled (Phillips et al., 2006). It is considerably more difficult to collect the true absence data because it is rarer than the presence data and requires well-planned sampling schemes covering the entire study site (Soberon and Peterson, 2005). This limitation and the increased availability of presence-only records from herbarium and museum collections have also led to the advancement in developing methods for modelling presence-only data (Elith et al., 2006). Presence/absence data of species is used when areas of interest have been surveyed systematically (Elith et al., 2011; Pearson et al., 2007).

The most commonly used environmental data in SDMs are climatic (e.g. temperature and precipitation) and topographical (e.g. elevation and aspect). Several modelling algorithms can be used with both continuous and categorical data. Many environmental datasets are now available for modelling due to the advancement in remote sensing and GIS technologies. The availability of future climate scenarios has also facilitated the assessment of climate change potential impact on biodiversity (Miller, 2010; Pearson, 2010).

1.5.3 Modelling algorithms

A number of modelling algorithms and software packages have been developed to statistically identify relationships between species distribution and environmental predictors. The key main difference among modelling algorithms is types of input data (Table 1.3). Modelling methods of presence-only data can also be classified into three types: methods that solely rely on records of species presence, methods that use background environmental data, and methods that randomly draw pseudo-absences from the study area. The use of background environmental data aims to assess how the environment with known species presence correlates to the environment of the entire study area, whereas methods using pseudo-absence data aim to identify differences between localities of species occurrences and randomly selected localities used in place of real absence data (Pearson, 2010). The choice of modelling method has to be made carefully because it can result in significantly different predictions of species range and distribution. Moreover, it is suggested that the good performance of the methods are a result of the model ability to fit complex responses, often including interactions among variables, and the selection of an appropriate suite of variables (Elith et al., 2006; Pearson et al., 2006).

Table 1.3. Some published methods and software for species distribution modelling (Miller, 2010; Pearson, 2010).

Model/ Software	Algorithms	Species data types	Key references
BIOMAPPER	Ecological Niche Factor Analysis (ENFA)	presence and background	Hirzel et al. (2002)
BIOMOD	Multiple methods	presence and absence (or pseudo-absence)	Thuiller (2003)
DOMAIN	Gower Metric	presence-only	Carpenter et al. (1993)
GARP	Genetic algorithm (GA)	pseudo-absence	Stockwell (1999)
MAXENT	Maximum entropy	presence and background	Phillips et al. (2006)
Implemented in R	Regression: generalised linear model (GLM), generalised additive model (GAM), boosted regression trees (BRT), multivariate adaptive regression splines (MARS)	presence and absence (or pseudo-absence)	Elith et al. (2006); Elith and Leathwick (2007); Lehmann (2003)
OpenModeller	Multiple methods	depends on method implemented	de Souza Muñoz et al. (2011)
SPECIES	Artificial Neutral Network (ANN)	presence and absence (or pseudo-absence)	Pearson et al. (2002)

1.5.4 Model assessment

The accuracy of model predictions can be assessed by examining the ability of the models in predicting the actual observations. This is done by using the models with independent datasets ideally obtained by collection from different areas or from the surveys with different sampling strategies (Guisan and Zimmermann, 2000). However, a truly independent dataset is often unavailable. Thus, the modelling dataset (train or calibration data) can be partitioned to generate an independent dataset (test or evaluation data) for model evaluation. Various strategies have been used for partitioning data, including bootstrapping, k-fold cross-validation and jackknife. The Bootstrapping method involves iterative resampling a dataset with replacement. The k-fold cross-validation method splits data into k partitions. k-1 partitions are then used as a training dataset to fit the model, while the one left out partition is used for model evaluation. Jackknife or leave-one-out cross-validation is another form of k-fold cross-validation, in which k is the number of all observations. One observation is excluded from each model calibration and the operation is repeated for k times. The choice of data partitioning strategy often depends on the number of sample sizes (Guisan et al., 2017; Pearson, 2010).

Two main types of accuracy metrics are used to assess the model predictive performance: confusion matrix and receiver-operating characteristic (ROC). Confusion matrix is used to summarise the frequencies of the four possible types of predictions from the analysis of test data, including (a) true positive, (b) false positive, (c) false negative, and (d) true negative (Table 1.4) (Miller, 2010; Pearson, 2010). A number of statistical tests are employed to assess the model accuracy using these frequencies in the confusion matrix. The commonly used tests are, for example, Kappa (difference between prediction accuracy and chance agreement), sensitivity (proportion of observed present correctly predicted), specificity (proportion of observed absent correctly predicted), and True skill statistic (TSS) (Miller, 2010). However, since SDMs produce a result of continuous predictions, a threshold is used to convert continuous values to the binary prediction of present or absent (Table 1.5). A threshold of occurrence should be selected based on the type of species data and the objectives of the study (Liu et al., 2015; Pearson, 2010).

Table 1.4. Confusion matrix used to summarise the frequencies of the four types of prediction (Pearson, 2010).

	Observed present	**Observed absent**
Predicted present	(a) True positive	(b) False positive
Predicted absent	(c) False negative	(d) True negative

Table 1.5. Some published methods for setting thresholds of occurrences to convert the continuous prediction to the binary prediction (Pearson, 2010).

Method	**Description**	**Species data types**
Fixed value	An arbitrary fixed value (e.g. probability = 0.5)	Presence-only
Lowest predicted value	The lowest predicted value corresponding with an observed occurrence record	Presence-only
Fixed sensitivity	The threshold at which an arbitrary fixed sensitivity is reached (e.g. 0.95, meaning that 95% of observed localities will be included in the prediction)	Presence-only
Sensitivity-specificity equality	The threshold at which sensitivity and specificity are equal	Presence/absence
Sensitivity-specificity sum maximization	The sum of sensitivity and specificity is maximized	Presence/absence
Maximize Kappa	The threshold at which Cohen’s Kappa statistic is maximized	Presence/absence
Average probability/ suitability	The mean value across model output	Presence-only
Equal prevalence	Species’ prevalence (the proportion of presences relative to the number of sites) is maintained the same in the prediction as in the calibration data.	Presence/absence

However, the model assessment will be sensitive to the method used to select the threshold for continuous-to-binary prediction conversion. Hence, a statistical test that provides a single measure of model predictive performance across all possible thresholds is potentially useful. This can be achieved by using the Area Under the Receiver Operating Characteristic Curve (AUC). Also, the receiver-operating characteristic curve (ROC) is suggested to be threshold and prevalence-independent (Fielding and Bell, 1997; Manel et al., 2001). It is derived from plotting sensitivity against (1-specificity) across the range of available thresholds. Hence, the ROC curve indicates the relationship between the proportion of observed presences correctly predicted (sensitivity) and the proportion of observed absences incorrectly predicted (1-specificity). The AUC assesses how well the model can accurately distinguish sites at which a species is present and absent (Miller, 2010; Pearson, 2010). The AUC ranges from 0-1, in which the AUC score of 1 reflects the model ability in perfectly discriminating between the present and absent sites of species, while AUC < 0.5 indicates a model performance that is no better than random (Fielding and Bell, 1997; Swets, 1988).

1.6 The use of fossil record and museum collection

To better understand the impacts of climate change on species distribution, it is important to study the effects of past environmental changes on biodiversity. An understanding of responses of species in the past provides useful information for predictions of their potential reaction to future changes (Jablonski and Whitfort, 1999). The fossil record is a valuable source for studying the world's past and the history of life since data can be drawn about palaeoenvironmental conditions and species communities that occurred at specific geological times. For instance, the discovery of fossil *Pongo* teeth and other primate fossils at Lenggong Valley and Batu Caves, two cave sites in Peninsular Malaysia, provides evidence for the persistence of forest habitat in that region during the Pleistocene and indicates that environmental changes affecting Javan species at that period of time had not reached Peninsular Malaysia until 33 ka (Ibrahim et al., 2013). It is suggested that the conversion of forest to savannah habitat due to climate changes is also the cause of the local extinction of *Pongo* in Java during the Late Pleistocene (Storm et al., 2005). Furthermore, fossil records can be informative in helping estimate species distributions and the period of a species extinction in a specific region, as well as the determining factors contributing to species loss. *Gigantopithecus blacki* fossils discovered in South China, for example, suggest that the largest extinct primate species had a much wider distribution before it underwent major range contraction during the Middle Pleistocene and disappeared in the Late Pleistocene (Zhao and Zhang, 2013). Changes in the climate and the colonization of the genus *Homo* during the late Early Pleistocene are believed to have significantly impacted the habitat and diet of *G. blacki* (Zhao and Zhang, 2013).

Museum collections provide unique and invaluable information for research in many fields, including biodiversity and global climate change. They are an important source of baseline data for several regions in the world over a long time span (Shaffer et al., 1998; Suarez and Tsutsui, 2004). Examining museum specimens allows researchers to document the impact of past environmental changes on species biodiversity and provides valuable insight into species' potential response to future changes (McCarty, 2001; Suarez and Tsutsui, 2004). Records from museum collections have been used to investigate species range shifts for many plant and animal species. For example, occurrence records of gibbons across China in long-term archives indicate that at present, gibbons occupy smaller, more restricted distribution ranges compared with those in the past. The species were thought to have experienced a range contraction since the mid-eighteenth century and a severe population decline in the late nineteenth century (Chatterjee et al., 2012; Turvey et al., 2015). For some species, museum collections have provided evidence for habitat loss during the historical time. Specimens of small mammals from the six Illinois counties across Chicago suggest that the local extinction or the population decline of these species was caused by the loss of their prairie habitat in the region (Pergams and Nyberg, 2001). The impact of climate change on the species' biology in some cases can be illustrated by museum collections. By examining 3450 nest records of tree swallows (*Tachycineta bicolar*) from nest record cards in museums, universities and ornithological societies, Dunn and Winkler (1999) found that increased temperature was likely to have caused an advance in the egg-laying date of the species between 1959 and 1991. Furthermore, fossil and museum records are an important datasource that enables investigation of the underlying assumption of modern biogeography. It is suggested that environmental factors can determine specie distributions when species are likely to maintain ecological niches across evolutionary times (Wiens et al., 2010). Range shift may result from species movement to track niches in order to prevent its own extinction (Martínez-Meyer et al., 2004). Data on past species occurrences can be used to project modern distribution of species to be compared with the actual current distribution, which allows us to examine this principle of niche conservatism.

Although fossil records and data from museum collections may have many limitations, as some of them contain inaccurate or no geographical coordinates, and are biased towards specific areas, time periods and species (Newbold, 2010), using this data allows for the tracking of species responses across environmental conditions over a longer timescale. This can enhance the understanding of species range dynamics and vulnerability to environmental changes (Newbold, 2010; Turvey et al., 2015).

1.7 Thesis aims and objectives

Today's Southeast Asian biodiversity has survived the period of megafauna extinction, caused by the fluctuation in environmental conditions and early human impact (Louys et al., 2007). The study of current species distribution alone may then lead to a biased understanding of species' niche requirements and their adaptive ability. Past baseline data can be used to indicate where species occurred during the times when there was no or little anthropogenic pressure. The study in Chapter 3 of this thesis will include fossil and historical data to investigate how large mammals in Southeast Asia responded in their range shifts to past environmental changes and how their current distributions are likely to be affected by projected future changes.

Predictions of species responses to climate change generated by SDMs generally assume that species climatic niches will remain similar across time. However, the evaluation of model ability to predict potential distribution of species in the future is challenging because predicted events have not yet occurred. Several studies, therefore, have drawn on independent datasets to evaluate the predictive accuracy of models (Araújo et al., 2005; Martínez-Meyer et al., 2004; Newbold, 2010). In Chapter 4, fossil data will be used as independent datasets to forecast current species distribution and assess the predictive accuracy of modelling techniques used. Modern data of species occurrences will also be used to hindcast past distribution of species.

Another challenge in the study of species distribution in Southeast Asia is the lack of well-documented data. Not only are there insufficient studies and surveys of palaeo-records, but present-day records of fauna species are also variable in quality and often lack site-specific locality details. Species' geographic range maps, available from online databases such as the IUCN Red list website, have been increasingly used in macroecological research studies. However, this data type tends to be biased in its representation of the actual species distribution and may reduce the models' predictive accuracy of current species distributions and the reliability of projected distributions in the future. Hence, a further aim of this thesis in Chapter 5 is to determine how much model outputs vary, depending on types of input data. Models resulting from using point locality data collected from local sources and published works of literature will be compared with results derived from using IUCN polygon range maps. Variations from the incorporation of different future climate scenarios will also be examined.

Lastly, as faunal species shift their range in response to environmental changes, the conservation value of protected areas is also likely to change because the areas may no longer be suitable for the species. A case study in Chapter 6 will feature the current effectiveness of protected areas in Thailand in conserving biodiversity and how the conservation values may change in the future, with the employment of a zonation reserve-design software as the assessment tool. Additionally, high priority areas for conservation will also be identified.

In this thesis, Southeast Asia is defined as China, Myanmar, Thailand, Laos, Cambodia, Vietnam, Malaysia, Singapore, Brunei, Indonesia and the Philippines. I focus on large mammal species and fulfil the following aims by using compiled fossil, historical and present records of the species and SDM techniques for the analyses. The aims of this thesis are as follows:

1. To examine the impact of climate change on large mammal distributions in Southeast Asia across three different timescales; past (~120,000-140,000 years BP), present (AD 1945 to present) and future (2050).
2. To examine the predictive ability of SDM methods and test the hypothesis of niche conservatism.
3. To determine prediction discrepancies derived from different types of data.
4. To assess conservation values of currently-protected areas and how these would be likely to change under future climate scenarios, and to identify high priority areas for conservation in Thailand.

Chapter 2: Material and Methods

2.1 Species data

2.1.1 Data collection

Large mammals in this thesis were generally defined as any mammal species that are identifiable under typical field conditions following Dorst and Dandelot (1970). Species records were also compiled from published literature that justified any mammal species as large mammals. A database was then established from this species list. Species data required information that encompasses taxonomy, geo-referenced location, year of survey/age of fossil and datasource (Table 2.1). In this study, species records were obtained from published literatures, museum collections and online databases.

Volumes of published literature included historical archives, books, research articles, and reports published by local authorities and/or NGOs. Records from these literatures were extracted using the following inclusion criteria: scientific name of species, precise location of discovery, and time. Records were excluded if they were missing one or more of these categories. Museum collection records were obtained from four museums: The Natural History Museum (UK), the American Museum of Natural History (US), the Museum of Comparative Zoology (US), and the Smithsonian National Museum of Natural History (US), where species specimens with point locality and open access databases are freely available.

The Global Biodiversity Information Facility (GBIF) is one of the largest online databases, providing a platform for both researchers and the general public to share information of where and when all types of species have been recorded. As of April 2021, the GBIF contains over 1.6 billion of species occurrence records and at least 5,700 peer-reviewed publications have been generated using the species data from this site. A large number of species records in the GBIF are derived from a wide variety of sources, ranging from specimens deposited in museums, universities, institutions and botanic gardens to geotagged photos taken from smartphones and shared by amateur naturalists. The GBIF database also contains fossil occurrence data obtained from many groups of palaeontologists such as The Palaeobiology Database (PalaeoBioDB). Records in the GBIF have been accrued from 1,676 publishing institutions across the world (GBIF, 2021). Another important online database used in this study was the VertNet database. VertNet is a collaborative project funded by the

National Science Foundation (NSF) in the USA; It provides a tool for exploring and sharing biodiversity data. At present, the VertNet database consists of more than 21 million records from 125 publishers worldwide (VertNet, 2021).

Records of the species data in this study were compiled with the awareness that there are other potential datasources available for large mammal species. However, this study mainly focused on the sources or databases where species data have been recorded with geo-referenced location. Other databases where geo-referenced location data were not co-recorded with other types of species data, were excluded from the analyses of this study.

Table 2.1. A template for collecting species records and geo-referenced location.

Family	Genus	Species	Latitude	Longitude	Year	Source

2.1.2 Data cleaning

Data extracted from the above listed sources were amassed into an excel spreadsheet and each record was subjected to rigorous cleaning. Large mammal species records with an inaccuracy in geographic coordinates of more than 5,000 metres were excluded from the database in this study to standardise the resolution of environmental data and maps of the study areas. Records with anomalous geographic positions, for example, the coordinates of recent data that fall in the ocean where any terrestrial species are unlikely to be found, were also removed from the dataset. The GPS coordinates were then plotted onto the Southeast Asia map with 2.5 arc-minute resolution grid (~5 km), displaying the exact positions of the species in the study area. In order to prevent duplication and minimise recording error, each grid cell of the map containing species occurrence records was determined by the centre point coordinates. Only species with more than 10 of these centroid points were included in the analyses because previous studies have shown that useful models could be produced with as few as 10 species localities (Hernandez et al., 2006; Pearson et al., 2007; Stockwell and Peterson, 2002).

Species records were collected based on two-time intervals: fossil (Pleistocene ~120,000 – 140,000 years BP) and modern (AD 1945 - present). The total number of records after the data cleaning processes was 556 fossil and 6,939 modern points. There were records of 24 large mammal species from 12 families: Bovidae, Canidae, Cercopithecidae, Cervidae, Elephantidae, Felidae, Hominidae, Hylobatidae, Lorisidae, Suidae, Tapiridae and Ursidae. While the majority of fossil records belonged to the Suidae (94 out of 556 records), most of the modern records were from 5 bovid species (Table 2.2). In terms of collection volume, China holds the largest number of fossil records in the region (366/556 records, 65.8%) due to a long history in paleontology. Chinese people have started to collect mammalian fossils, which were known as dragon bones in the past, for 2,000 years for use in traditional medicine (Pei, 1957). On the other hand, about 95% of modern records were gathered from Thailand because of the accessibility to large mammal survey data in the country between 2004 and 2007.

Table 2.2. Large mammal species with presence locations of more than 10 points.

Family	Genus	Species	No. of presence points	
			Fossil[*]	Modern
Bovidae	*Bubalus*	*bubalis*	14	15
	Capricornis	*sumatraensis*	12	212
	Bos	*gaurus*	NA	1,187[**]
	Bos	*javanicus*	NA	142[**]
	Naemorhedus	*caudatus*	NA	36[**]
Canidae	*Cuon*	*alpinus*	26	124
	Canis	*aureus*	NA	512[**]
Cercopithecidae	*Macaca*	*mulatta*	49	81
	Macaca	*nemestrina*	14	46
	Trachypithecus	*cristatus*	NA	27[**]
	Trachypithecus	*phayrei*	NA	32[**]
Cervidae	*Muntiacus*	*muntjak*	34	796
	Rusa	*unicolor*	52	364
Elephantidae	*Elephas*	*maximus*	41	495
Felidae	*Panthera*	*pardus*	19	155
	Panthera	*tigris*	67	107
Hominidae	*Pongo*	*pygmaeus*	28	14
Hylobatidae	*Nomascus*	*concolor*	43	31
	Hylobates	*pileatus*	NA	16[**]
Lorisidae	*Nycticebus*	*pygmaeus*	NA	39[**]
Suidae	*Sus*	*scrofa*	94	1,316
Tapiridae	*Tapirus*	*indicus*	16	214
Ursidae	*Ursus*	*thibetanus*	47	273
	Helarctos	*malayanus*	NA	705[**]
	Total		**556**	**6,939**

[*] NA in fossil data indicates insufficient number of records for inclusion in the analyses.

[**] Number of occurrence points obtained at 30 arc-second resolution (~1 km) for the analyses only in Chapter 6.

2.1.3 Ecology of large mammal species

Bubalus bubalis is closely related to *Bubalus arnee*. Since 2003 the IUCN has considered *B. bubalis* as the domestic form of Asian water buffalo, while *B. arnee* is the wild form (Kaul et al., 2019). The genus Bubalus is suggested to have a wide distribution range across Europe and Asia during the Pleistocene (Cockrill, 1981). However, the dramatic changes in ecological and climatic conditions during the glacial periods are believed to have substantial effects on the distribution of the genus. There had been a decline in the population and range size when climates became drier and colder. The population then began to recover during the warm period of the Holocene post-glacial phase between 11 – 6 kyr BP in Southeast Asia and the Indian subcontinent (Kaul et al., 2019; Wang et al., 2017; Zhang et al., 2020). Domestication of each species from this genus has been estimated to independently occur 7 – 3 kyr BP, overlapping with the early development of rice cultivation and domestication (Wang et al., 2017). Today, *B. bubalis* is one of the important livestock species, primarily raised as a working animal and for the production of milk and meat. Asia is home to 97% of the global population, while the remaining 3% are found in Africa and South America (Zhang et al., 2020). Nevertheless, the rapid expansion of the domestic water buffalo population due to an increasing demand for agriculture production has put the wild form of the species under severe threat of losing genetic diversity. Competition and interbreeding with domestic and feral buffaloes have led to a decline in the wild species population and a fragmentation of the species habitat (Kaul et al., 2019; Scherf, 2000).

Capricornis sumatraensis is also known as mainland serow or Sumatran serow (Duckworth et al., 2008; Phan et al., 2020). It has been identified in fossil records from many Pleistocene sites across China and Southeast Asia, suggesting that the species had a wide distribution throughout the region from the Early Pleistocene to Late Pleistocene (Bacon et al., 2008; Bocherens, 2017; Tougard et al., 1998; Wattanapituksakul et al., 2018). Previous studies have shown that the serow was one of the mammal species that adapted to the changing climatic and environmental conditions during the Pleistocene by migrating southward when the sea level was low and the climates became cooler (Tougard, 2001). Nowadays, although the mainland serow occupies habitats across 11 countries, including China, Southeast Asia and the Himalayan region, the species population has been found to be highly fragmented and significantly in decline over the past three generations due to poaching, habitat loss and destruction throughout its entire distribution range (Phan et al., 2020).

Bos gaurus (gaur) is the largest extant species in the Bovidae family. Fossil records of *B. gaurus* found in many different sites across India and China were dated to the Pleistocene (Ahrestani, 2018). Historically, the species was widely distributed throughout mainland South and Southeast Asia (Ashokkumar et al., 2011). However, the species has become extinct in a few Asian countries such as Sri Lanka and possibly Bangladesh. Although gaur can tolerate some habitat disturbances, for example, hunting, rugged terrain and dense forest, hunting pressure in some parts of its distribution has been too strong for the population to sustain (Duckworth et al., 2016). *B. gaurus* is threatened by poaching for its horns and meat, disease and competition for food resources, which have led to a considerable decline of more than 80% in the global population over the past 100 years. The gaur populations are now restricted to fragmented habitat patches within protected areas (Ahrestani, 2018; Duckworth et al., 2016; Groves and Grubb, 2011).

Based on fossil evidence and ancient cave art from previous studies, *Bos javanicus*, also known as banteng, is believed to widely occupy habitats in Southern China (Yunnan), Northeast India, mainland Southeast Asia, peninsular Malaysia and the islands of Borneo, Java and Bali during times of lowered sea levels in the Pleistocene (Chazine, 2005; Gardner, et al., 2016). Nevertheless, banteng has been reported to experience a drastic decline in its ancestral distribution range and local extinctions. Even large parts of its range in the early 1990s are no longer occupied (Pedrono et al., 2009). There has been at least 50% reduction in the species population over the past 21 years (Gardner, et al., 2016). The species is now under a serious threat of becoming extinct in several Asian countries in the near future due to illegal hunting for commercial purposes and extensive habitat degradation caused by agriculture and wood plantation (Gardner, et al., 2016; Pedrono et al., 2009). The current global population of banteng is estimated to be 8,000 animals, more than 50% of which are in Eastern Cambodia (Gray et al., 2012).

Naemorhedus caudatus spp. griseus (Chinese goral) is a widespread species found to occur in China, India, Myanmar, Thailand and Vietnam. Even though little information is known about the global population of the species, it is believed that there has been an insignificant decrease over the past three generations, owing mainly to excessive hunting for its meat, fur and uses in traditional medicines (Duckworth et al., 2008). Fossil records of *Naemorhedus* have been reported in different sites in China and across many countries in Southeast Asia (Bacon et al., 2008; Colbert and Hooijer, 1953; Suraprasit et al., 2020; Tougard, 2001; Tougard et al., 1998; Wattanapituksakul et al., 2018). This suggests that *Naemorhedus* is one of the typical members of the

Southeast Asian mammal assemblages during the Early to Late Pleistocene (Suraprasit et al., 2020).

Cuon alpinus (dhole) was once widely distributed across South and East Asia. It occurred as far north as the southern parts of Russia (Kamler et al., 2015). The species is believed to be one of the large mammal species that were wiped out from its historical range during the Late Pleistocene mass extinction events *c.* 12,000 – 18,000 years BP (Iyengar et al., 2005). Although dhole is known to be capable of occupying a wide range of habitats, including mountainous alpine regions, open steppes, shrubland and dense forest, the present range of the species has been restricted to scattered areas due to habitat fragmentation, depletion of prey populations, and increased disturbance from human activities (Iyengar et al., 2005; Kamler et al., 2015). Approximately 25% of the dhole's historical range is currently occupied today. The total population of the species is estimated to be 4,500-10,500 individuals and most of the known subpopulations are relative small and have an extreme fluctuation in numbers (Kamler et al., 2015).

Canis aureus (golden jackal) is one of the most widespread canid species, commonly found throughout Africa, Europe and Asia. The species can cope with a wide variety of habitats and environmental conditions, including areas with human disturbance and presence (Moehlman and Hayssen, 2018). However, high population densities are often observed in habitats with abundant food resources and cover. Currently, there is no known threats causing a significant decline in the population of golden jackal (Hoffmann et al., 2018). The species distribution rage is found to gradually decline in some parts of its range, whereas the range expansion is reported in other areas. It is also suggested that increased warming due to climate changes is likely to allow further dispersal of the species (Arnold et al., 2012). Therefore, golden jackal is listed as Least Concern on the IUCN Red List of Threatened Species (Hoffmann et al., 2018). Fossil records of the species are controversial regarding their specific attribution. In North Africa, fossil remains identified as *C. aureus* were dated to the Upper Pleistocene (Moehlman and Hayssen, 2018).

Macaca mulatta (rhesus macaque) is classified by the IUCN as a Least Concern species because it has a large population and is commonly found throughout South, Southeast and East Asia (Singh et al., 2020). The species occurs in a wide range of habitats and appears to have an extremely diverse diet. It can tolerate high levels of disturbance and even coexist with human settlement. These highly adaptive abilities have been an important evolutionary strategy that causes rhesus monkey to be among the most widely distributed and successful primates in the world (Hasan et al., 2013). Although the species population is currently not threatened, human-primate conflict is a critical issue in many areas. The rhesus monkey is often found to cause damage to crop plants and a nuisance to people (Devi and Saikia, 2008; Hasan et al., 2013; Mazbah Uddin and Ahsan, 2018; Priston and McLennan, 2013). Historically, the species also had an extensive geographic range. Most fossil records of rhesus monkeys discovered in China were found to fall within the present range of the species. Some fossil remains dated to the Late Pleistocene to Holocene have been reported from as far north as North China (Tong, 2014).

Macaca nemestrina (Southern pig-tailed macaque) occurs in four Southeast Asian countries, including Brunei, Indonesia, Malaysia and Southern peninsular Thailand (Roos et al., 2014). Even though the pig-tailed macaque is found commonly in some parts of its range, the populations in many areas have experienced a drastic decline due to habitat loss and hunting for food and illegal pet trade. Extensive habitat fragmentation and degradation from the expansions of palm oil plantations, agriculture and loggings are major threats to the species' existence (Ang et al., 2020; Ruppert et al., 2018). Now, the macaque is believed to undergo a population reduction of more than 30% over the past three generations (~33 years). In addition, evidence from fossil records indicates that during the Holocene, the species populations were more abundant in some parts of its range compared to today (Ang et al., 2020).

Trachypithecus cristatus (silvery lutung/ silvered leaf monkey) is the most widely distributed species in the genus *Trachypithecus*. It occurs from mainland Southeast Asia to the Sunda region (Roos et al., 2008). Fossil remains of this genus dated to the Pleistocene have been reported in China, Vietnam, Laos, Thailand, and Indonesia. It is suggested that changes in sea levels due to glacial-interglacial cycles during the Pleistocene had led to the speciation of *Trachypithecus* (Roos et al., 2008). At present, little is still known about *T. cristatus*, but the total population is likely to decrease at a rate of more than 30% over the past three generations (~36 years) and a continued population decline is expected in the future (Meijaard and Nijman, 2020). This led to a reclassification of the species in 2020 from Near Threatened to Vulnerable in the IUCN category (Meijaard and Nijman, 2020; Nijman and Meijaard, 2008). Major threats of the silvery lutung are habitat loss, hunting for meat, uses in traditional medicines, and capture for pet trade. Habitats of the species are severely threatened by forest fires, logging and large scale land clearance for palm oil plantations (Harding, 2010; Meijaard and Nijman, 2020).

Trachypithecus phayrei (Phayre's leaf-monkey) is listed as one of Endangered species by the IUCN because it suffers from a global population decline by more than 50% over the past three generations (~36 years) (Bleisch et al., 2020). The species population in some parts of its range has been found to decrease by more than 80% over the last 20 years, causing it to be even more vulnerable in highly fragmented habitats (Bleisch et al., 2020; Molur et al., 2003). Habitat fragmentation and degradation due to human settlements and agricultural land expansion are major threats to the species (Molur et al., 2003). In the northern part of Thailand, the species has been nearly hunted out, indicating that illegal hunting for food, medicines and pet trade constitute important threats to the species. Phayre's leaf-monkey now occupies habitats in 7 Asian countries, including Bangladesh, China, India, Laos, Myanmar, Thailand and Vietnam (Bleisch et al., 2020). Despite being one of the most widespread member of the genus *Trachypithecus*, few studies have been conducted on the species' ecology, behaviour, genetics and systematics. A recent study based on mitogenome sequencing of the species supports the hypothesis for speciation of the four *Trachypithecus* species groups, which occurred at a similar time in the Early Pleistocene and were highly associated with changes in environmental conditions such as forest cover and sea level (Roos et al., 2020).

Muntiacus muntjak (Southern red muntjac) occurs commonly throughout parts of its distribution range in Brunei, Indonesia, Malaysia, Thailand and Vietnam (Beharrell and Ryder, 2004; Timmins et al., 2016). Evidence from fossil remains suggests that muntjac distribution during the Pleistocene was very similar to its current range. Many fossil records identified as the species have been collected from various sites in Malaysia, Indonesia, Vietnam and Thailand (Long et al., 1996; Wirkner and Hertler, 2019). Recent studies have shown that *M. muntjak* is one of the most common species that were frequently recorded during camera trap surveys (Kawanishi and Sunquist, 2004; Ngoprasert et al., 2007; Timmins et al., 2016). The Southern muntjac can tolerate high levels of disturbances. It was found to exist in a wide variety of habitats even in heavily degraded areas such as logged forests and plantation areas (Mohd-Azlan, 2006; Timmins et al., 2016). Even though the species is not threatened with extinction in the near future, it is widely hunted for meat and body parts across its range. Muntjac has been suggested to be among the most preferred wild meat choices in Southeast Asia (Kawanishi and Sunquist, 2004; Timmins et al., 2016).

Rusa unicolor (Sambar deer) occupies a wide range of habitats throughout South and Southeast Asia. It also occurs commonly across the Southern parts of China to Taiwan. In these recent years, sambar has been reported to experience a rapid decline in population, leading to its small population sizes and local extinctions in large parts of its distribution range. Despite being highly adaptive, the species currently occupies less than 50% of its historical range in the past century (Kawanishi et al., 2014). The sambar population is also found to be highly fragmented in most of its range. Predation and hunting are two major threats to the survival of the species. The sambar deer is a significant prey species for tigers across its global southern range. The species accounts for 30 – 50% of diet options for tigers (Andheria et al., 2007; Bagchi et al., 2003; Hayward et al., 2012; Timmins et al., 2015). Furthermore, overhunting of sambar observed in many parts of its range has put the species at high risk of local extinction (Kawanishi et al., 2014).

Elephas maximus (Asian elephant) is the only extant species of the genus *Elephas*. The species is believed to have diverged from the extinct elephant species since the Late Pleistocene. The Asian elephant occupied habitats ranging from the West of Indian subcontinent to Southeast Asia and China 6,000 years ago, but nowadays it has disappeared almost entirely from its historical range (Sukumar, 2006; Williams et al., 2020). Major threats to elephants include habitat loss and fragmentation, human-elephant conflict, and poaching for illegal trade. Changes in land cover across Asia due to rapid human population and economic growth have led to a reduction of suitable habitats for elephants (Sukumar, 2006). Human-elephant conflict arises from an overlap in spaces and has caused fatality and injury in both human and the animal every year. Apart from ivory, the elephant is poached for other products such as skin and meat. The elephant population is now restricted to fragmented habitats in 13 Asian countries, where 60% of the global population are in India (Sukumar, 2006; Williams et al., 2020).

Panthera pardus (leopard) is a highly adaptive species that can tolerate extremely harsh conditions, even in areas where other large carnivore species have been wiped out. It has a wide range of distribution from Africa to Asia, covering 8 million km^2. However, leopard has disappeared largely from its historical range and population of the species, suffered a dramatic fall in numbers and become isolated. It is estimated that suitable habitats for leopard have reduced by more than 30% over the past three generations of the species (~22.3 years) (Stein et al., 2020). The leopard is mainly threatened by anthropogenic activities and prey base depletion. The species is hunted for illegal wildlife trade of its skin and bones (Nowell, 2007). The density of leopards has been found to be associated with prey abundance. A decrease in prey abundance is likely to result in a reduced density of large carnivore species (Carbone et al., 2011).

Panthera tigris (tiger) was once widely distributed across Asia. However, the species has disappeared from large parts of Southwest, Central, Southeast and East Asia over the past 100 years. It is now found only in 7% of its historical range (Sanderson et al., 2006). A breeding range of the species has also been estimated to drastically decline by more than 50% during the past three generation (~21 years). The global tiger population is approximately 3,200 with estimates of less than 2,500 mature individuals. Hence, tiger is listed as Endangered by the IUCN (Goodrich et al., 2015). Poaching for illegal wildlife trade is an important factor that has driven the tiger to local extinction and threatened the survival of the species in many areas. Particularly in Southeast Asia, tigers have been heavily hunted for high value products, including their skin, bones and claws (Nowell, 2007). In addition, prey abundance is one of the key requirements for the tiger population to persist. The tiger primarily relies on large ungulates such as the gaur, the sambar and the chital but at least 40% of its prey species are currently threatened and undergoing a population decline (Wolf and Ripple, 2016).

Pongo pygmaeus (Bornean orangutan) is a critically endangered species, which is endemic to the island of Borneo in Indonesia (Kalimantan) and Malaysia (Sarawak and Sabah). It is one of large mammal species currently facing a drastic population decline. It has been suggested that the orangutan has likely experienced a loss of more than 80% of its population over a period of 75 years. Today, orangutan populations remain in highly scattered habitat patches across its distribution range (Ancrenaz et al., 2016). Without effective conservation actions, it is suggested that many populations of the species will disappear in the next 50 years (Abram et al., 2015). The two major threats of the species survival are habitat loss and hunting. The native forests of Borneo, the orangutan’s primary habitat, have been reported to reduce by 30% between 1973-2010 due to logging, forest fire and conversion to plantations (Gaveau et al., 2014). At this rate, it is predicted that more than 60% of orangutan habitat will disappear by 2025 (Ancrenaz et al., 2016). Furthermore, illegal hunting is found to contribute to 12% of the estimated species population decrease by 2025. The average number of orangutans killed in Kalimantan per year is between 1970 – 3100 (Ancrenaz et al., 2016; Meijaard et al., 2011).

Nomascus concolor (black crested gibbon) is found to occupy a discontinuous habitats in southwestern China, North-western Laos and Southern Vietnam. Based on fossil records, the distribution of the genus *Nomascus* is believed to be widely over a large area of Southern and Central China up to the Yellow River 1,000 years ago (Jablonski and Chaplin, 2009; Pengfei et al., 2020). Today, the black crested gibbon is listed as one of Critically Endangered species under the IUCN category because the population has been estimated to decline by more than 80% over the last three generations (45 years). The current population of the species is estimated at 2,000 individuals, most of which reside in China. The species subpopulations have been reported to be small and isolated (Jiang et al., 2006; Pengfei et al., 2020). Major threats of the black gibbon are habitat loss and hunting. The species is generally fastidious in its habitat choice, causing it to be very sensitive to habitat degradation and fragmentation. A previous study shows that deforestation in recent history has resulted in reduced and isolated populations (Jiang et al., 2006). Even though there is a local taboo against hunting or eating the black gibbon, the animal has been hunted for meat, illegal pet trade, and uses in traditional medicines (Pengfei et al., 2020; Rawson et al., 2011).

Hylobates pileatus (pileated gibbon) is a generalist species that can adapt to a variety of habitat types (Traeholt et al., 2005). The species occurs in parts of three Southeast Asian countries: Cambodia, Laos and Thailand. During 1970 – 2015 the pileated gibbon has been estimated to experience a severe decline by more than 50%, leading to a classification of the species in the Endangered category by the IUCN (Brockelman et al., 2020). Similar to other gibbon species, the pileated gibbon is mainly threatened by habitat loss and fragmentation, and hunting for pet trade. Fragmented habitats may facilitate human access to previously remote forested areas, resulting in an increase in hunting pressure (Traeholt et al., 2005). Although all populations of the pileated gibbon in Thailand inhabit areas within protected zones, land encroachment and hunting by exploiters of minor forest products are still a significant problem (Phoonjampa and Brockelman, 2008; Traeholt et al., 2005).

Nycticebus pygmaeus (pygmy slow loris) is a nocturnal primate species, found in parts of Cambodia, China, Laos and Vietnam. Previous studies indicate that the species is likely occur at low abundances throughout most of its distribution range (Nekaris et al., 2008; Starr et al., 2011). A dramatic reduction of the pygmy loris population is estimated to be more than 50% over the past three generations (24 years). Hence, it has been reclassified from Vulnerable to Endangered species by the IUCN since 2020 (Blair et al., 2020). The pygmy loris is severely threatened by illegal hunting throughout its range for pet trade and uses in traditional medicines. The animal has been found to be available for sale in traditional medicine stores and local markets (Blair et al., 2020; Starr et al., 2010). Its parts are believed to cure more than 100 diseases such as stomach problems, to heal wounds and broken bones, and to help regain strength after childbirth (Starr et al., 2010). Moreover, captive pygmy lorises are used as photo props or entertainment to attract tourists (Nekaris and Starr, 2015).

Sus scrofa (wild boar) has the widest distribution range of all pigs. It occurs in an extremely wide range of habitat types from North Africa to Western Europe, the Mediterranean basin to Eastern Russia and Japan, and throughout Southeast Asia (Keuling and Leus, 2019). The species is found abundantly across its range. Although wild boar population can become reduced where hunting pressure is high, the species has the highest reproductive rate among ungulates and is able to double its local density in one year (Massei and Genov, 2004). Little information is known about the trend and total population of the species. Currently, there are also no known major threats to the species at a global scale. However, the wild boar may be threatened locally from various factors such as habitat destruction, human-animal conflict, contagious diseases, and genetic contamination with domestic pigs (Keuling and Leus, 2019).

Tapirus indicus (Malay tapir) is believed to split from closely related tapir species during the Pleistocene ice ages (Brooks et al., 1997). Currently, it is found in Southern and Central Sumatra of Indonesia, the mainland of Peninsular Malaysia, Thailand and Myanmar. The Malay tapir was reported in Cambodia, China, Vietnam and Laos during the past 100 years but the populations in these four countries are suspected to have gone extinct (Brooks et al., 1997; Duckworth et al., 1999; Traeholt et al., 2016). The species is listed as Endangered by the IUCN because of the estimated population decline by more than 50% over the last three generations (36 years). A continuing decline by at least 20% is also expected in the next 24 years (Traeholt et al., 2016). Today, Malay tapir populations are extremely isolated in discontinuous and fragmented habitats. The species is threatened by habitat loss and deleterious effects of inbreeding. The rate of the species population decline has been found to be proportional to the loss of tropical rainforest cover in Southeast Asia due to deforestation and land conversion to plantations and human settlement at the same period (Brooks et al., 1997; Traeholt et al., 2016).

Ursus thibetanus (Asiatic black bear) distribution range has been restricted to Asia since historical time, even though fossil records of the species suggest that the black bear also occurred in Europe during the early Pliocene to Late Pleistocene (Fourvel et al., 2013; Garshelis and Steinmetz, 2020). Overall, the species population has been on a declining trend, with more than 30% decrease over the past 30 years. The most extreme population decline was reported to be more than 60% in

Bangladesh, where the species was also predicted to become extinct in the near future (Garshelis and Steinmetz, 2020; Islam et al., 2013). The Asiatic black bear has been hunted extensively, especially in China and Southeast Asia for bear bile and body parts to be used in traditional medicine and food. There has been a local belief that bear bile can reduce fever and inflammation, detoxify liver, arrest convulsions, improve eyesight and dissolve gall stones. In Vietnam, the number of bears killed and/or taken from the wild was suggested to be as high as 1,000 per year. Habitat loss and degradation is an additional threat to the species across its range (Garshelis and Steinmetz, 2020; Scotson, 2008).

Helarctos malayanus (sun bear) has been suggested to occupy a wider distribution range during the Pleistocene and historical time than it does today. Evidence from fossil records indicates that the species extended farther north than Yunnan in China, and Assam in India was a limit of its northwestern range. Nevertheless, the sun bear has undergone local extinctions in many areas and is now found to occur discontinuously across its former range (Scotson et al., 2017). The sun bear heavily relies on forested habitats; therefore, the highest deforestation rate of Southeast Asia among the tropics has led to the species population decline by approximately 35% over the past 30 years (Scotson et al., 2017; Sodhi et al., 2004). Furthermore, the sun bear is one of the most targeted bear species by poachers. It is exploited illegally for commercial pet trade, meat and traditional medicines (Burgess et al., 2014). Deforestation and habitat degradation together with hunting have been suggested to accelerate the rate of species population decline even more in the future (Scotson et al., 2017).

Additional information on habitat preferences and home ranges of large mammal species in this study is shown in Table 2.3. The variation in home range size depends on habitat types, time of the year and sex of the animals.

Table 2.3. Summary of species habitat preferences and home ranges

Species	**Current habitat preferences**	**Home range (km^2)**	**References**
Bubalus bubalis	Forest, savanna, grassland, wetlands (inland)	3 – 8	Choudhury, (2014); Kaul et al. (2019)
Capricornis sumatraensis	Forest, shrubland, grassland, rocky areas (e.g. inland cliffs, mountain peaks), artificial/ terrestrial	0.11 – 0.16	Cunningham (2011); Phan et al. (2020)
Bos gaurus	Forest, savanna, shrubland, grassland, artificial/ terrestrial	32 – 169	Duckworth et al. (2016); Sankar et al. (2013)
Bos javanicus	Forest, grassland	20 – 44	Gardner (2014); Gardner, et al. (2016)
Naemorhedus caudatus	Forest, shrubland, grassland, rocky areas (e.g. inland cliffs, mountain peaks)	0.58 – 1.03	Duckworth et al. (2008)
Cuon alpinus	Forest, shrubland, grassland	60 – 80	Kamler et al. (2015)
Canis aureus	Forest, savanna, shrubland, grassland, artificial/ terrestrial	9.2 – 20.5	Charaspet et al. (2019); Hoffmann et al. (2018)
Macaca mulatta	Forest, savanna, shrubland, artificial/ terrestrial	0.65 – 1.98	Timmins et al. (2008); Singh et al. (2020)
Macaca nemestrina	Forest, artificial/ terrestrial	1 – 3	Ang et al. (2020)
Trachypithecus cristatus	Forest, artificial/ terrestrial	0.20 – 0.43	Harding (2010); Meijaard and Nijman (2020)
Trachypithecus phayrei	Forest, savanna, artificial/ terrestrial	0.58 – 1.07	Bleisch et al. (2020); Carl (2009)
Muntiacus muntjak	Forest, artificial/ terrestrial	0.63 -1.68	McCullough et al. (2000); Timmins et al. (2016)

Rusa unicolor	Forest, savanna, shrubland, grassland, wetlands (inland), artificial/ terrestrial	2.4 – 42.8	Chatterjee et al. (2014); Timmins et al. (2015)
Elephas maximus	Forest, shrubland, grassland, artificial/ terrestrial	250 - 600	Alfred et al. (2012); Williams et al. (2020)
Panthera pardus	Forest, savanna, shrubland, grassland, rocky areas (e.g. inland cliffs, mountain peaks), desert	8.8 – 18.0	Grassman (1999); Stein et al. (2020)
Panthera tigris	Forest, shrubland, grassland	70 – 294	Goodrich et al. (2015); Simcharoen et al. (2014)
Pongo pygmaeus	Forest	9 – 40	Ancrenaz et al. (2016); Singleton and Schaik (2001)
Nomascus concolor	Forest	1.0 – 2.6	Fan and Jiang (2008); Pengfei et al. (2020)
Hylobates pileatus	Forest	0.3 – 1.0	Brockelman et al. (2020); Traeholt et al. (2005)
Nycticebus pygmaeus	Forest, artificial/ terrestrial	0.12 – 0.22	Blair et al. (2020); Starr et al. (2011)
Sus scrofa	Forest, savanna, shrubland, grassland, wetlands (inland), desert, artificial/ terrestrial, artificial/ aquatic and marine	5 – 20	Keuling and Leus (2019)
Tapirus indicus	Forest, grassland, wetlands (inland)	12.75	Brooks et al. (1997); Traeholt et al. (2016)
Ursus thibetanus	Forest, shrubland, grassland, wetlands (inland), artificial/ terrestrial	24 – 71	Garshelis and Steinmetz (2020); Hwang et al. (2010)
Helarctos malayanus	Forest, shrubland, artificial/ terrestrial	6.2 – 20.6	Scotson et al. (2017); Wong et al., (2004)

2.2 Environmental data

Large mammal species are suggested to face a high risk of extinction because several of their ecological traits have been associated with species vulnerability, including long generation times, low reproductive rates and large body size (Cardillo, 2005). Until recently, global climate change has become another important threat to biodiversity. Change in climatic conditions can modify many of the key life history traits and ecological factors which in turn determine species extinction risk (Isaac, 2009). There has been evidence that climatic changes have had a significant impact on the geographical range and distribution of large mammals (Chen et al., 2011; Davies et al., 2009; Hetem et al., 2014; Root et al., 2003). Many large mammal species in Southeast Asia are affected by changes in climatic conditions, in particular temperature and precipitation (Table 2.4). These climate variables directly and indirectly influence distribution ranges of the species. For example, the occurrence of Malay tapirs in Thailand was found to be positively associated with annual rainfall, whereas the three ungulate species, namely the gaur, the sambar and the red muntjac, were found in drier habitats (Lynam et al., 2012). Changes in environmental conditions may also have an indirect impact on large mammal distribution by influencing the seasonality and growth of food plants and altering biotic interaction. Climate change will likely lead to distribution range and prey overlaps in two leopard species, the common leopard and the snow leopard, resulting in an increase in species competition (Lovari et al., 2013). Hence, six climatic variables obtained from WorldClim were chosen for the analysis according to species ecological requirements or climatic variables that were used for distribution modelling of the species in previous studies (Table 2.5).

Table 2.4. Direct and indirect influence of climatic variables on large mammal distributions.

Species	Climatic predictors	Reference
Bubalus bubalis	Seasonal temperature	Kaul et al. (2019)
Capricornis sumatraensis	Seasonal temperature	Wu and Zhang, (2004)
Bos gaurus	Seasonal temperature, precipitation	Prayurasiddhi (1998)
Bos javanicus	Annual rainfall, annual mean temperature	Aulia Rahman (2020)
Naemorhedus caudatus	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)
Cuon alpinus	Annual precipitation	Jenks et al. (2012)
Canis aureus	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)
Macaca mulatta	Temperature, precipitation	Korstjens and Hillyer (2016)
Macaca nemestrina	Temperature, precipitation	Korstjens and Hillyer (2016)
Trachypithecus cristatus	Temperature, precipitation	Korstjens and Hillyer (2016)
Trachypithecus phayrei	Temperature, precipitation	Korstjens and Hillyer (2016)
Muntiacus muntjak	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)
Rusa unicolor	Annual rainfall, Rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)

Elephas maximus	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)
Panthera pardus	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)
Panthera tigris	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al., (2012)
Pongo pygmaeus	Mean annual temperature, monthly wet dry season rainfall	Gregory et al. (2012)
Nomascus concolor	Annual mean temperature, annual precipitation	Bryant et al. (2015)
Hylobates pileatus	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)
Nycticebus pygmaeus	Precipitation, temperature	Reinhardt et al. (2016)
Sus scrofa	Annual rainfall, rainfall in wettest quarter, rainfall in driest quarter, mean temperature	Trisurat et al. (2012)
Tapirus indicus	Annual rainfall	Lynam et al. (2012)
Ursus thibetanus	Annual temperature and precipitation	Escobar et al. (2015)
Helarctos malayanus	Temperature, precipitation	Scotson et al. (2017)

Table 2.5. WorldClim's climatic variables chosen for the analysis

Code	Environmental variable
BIO1	Annual Mean Temperature
BIO5	Maximum Temperature of Warmest Month
BIO6	Minimum Temperature of Coldest Month
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month

2.3 Species distribution modelling

Since species are facing a rapid change in environmental conditions, assessment of the impacts of various climate scenarios has become one of the focused areas of current macroecological research. A number of models have been proposed to provide a better understanding of the potential effects of these changes on species distributions in order to alleviate adverse effects on biodiversity. Species distribution models (SDMs) have been developed extensively over the past few decades and become a widely used technique in tackling the issue of climate change and biodiversity loss (Araújo et al., 2011, 2006; Chatterjee et al., 2012; Davis et al., 2014; Klorvuttimontara et al., 2011; Meier et al., 2012; Peterson, 2003; Thorn et al., 2009).

2.3.1 Target group background data (TG)

In order to model species distributions, additional data representing the range of the environmental variables in the study area is required. It is called background or pseudo-absence data. These data are usually obtained by randomly selecting points from the entire study region. However, occurrence records are often biased toward more accessible areas (Phillips et al., 2009). Here, our fossil records were also biased towards China, while modern records were clustered in Thailand. Many of fossil remains have been discovered and archived in China long before the development of palaeontology because there is a local belief in finding the dragon bones to use as medicament. The field of palaeontology in China has later been widely recognised by the public and grown rapidly over the past two decades (Zhou and Meng, 2014). Clustered records in Thailand were from the extensive surveys of large mammals throughout all protected areas in the country between 2004-2007. The spatial bias of data records can lead to environmental bias and potentially less accurate model predictions. Therefore, a novel background data, called target-group (TG) background data, has been proposed to cope with biased occurrence data (Phillips et al., 2009).

The TG approach is designed to obtain background data with the same bias as the presence data, so they have the same environmental bias. To illustrate, if occurrence data are only taken from easily accessed parts of the study area, then background data should be taken from the same sites (Ferrier et al., 2002; Phillips et al., 2009). The underlying assumption of this approach is that a model based on biased occurrences and background data with the same bias will focus on any differentiation between the distribution of the occurrences and that of the background, but will not focus on the sample selection bias. For example, if the species occupies specific habitats within the sampled area, the model will emphasise these habitats rather than areas that are more heavily sampled (Phillips et al., 2009). The TG approach has been found to improve model performances in the studies of various species and across geographic areas (Mateo et al., 2010a; Phillips et al., 2009; Ranc et al., 2017). TG can be estimated by using a combination of all occurrence records for a target group species that are collected or observed using the same methods. It has been suggested that when modelling species distribution using presence-only data, the selection of background data approach is as important as the selection of modelling method. (Phillips et al., 2009).

2.3.2 Modelling techniques

In this thesis, a total of 7 modelling techniques in two platforms (BIOMOD package in R and Maxent software) were used to identify impacts of climatic changes on large mammal distributions. They were chosen based on their frequency of usage in the study of species distributions and the promising ability to produce useful predictions. All the 7 models were implemented in the package 'BIOMOD' in R (Thuiller et al., 2009) only in Chapter 5 because large datasets used in this chapter could not be processed in the Maxent software. The Maxent software (Phillips et al., 2006) was used for the analyses of the remaining chapters due to small samples of some species in the study. Maxent have been found to produce useful predictions even with small sample sizes, as low as 5 records (Pearson et al., 2007). The Maxent software is also known to be practical and particularly intuitive (Merow et al., 2013). The 7 modelling techniques employed here included Surface Range Envelope (SRE, also known as Bioclim), Generalised Linear Model (GLM), Generalised Additive Model (GAM), Classification Tree Analysis (CTA, also referred as CART), Random Forest (RF), Multivariate Adaptive Regression Splines (MARS), and Maxent.

Surface Range Envelope (SRE)

SRE is equivalent to Bioclim, which is the most commonly used envelope modelling approach (Shabani et al., 2016). Bioclim has been designed to handle presence-only data. It correlates species known occurrences with climatic variables to define sets of environmental conditions within which a species can survive and maintain a viable population. However, this modelling technique is known to use the realised niche to characterise bioclimatic envelope because it focuses only on climatic variables and does not include other non-climatic predictors influencing the distribution of species such as biotic interactions and species dispersal (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003; Shabani et al., 2016). Hence, Bioclim and similar environmental envelope models sometimes refer to the climate profile of the species. The technique constructs a fitted, species-specific, minimal rectilinear envelope in a multidimensional climatic space bounded by the minimum and maximum values of all species occurrences (Boxcar) (Guisan and Zimmermann, 2000; Shabani et al., 2016).

Generalised Linear Model (GLM) and Generalised Additive Model (GAM)

GLM is a linear regression model, allowing the analysis of a response variable which can be non-linear to a single or a combination of environmental predictors (explanatory variables). A parametric link function in GLM used to find a relationship between the mean of the response and the explanatory variables allows (1) transformation to linearity, and (2) the predictions to be limited within the value range of the observed response variable; for example, 1/0 when using presence-absence survey data. GLM is a flexible and suitable model for the analysis of ecological relationships because the model can also handle non-normal structures of ecological data such as binomial and Poisson (Guisan et al., 2002; Guisan and Zimmermann, 2000; McCullagh and Nelder, 1989).

Alternative regression technique, GAM, is a non-parametric extension of GLM. This technique assumes that the functions are additive, and the components are smooth. GAM applies smoothers to each explanatory predictor and additively calculates the mean of the response variable, which allows more flexibility in the modelling processes. The model can handle highly non-linear and non-monotonic relationships between the response and the combination of explanatory variables. GAM is data- rather than model-driven because the form of the relationship of variables are determined by data rather than assuming some type of parametric relationship (Guisan et al., 2002; Guisan and Zimmermann, 2000; Yee and Mitchell, 1991).

Multivariate Adaptive Regression Splines (MARS)

MARS is a promising modelling approach, suggested to be suitable for high dimensional problems, for instance, a large number of inputs (Hastie et al., 2009). It is used to generate a local model in which relationships between response and explanatory variables are either linear or non-linear by using a combination of linear regression, mathematical construction of spline and binary recursive partitioning (Heikkinen et al., 2006). The technique builds multiple linear regression models fitting each partitioned group of the predictor variables (spline). The splines are connected to form piece-wise regression, known as basic functions. The points connected between regression lines are called knots, marking the end of one region of data and the beginning of another with different natures of the function (Mateo et al., 2010b; Zhang and Goh, 2016). The number and the location of the required knots are searched by using a forward/backward stepwise way: firstly, overfitting the models to produce more knots than needed, and then removing knots that contribute the least to the overall model efficiency (Mateo et al., 2010b; Prasad et al., 2006).

Classification Tree Analysis (CTA)

CTA is also referred to as classification and regression trees (CART). It uses recursive partitioning to split the data into increasingly homogenous subsets of response, such as presence or absence, according to their relationship to a set of environmental variables (explanatory predictors) (Heikkinen et al., 2006; Thuiller et al., 2003). The advantages of CTA include the ability to handle both numerical and categorical variables, and to provide insights into complex interactions and hierarchical relationships between species and predictors, which can then lead to the identification of variables with the greatest influence on species presence. CTA is one of the few modelling techniques that can model interactive effects of two or more variables (Heikkinen et al., 2006; Prasad et al., 2006; Thuiller et al., 2003). However, this technique has a high tendency of overfitting, since it is prone to overfit in three directions: searching for best predictors, for best split, and repeating for multiple times (Araújo et al., 2005).

Random Forest (RF)

RF is one of the most accurate classification or regression tree-based models, designed to generate predictions that do not overfit data (Breiman, 2001). In RF, multiple decision trees are constructed by using bootstrap aggregation (bagging) to select subsamples from the original dataset of predictor and response. When the trees are fully grown to maximum size without pruning, the predictions are produced by averaging all decision trees or using the majority vote from each tree in the case of classification model. Typically, about one third of data will not be selected by the algorithm; this is called out-of-bag samples. It is then used to evaluate model performance by determining variable importance and error rates (Breiman, 2001; Cutler et al., 2007; Prasad et al., 2006; Shabani et al., 2016).

Maxent

Maximum entropy model (Maxent) is a general-purpose machine learning method that estimates a target probability distribution across a geographic area from incomplete information (Phillips et al., 2006). The model aims to find the probability distribution of maximum entropy (i.e. closest to uniform) subject to constraints that are the inferences from available information such as environmental variables and species occurrence records of the target distribution (Pearson et al., 2007; Phillips et al., 2006). It is not only the mathematical formulation underlying Maxent that is clearly defined and simple; there are also many advantages that render Maxent suitable for modelling species distributions, including: (1) it can be applied for either presence-only or presence/absence datasets with both continuous and categorical variables at all scales; (2) there is a feature to avoid overfitting; (3) continuous model output allows great flexibility in manipulating and interpreting predictions; and (4) a currently active research area in machine learning and statistics for maximum entropy modelling can contribute to knowledge and advancement of the software (Phillips et al., 2006).

2.3.3 Modelling methods

Maxent version 3.4 (available at https://biodiversityinformatics.amnh.org/open_source/maxent/) was used to generate the probability range map of species occurrence in relation to 6 climatic variables. All species were simply assumed to require the same niches across time to facilitate the analysis of changes in the spatiotemporal distribution of the species.

BIOMOD (Biodiversity modelling) provides a platform to perform ensemble forecasting of species distributions (Thuiller et al., 2009). It currently includes 11 modelling approaches and can work with both presence/absence and presence-only data (Thuiller et al., 2019). BIOMOD overcomes several limitations of each modelling approach by allowing greater flexibility in data manipulation and model evaluation; it is also implemented in freeware (Thuiller et al., 2009). The application of multiple models combined with an ensemble forecasting framework has been introduced to improve the robustness of model predictions (Araujo and New, 2007). The Biomod2 package in R was implemented to determine the current species distribution by using a combination of 7 modelling methods.

Chapter 3: Investigating the impact of environmental changes on large mammal distributions in Southeast Asia: Past, Present and Future

3.1 Abstract

1) The study of species responses to climate change is needed for planning effective conservation action in Southeast Asia, where high species richness is coupled with endemism. However, the biodiversity in the region has experienced environmental fluctuations with the passage of time. Investigating the impact of climate change only on current species distribution may lead to a biased understanding of species responses to environmental changes. Therefore, examining changes in the patterns and rates of species range shifts across time may provide a better understanding of the dynamics of species distribution.

2) Species records of large mammals across Southeast Asia were compiled from published literature, museum collections and online databases based on two time intervals: fossil (Pleistocene ~120,000 – 140,000 years BP) and modern (AD 1945 to the present). In total, there were 15 species that had sufficient fossil and modern records (>10 localities) for distribution modelling.

3) Maxent was used to model species potential distributions in relation to six climatic variables for the last interglacial, current and future climate conditions (RCP2.6 and RCP8.5). Project species distributions were then used to measure species richness and calculate the rate of species range shifts at each time interval.

4) Currently, the mean species richness decreased from 4.14 species per grid cell during the last interglacial to 2.46, and SDMs suggested that it would continue to decline to 2.41 in the future under RCP8.5. The rate of species range shifts was predicted to be approximately 33 – 105 times higher than the estimated rate for the past period depending on the future climate scenario.

5) Large mammals respond to climate change in an individualistic manner, suggesting that SDMs should be conducted for all threatened species. The predictions of increased rates of range shifts indicated that these species are vulnerable to warming climate due to their ecological characteristics and should be prioritised for conservation.

3.2 Introduction

3.2.1 Environmental conditions and biogeography of Southeast Asia

Extensive areas in Southeast Asia particularly have high levels of mammal species richness and endemism due to complex geological activities in the region (Myers et al., 2000; Schipper et al., 2008). The region has undergone considerable environmental changes over time, affecting the dispersal and distribution of flora and fauna (Chatterjee, 2016). The environmental conditions of Southeast Asia during the Pleistocene were largely influenced by glacial periodicity. Continuous cycles of glaciation and deglaciation caused variations in the region’s temperature, sea level and the extent of exposed land (Chatterjee, 2009). The periods of glaciation lowered sea level by 160 m during the middle Pleistocene and 120 m during the last glacial maximum (~20,000 years ago), allowing the connection between mainland Southeast Asia and the islands of Sumatra, Borneo and Java (Bird et al., 2005; Heaney, 1991). The expansion of glaciers also caused a reduction in temperature from about 2-6 °C below the present level (Heaney, 1991). During the late Pleistocene, the region was likely to experience increased seasonality, but the pattern of rainfall was varied depending on the location. These climate variables led to changes in the vegetation type and extent (Bird et al., 2005; Heaney, 1991). Evidence from fossil pollen records indicated the sensitivity of vegetation to environmental changes. It showed that during a period of lowered sea level, there had been an expansion of seasonal forests and savannah vegetation but a decrease in the extent of tropical rainforests in Southeast Asia (Heaney, 1991). The formation of land bridges and extent of rainforests subsequently affected species distribution and richness (Hassel-Finnegan et al., 2013).

At the present, Southeast Asia has experienced high human population density, with China alone holding nearly 20% of the global population (UN, 2017). Rapid population growth rates and economic development over the past four decades have led to dramatic habitat changes and ecological degradation, which in turn has resulted in extinctions and extirpations of many species in the region (Chatterjee et al., 2012; Gibson et al., 2013; Turvey et al., 2010; Zhang, 2000). Furthermore, humans have had a major influence on global warming since the mid-20th century by increasing greenhouse gas concentrations in the atmosphere (IPCC, 2013). The projected rate of climate change by the end of the 21st century is likely to exceed the average rates experienced during the past 10,000 years (IPCC, 2013). Today, the mean annual temperature and precipitation of Southeast Asia are higher than during the last interglacial by 1.4 °C and 3.5 mm, respectively. These environmental variables are the driving factor for changes in species distribution and range size. Numerous taxa have already exhibited significant spatial range shifts in response to on-going climate changes (Chen et al., 2011; Parmesan, 2006; Parmesan and Yohe, 2003).

3.2.2 The use of fossil records in the study of species distribution

Despite a highly dynamic environment during the Pleistocene, the megafaunal extinction in Southeast Asia was less severe compared to other parts of the world. The total number of large-bodied mammal genera that became extinct throughout the Pleistocene in Southeast Asia was equivalent to the extinctions only during the late Quaternary in North America (Louys, 2012). However, many extant species that persisted so well in the region over the past 1,000,000 years have now become threatened (Bleisch et al., 2008; Goodrich et al., 2015; Kamler et al., 2015; Stein et al., 2016; Traeholt et al., 2014). Hence, the study of the effects of the current climate change on species distribution alone may lead to a biased understanding of species responses to environmental changes.

Past baseline data such as fossil records can be used to indicate the presence of species during the times when there was no or little anthropogenic pressure. Fossil records are a valuable datasource that can provide useful information for the study of spatial and temporal changes in species distribution (Chatterjee, 2016). Evidence from fossil records indicated that the gibbon distributions in China have changed considerably since the Plio-Pleistocene. The species have disappeared from large parts of their historical ranges and are now restricted to narrow geographical ranges in the south-western part of the country (Chatterjee et al., 2012). Understanding these species responses to past climate changes has significant implications for conservation planning. It can improve our understanding of species' current range shifts and how they are likely to respond to future environmental changes (Chatterjee, 2016; Woodruff, 2010). Furthermore, examining changes in species distribution across time can yield insights into palaeoecological processes and macroevolutionary phenomena (Myers et al., 2015).

3.2.3 The dynamics of species distribution and range shifts

Environmental conditions are known to affect species geographical distributions and ranges. Range size and dynamic changes at the boundary of distributions reflect the tolerances of species to environmental factors (Brown et al., 1996). In the face of climate change, if species cannot adapt to new conditions to remain in their habitats, they may be forced to shift distributional ranges to where the climatic factors are within their limits (Hetem et al., 2014). Species extirpation and extinction may occur when a species fails to adapt or move to new locations. It may also indicate that species range shifts lag behind the velocity of climate change (Hetem et al., 2014; Williams and Blois, 2018). Temperature and precipitation have been found to contribute to species distribution across taxa by determining species distributions and patterns of range shifts (Hoegh-Guldberg and Bruno, 2010; Manel et al., 2012; Zhao et al., 2018). The processes and patterns of species tracking their favourable climatic conditions can provide the underlying background knowledge necessary to understand the dynamics of species distributions and range limits with implications for biodiversity conservation.

3.2.4 Effects of temperature and precipitation on species distributions

Changes in temperature and precipitation influence the biogeography of flora and fauna species. Many studies have shown that climate warming can result in shifts in species distributions and ranges (Hickling et al., 2006; Mason et al., 2015; Parmesan et al., 1999; Thomas, 2010; VanDerWal et al., 2013). Temperature plays a crucial role as a factor determining the extent and location of species range margins (Mason et al., 2015). In animals, an increase in temperature has a direct impact on the fundamental physiological functions of species such as locomotion, growth and reproduction (Deutsch et al., 2008). It was reported that the increased mean annual temperature of 0.21 °C per decade has caused 13 taxonomic groups in the UK to shift northwards by 23 km (Mason et al., 2015). Tropical species are even more vulnerable to temperature change compared to temperate species due to their narrow thermal tolerance. Currently, species in the tropics are likely to live close to the limit of their optimal temperature. Hence, tropical regions are predicted to confront the greatest risk of species loss (Deutsch et al., 2008).

Changes in precipitation may have direct and indirect impacts on species distribution. Extreme precipitation events such as flood and drought can also affect species phenology, survival rates and plant productivity, which in turn affect species distribution, richness and diversity (Bickford et al., 2010; Butt et al., 2015; Wang et al., 2013). In Asia, primate species richness has been positively associated with the mean annual rainfall (Wang et al., 2013). Reduced precipitation has resulted in a decrease in breeding cues and available breeding sites of amphibians in Southeast Asia (Bickford et al., 2010). Furthermore, precipitation may indirectly affect species through its influence on resource availability (Araújo et al., 2006).

3.2.5 Species distribution modelling (SDM)

The understanding of the relationship between species occurrences and the environmental variables at specific locations is important to biodiversity conservation. In order to prevent biodiversity loss, it is necessary to have prior knowledge of how species may respond to changing environments. Species distribution modelling (SDM) has been developed rapidly over the past few decades to inform conservation planning and management. It can be used to determine shifts in the spatial distribution of species in response to changes in environmental conditions. Among various modelling techniques, Maxent has become commonly used in macroecological studies for many groups of species across habitat types (Gouveia et al., 2016; Klorvuttimontara et al., 2011; Kuemmerle et al., 2011; Sesink Clee et al., 2015; Stigall, 2012a; Trisurat et al., 2012). As a powerful tool for explaining and predicting complex ecological processes and patterns, the Maxent model has a number of advantages over other traditional modelling methods (Olden et al., 2008; Phillips et al., 2006). One important advantage is the ability to implement models with a small number of species records (Pearson et al., 2007), which is beneficial particularly for poorly sampled areas in the tropics where species occurrences of various taxa are scarce.

3.2.6 Chapter aims and objectives

1. To examine the impacts of climate change on large mammal species richness across Southeast Asia over time: past (~120,000-140,000 years BP), present (AD 1945 to present) and future (2050).
2. To investigate the effects of climate change on the spatiotemporal patterns of species distribution and range size.
3. To compare rates of species range shifts across time and evaluate the risk of species extinction.

3.3 Materials and methods

3.3.1 Input data

A database of 15 large mammal species was amassed comprising a total of 556 fossil and 4,243 modern records (Table 3.1). Point locality data for each species across Southeast Asia were compiled from published literature, museum collections and online databases (see Appendix 1). Data were collected based on two time intervals: fossil (Pleistocene ~120,000 – 140,000 years BP) and modern (AD 1945 to the present). Species records with no GPS coordinates or coordinate uncertainty of more than 5,000 metres were excluded from the analyses. Point locality data for fossil distributions tended to be biased towards China because the field of palaeontology has been very active in this region. Modern records were clustered in Thailand because there were extensive surveys for large mammals throughout the country between 2004 and 2007 (Figure 3.1). However, modern data were relatively scarce in other countries despite several resources including GBIF, one of the largest databases for biodiversity data. Extremely high hunting pressure in the region may prevent local authorities from sharing information with open-access platforms.

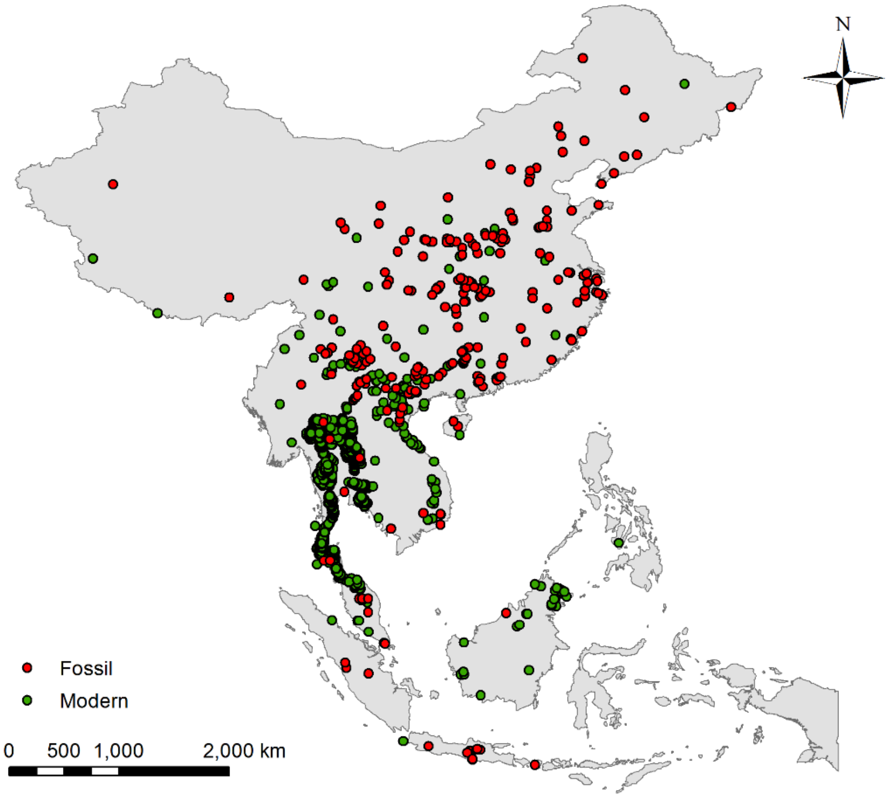


Figure 3.1. Map of the study areas showing the geographical distribution of fossil and modern records**.**

Table 3.1. Large mammal records used in the analyses.

Species	Common name	IUCN status[1]	No. of presence	
			Fossil	**Modern**
Bubalus bubalis	Asian water buffalo	EN	14	15
Capricornis sumatraensis	Sumatran serow	VU	12	212
Cuon alpinus	Dhole	EN	26	124
Elephas maximus	Asian elephant	EN	41	495
Macaca mulatta	Rhesus macaque	LC	49	81
Macaca nemestrina	Pig-tailed macaque	VU	14	46
Muntiacus muntjak	Barking deer	LC	34	796
Nomascus concolor	Black crested gibbon	CR	43	31
Panthera pardus	Leopard	VU	19	155
Panthera tigris	Tiger	EN	67	107
Pongo pygmaeus	Bornean orangutan	CR	28	14
Rusa unicolor	Sambar deer	VU	52	364
Sus scrofa	Wild pig	LC	94	1316
Tapirus indicus	Malayan tapir	EN	16	214
Ursus thibethanus	Asiatic black bear	VU	47	273

[1] IUCN status categories: EN, Endangered; VU, Vulnerable; LC, Least Concern.

After removing species records with inaccurate GPS coordinates, only species with more than 10 observations were accepted for inclusion in the analyses (Stockwell and Peterson, 2002). In addition to species occurrence data, pseudo-absence or background data, which are point data representing a range of environmental conditions in the study area, were required for modelling species distribution. Commonly, these points are randomly chosen from the entire study area. However, our species occurrences that were likely to be spatially biased toward China and Thailand, may lead to environmental bias and result in a less accurate prediction of species distributions (Phillips et al., 2009). A novel approach of using a target-group background has been proposed to improve model performance with biased data. The target-group background is background data with a similar bias to species occurrences (Phillips et al., 2009). In this study, the target-group background, which was comprised of all occurrence data at each time interval, was used for modelling. Full details on data collection and processing have been described previously in Chapter 2.

3.3.2 Environmental variables

Temperature and precipitation are thought to be significant factors influencing the distributions of tropical species. Therefore, in this study, we focused on climatic variables including mean, maximum and minimum values of annual temperature and precipitation (Table 3.2). Six climatic variables used in the analyses were WorldClim version 1.4 (available for download at http://worldclim.org/version1) at the 2.5 arc-minute resolution (~5 km). This spatial resolution was used to optimise processing time for modelling over the large geographical extent of the study area. The past environmental data for the last interglacial (LIG; ~120,000-140,000 years BP), which were originally available at the 30 arc-second resolution, were resampled to 2.5 arc-minutes by using the ArcGIS software (version 10.3). The current climate data were from the 1961-1990 period. Future climatic variables for 2050 included the average for 2041-2060. Two future scenarios (RCP2.6 and RCP8.5) derived from an average of all General Circulation Models (GCMs) were a focus here to account for some variations in species response to climate change (Beaumont et al., 2008). The RCP2.6 and RCP8.5 scenarios were considered as 'mild' and 'extreme' climate changes. RCP2.6 is a low emission scenario, which is expected to result from strong mitigation efforts to reduce greenhouse gas emission by the end of 21st century, whereas RCP8.5 is known as a business-as-usual scenario, predicting high greenhouse gas emission under high population growth and no climate policy (van Vuuren et al., 2011, 2007). In the next 30 years, the annual mean temperature across Southeast Asia is estimated to increase by approximately 1.8 and 4.7 °C, and the annual mean precipitation is likely to increase by 3.3 and 19.8 mm under RCP2.6 and RCP8.5, respectively.

Table 3.2. Environmental variables included in the models for the analyses.

Code	Environmental variable
BIO1	Annual Mean Temperature
BIO5	Maximum Temperature of Warmest Month
BIO6	Minimum Temperature of Coldest Month
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month

3.3.3 Modelling the spatiotemporal distribution of large mammals using Maxent

Maxent version 3.4 (available at https://biodiversityinformatics.amnh.org/open_source/maxent/) was used to generate the probability range map of species occurrence in relation to 6 climatic variables at three time intervals (last interglacial, current and future). All species were simply assumed to require the same niches across time to facilitate the analysis of changes in the spatiotemporal distribution of the species. For each large mammal species, the Maxent model was repeated 10 times with a cross-validation technique to make use of all species records and find the average probability of species occurrences. A minimum of 10 replicates has been recommended for many SDM approaches, including regression, classification, and machine-learning, in order to yield the best model predictive accuracy (Barbet-Massin et al., 2012).

Average probability maps of species occurrences were converted into binary maps of ‘suitable’ and ‘not suitable’ habitats for the species based on threshold values. A threshold approach used in this study was the maximising of the sum of sensitivity and specificity (maxSSS). MaxSSS threshold was suggested to be an appropriate approach when only presence data are available because it has produced similar threshold values when using either presence/absence or presence-only data (Liu et al., 2013). Grid cells with the probability of species occurrence less than the threshold value were classified as unsuitable habitats for the species or absence. Those cells with the probability equal to or greater than the threshold were classified as suitable habitats or presence. Habitat suitability maps of the species across time intervals were compared to investigate the impact of climatic changes on species distribution and examine the potential areas that may be suitable for the focal species in the future. Maps of species richness over three time intervals were built by overlaying distributional range maps of 15 large mammal species.

3.3.4 Calculating range shifts

Shifts in the centre point of a predicted suitable distribution area were used to determine the rate of range shifts for each species between time periods. After reclassification of the projected distribution to suitable and unsuitable habitats, we determined the centroid of the predicted suitable habitat for each species at each time interval using the “Calculate Geometry” tool in ArcMap (version 10.3). The shift distance in each adjacent time period (120,000 – 140,000 years BP and AD 1945 – 2050) was estimated as the geodesic distance between the centroids using the “Near” tool, i.e. distance between the centroids of projected Quaternary and current distributions. The shift distance was then divided by the elapsed time between adjacent time intervals to calculate rates of species range shifts.

3.4 Results

3.4.1 Occurrence records and species richness

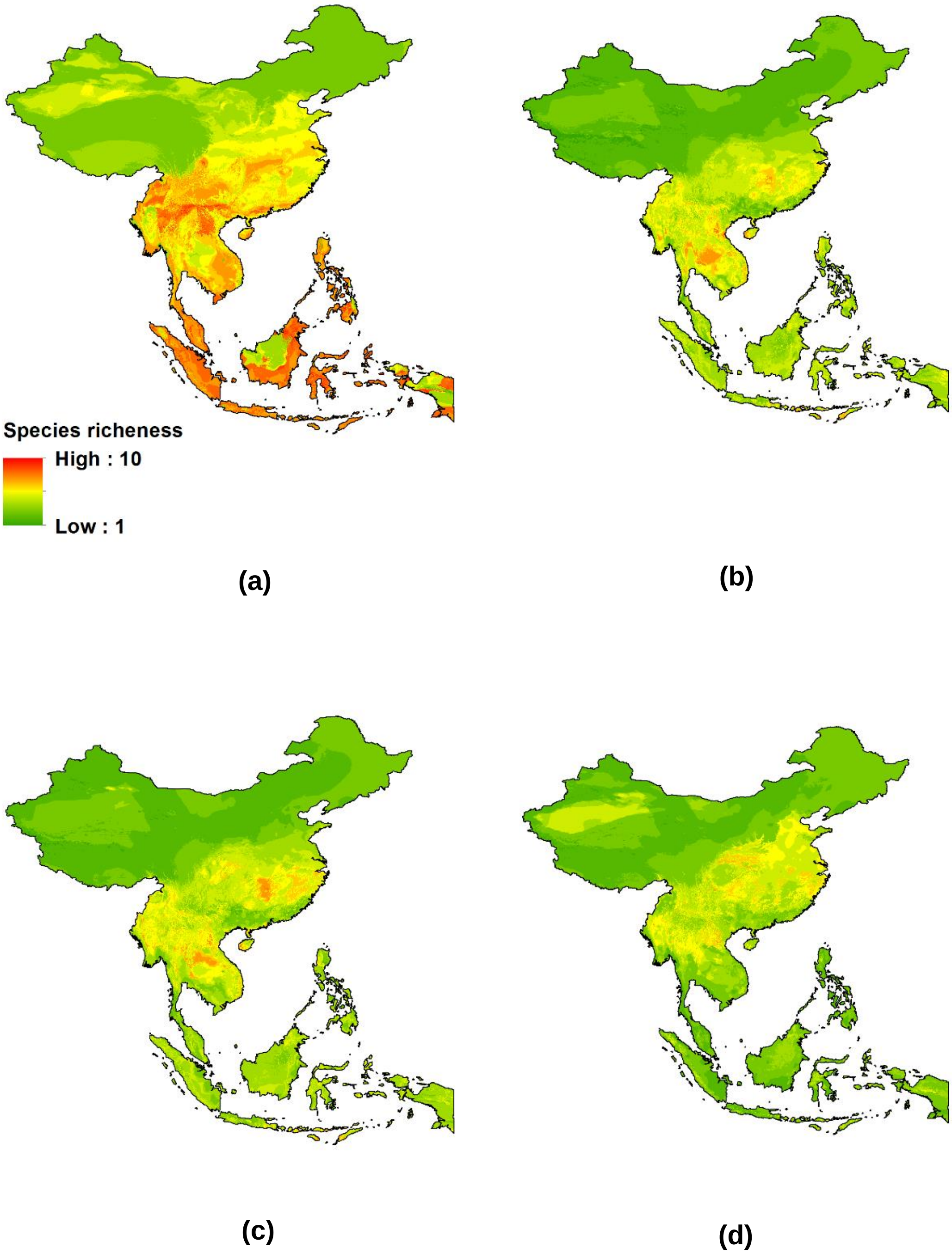
Sus scrofa (wild pig) was the most common species found in both time intervals. Its occurrence records accounted for approximately 17% and 31% of the total species records in the fossil and modern periods, respectively. The wild pig is a terrestrial mammal that has the largest geographic distribution. Its dispersal has been facilitated to all over the continent by humans (Oliver and Leus, 2008). In contrast, *Bubalus bubalis* (water buffalo) is a species that is rarely encountered. Records of this species were relatively low for all periods of time, potentially showing its rarity in the region. The confusion over scientific nomenclature of the species may be another possible reason for the small number of records. Linnaeus originally described the species and named it as *Bos bubalis* in 1758 but Kerr introduced the scientific name *Bos arnee* in 1792 (Choudhury, 2014). The International Commission on Zoological Nomenclature recently accepted the species name as *Bubalus arnee* in 2003, leading the IUCN to reconsider the wild forms of water buffalo as *B. arnee*, while *B. bubalis* has been suggested to be the domestic form of the species (Kaul et al., 2019).

Overall, the mean species richness of large mammals across Southeast Asia was found to decrease from the last interglacial and a continuous decline was predicted under the RCP8.5 climate scenario. During the last interglacial, the mean species richness was 4.14 species per grid cell (SD = 2.08); it declined to 2.46 (SD = 1.48) at the present time. In the future, the mean species richness was predicted to slightly increase from the present under RCP2.6, whereas it was expected to further decline under RCP8.5 (Table 3.3).

Table 3.3. Summary statistics for predicted species richness.

Time interval	Mean	SD
Last interglacial	4.14	2.08
Present	2.46	1.48
Future (RCP2.6)	2.48	1.42
Future (RCP8.5)	2.41	1.30

The map of species richness during the Quaternary indicates that the area with the highest biodiversity of large mammals was widely spread out over the region, ranging across the southern part of Southeast Asia to eastern China (Figure 3.2a). However, the high richness area has been shown to currently shift northwards and is now restricted to fragmented areas in the middle part of the region (Figure 3.2b). In the future, the areas of high species richness were expected to contract even more under RCP2.6, while RCP8.5 predicted a larger area with lower biodiversity (Figure 3.2c, d).



(a) (b)

(c) (d)

Figure 3.2. Maps of large mammal species richness across Southeast Asia over three time intervals: (a) Last interglacial, (b) Current and (c, d) Future (RCP2.6 and RCP8.5, respectively).

3.4.2 Species distribution of large mammals: past, present and future

Species distribution maps generated from using point locality information and climatic variables in this study illustrated changes in the distributions of large mammal species across time (see Appendix 2.1 for predicted distribution maps of all species). Currently, the range size from 11 species has reduced from the last interglacial. *Panthera pardus* is one of the species that have been most severely impacted by changing climatic factors; its species range size was found to decrease about 84% from the Quaternary period. In the past, leopard (*P. pardus*) was widely distributed across the region. Large areas in China were shown to be suitable habitats for the species (Figure 3.3a, left panel). However, the predicted current distribution showed a dramatic reduction in suitable habitats of leopards from its Quaternary range, implying the extirpation of the species from large parts of China and several countries in the region. Species ranges of the remaining populations have contracted markedly and they are now restricted to fragmented habitats (Figure 3.3a, right panel). This prediction is concordant with the recent assessments of leopard status by the IUCN, which lists the leopard as a vulnerable species (VU) due to a severe decline in population and range size (Stein et al., 2020).

Conversely, *Nomascus concolor* (black crested gibbon) is one of the species found to have an increase in its range size from the last interglacial. The current distribution of its suitable habitat was estimated to have expanded by approximately 26% compared to the past. Modern-day populations of the species were predicted to distribute widely across southern China (Figure 3.3b). However, at the present, small populations of the species have been found to occur discontinuously in Yunnan Province of China, north-western Laos and northern Vietnam (Rawson et al., 2011). They are fragmented by extensive areas of unsuitable habitats. The gibbon has experienced a severe population decline and rapid habitat loss due to a series of deforestation in recent history (Jiang et al., 2006).

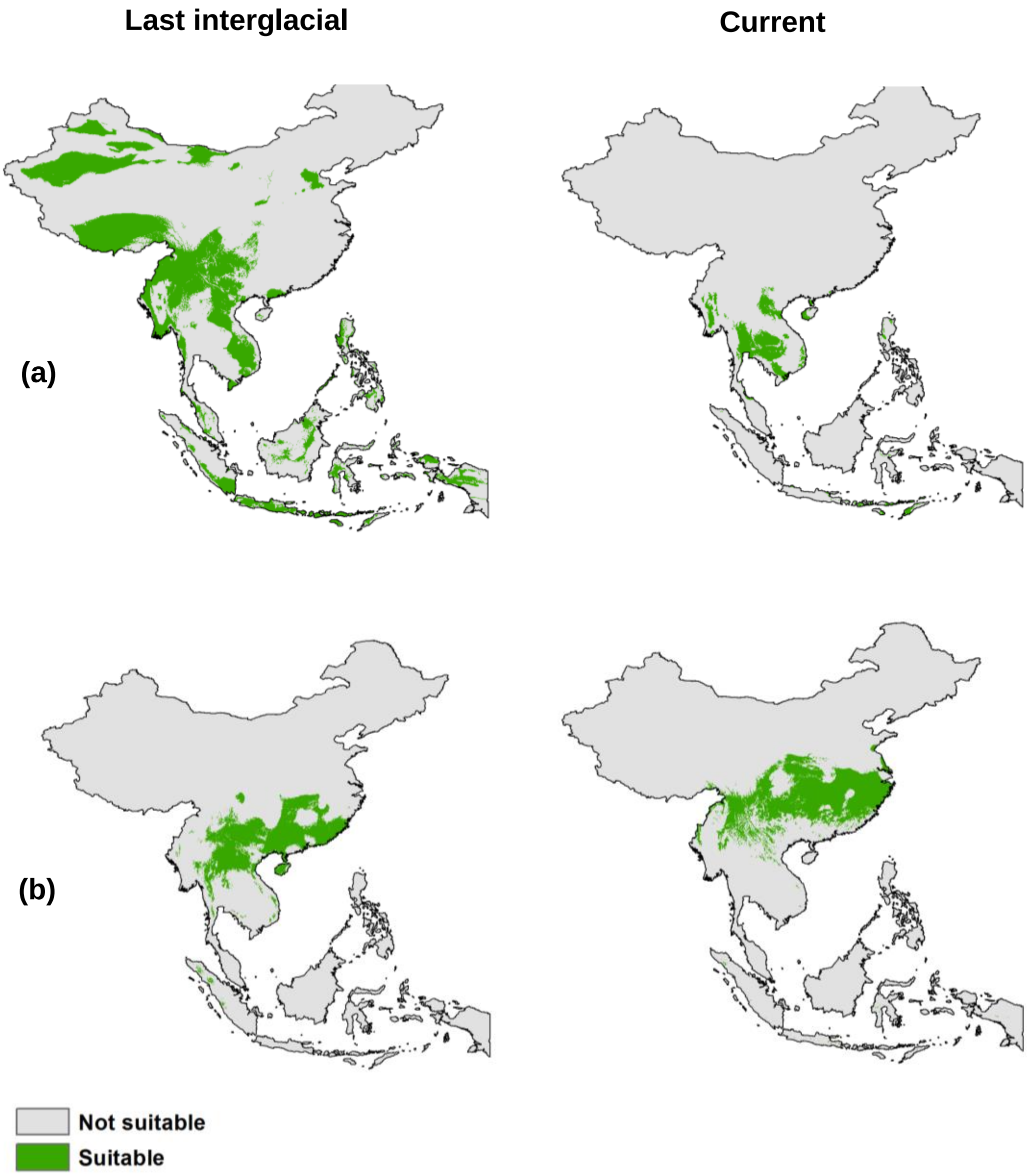


Figure 3.3. Maps of the study area showing the predicted distribution of suitable habitats for large mammals during the last interglacial (left) and current conditions (right). The selected species show different responses in range shifts to the changing climatic factors. During the current warming, (a) *P. pardus* shows a decreasing species range size whereas (b) *N. concolor* shows an increasing range size.

In post hoc analyses, grid cells listed as suitable habitats for the species were counted and percentage changes in the total area of species range from the previous time interval were calculated (Table 3.4). The results indicated that in the future, the range size of at least 6 species, including *E. maximus*, *N. concolor*, *P. tigris*, *P. pygmaeus*, *T. indicus* and *U. thibetanus*, was expected to reduce even further depending on the climate scenario. Under RCP8.5, tigers (*P. tigris*) were predicted to be one of the most affected species. The distribution of the species' suitable habitats was expected to decrease by 81%, suggesting that tigers are at extremely high risk of disappearing in the next few decades. Tiger extinction is highly likely to occur given the current small populations of less than 3,200 individuals worldwide (Goodrich et al., 2015). Small fragmented areas in Myanmar, Laos and Vietnam will be the only suitable habitats for the species (Figure 3.4a). Under RCP2.6, the greatest range contraction was found to occur in *T. indicus* (Malayan tapir, ~33% decrease in range size) followed by *N. concolor* (black crested gibbon, 31%). On the contrary, there were species predicted to gain more suitable habitats in the future. For example, *C. alpinus* was predicted to expand its range to southwestern China. The extent of the area of the species' suitable habitat was expected to increase by about 8% under both future climate scenarios (Figure 3.4b). Furthermore, there were species including *R. unicolor* (sambar deer) that showed either positive or negative responses to climate changes depending on the climate scenario (Figure 3.4c).

Table 3.4. Percentage changes in suitable habitats of large mammal species from each time interval.

Species	**Percentage changes in no. of suitable grid cells from the previous time interval**		
	Current	**RCP2.6**	**RCP8.5**
Bubalus bubalis	-79.6	29.6	28.6
Capricornis sumatraensis	-12.1	-6.2	6.1
Cuon alpinus	-93.6	8.3	7.9
Elephas maximus	-35.4	-11.0	-75.6
Macaca mulatta	167.5	1.1	-5.4
Macaca nemestrina	86.4	2.0	13.1
Muntiacus muntjak	-87.9	80.7	166.1
Nomascus concolor	26.2	-31.3	-53.7
Panthera pardus	-84.3	9.7	-22.0
Panthera tigris	-66.7	-23.0	-81.1
Pongo pygmaeus	-47.3	-5.0	-21.6
Rusa unicolor	-16.0	13.1	-63.2
Sus scrofa	-88.0	65.2	105.7
Tapirus indicus	-45.2	-32.5	-87.6
Ursus thibethanus	32.1	-2.1	-5.5

Minus sign indicates the contraction of species' suitable habitat from the previous time interval.

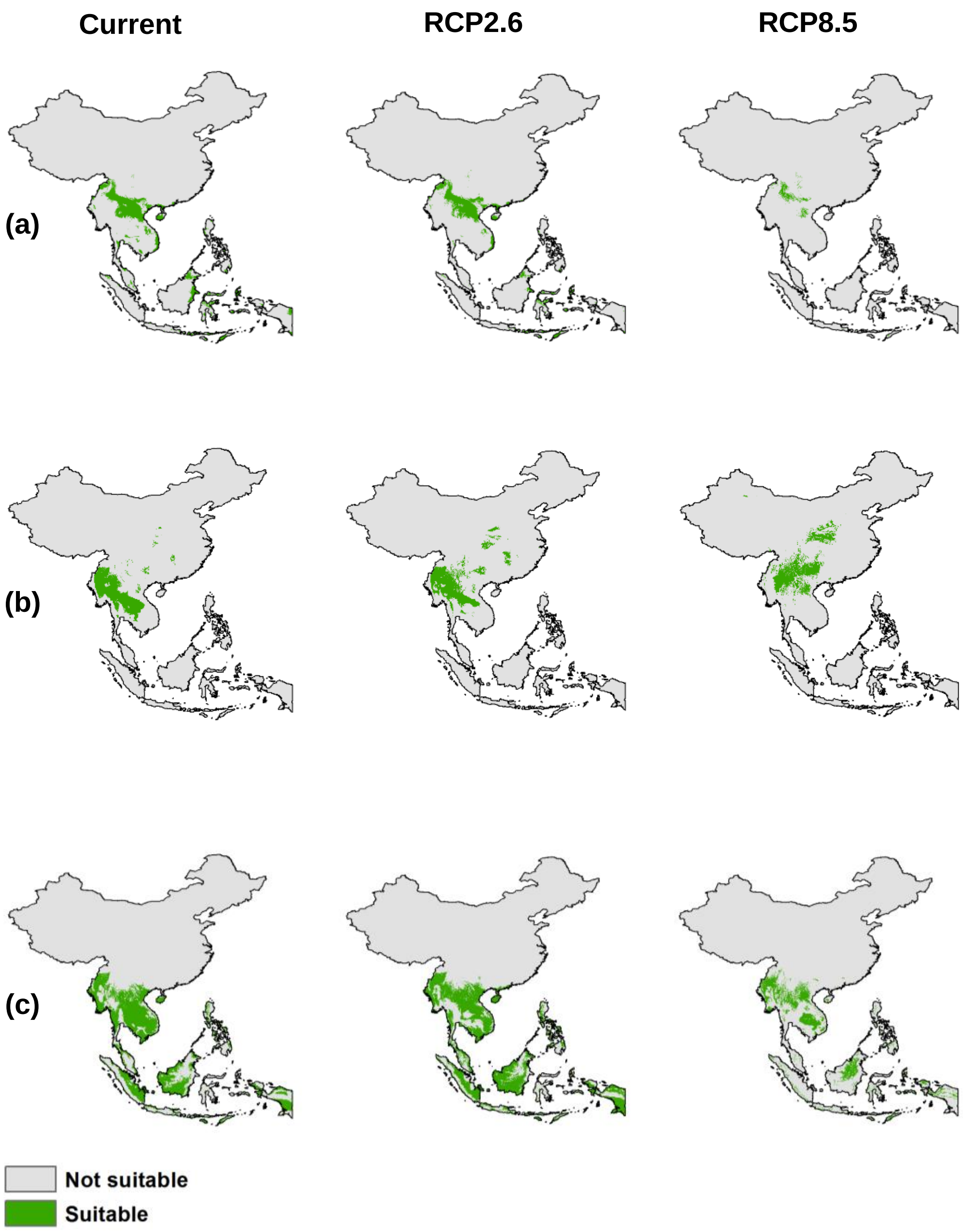


Figure 3.4. Maps of the predicted distribution of large mammals under the current (left), RCP2.6 scenario (middle) and RCP8.5 scenario (right). The selected sample species show different responses in range shifts to future climate changes. Under the future climate scenarios, (a) *P. tigris* shows a decrease in range size, (b) *C. alpinus* shows an increase in range size, and (c) *R. unicolor* shows an inconsistent pattern of response depending on the future scenarios.

3.4.3 Rate of range shifts

Based on the predicted distributions of suitable habitats for large mammals at each time interval and subsequent calculations for rates of range shifts, the species responded either positively or negatively to climate changes by shifting their ranges at varying rates across all time intervals (see Appendix 2.2 for the rates of all species range shifts). Despite environmental fluctuations during the Quaternary period, the species shifted their distribution at a slower rate (0.06 km/yr) compared to the present (2.0 km/yr and 6.3 km/yr under RCP2.6 and RCP8.5, respectively) (Table 3.5) when climate change was estimated to occur at a rate 10 times faster than the past 65 million years (Diffenbaugh and Field, 2013). Wild pigs, for example, were predicted to have the greatest range shift in two of the three observed time periods. The species was estimated to obtain the highest rate of range shift for the period of the last interglacial (0.13 km/yr) and AD 1945-2050 under RCP2.6 (5.5 km/yr). *P. tigris* was predicted to have the greatest rate of range shift, 12.7 km/yr, in another examined time period (AD 1945-2050 under RCP8.5).

Table 3.5. Summary statistics for the shift rates (km/yr) of large mammal species during each time period.

Time interval	**Average**	**Maximum**	**Minimum**	**Median**
1945 – 2050 (RCP8.5)	6.3	12.7	0.5	6.5
1945 – 2050 (RCP2.6)	2.0	5.5	0.3	1.6
120,000 – 140,000 years BP	0.06	0.13	0.01	0.06

3.5 Discussion

3.5.1 The pattern of species geographic distribution under changing climatic conditions

Results from these analyses indicate that species richness and the distribution of large mammals in Southeast Asia have been dramatically affected by changing climatic variables. The habitat suitability of large mammals has also changed markedly since the Quaternary period. Many species have experienced severe range contraction, local extirpation or are at a high risk of extinction. However, the patterns and rates of range shifts in response to changing climatic variables varied among and within species. Several species (i.e. sambar deer) showed an inconsistent pattern of range shifts under the given climate change scenarios even though the temperature and precipitation were predicted to increase in all situations. The varying responses of large mammals predicted in this study are concordant with results from previous studies (Lyons, 2003; Moritz et al., 2008; Williams and Blois, 2018). It has been suggested that mammals tend to shift their distribution in an individualistic manner, reflecting species movement to track their climatic niches (Lyons, 2003; Moritz and Agudo, 2013). These findings also exemplify the importance of conducting SDMs for all threatened species, and support the assertion that forecasting the impacts of future climate change on species should be integrated into conservation planning (Chatterjee et al., 2012).

3.5.2 The rates of species range shifts across time

The rates of range shifts were predicted to rise considerably for all species in the future regardless of the climate change scenario. This may reflect the sensitivity of species to environmental changes. Tropical species tend to have a low tolerance to warming and now live closely to their upper temperature limits (Deutsch et al., 2008; Dillon et al., 2010; Khaliq et al., 2014). Hence, even with a small change in environmental variables, the species may need to move more quickly to track their suitable spaces. The Malayan tapir population in Thailand has shown evidence supporting a climatic limitation of species distribution. The species has been found to shift from having a wide-ranging altitude to being restricted to the wetter and higher altitude areas, corresponding with a more marked dry season in its Thai range (Lynam et al., 2012; Steinmetz et al., 2008; Traeholt et al., 2016).

Furthermore, in this study, many species were expected to have large range shifts and the species with the greatest range shift do not remain the same across time periods. The average range shifts for the future were approximately 33 - 105 times higher than the predicted rate for the past period depending on the climate scenario. In the past, large mammals might have sufficient time to cope with changing environmental conditions, but the future warming was estimated to occur at a high rate over a short time scale and exceed the warmest temperature of the early Holocene (IPCC, 2014; Marcott et al., 2013; Williams and Blois, 2018). The higher rate of range shifts is therefore likely to require species to adapt rapidly to these changes. Furthermore, the average rate of species range shifts from this study was higher than the estimated rate for mammals in North America at the similar period of time as suggested by Williams and Blois (2018; 3.35 km/yr for 1950 - 2050 RCP8.5). The large difference in the rates of range shifts is likely due to the ecology of the focal species. The species observed here potentially have a much larger home range than the species in the study of Williams and Blois (2018). Asian elephants (*Elephas maximus*), for example, were estimated to occupy a home range size of 250 – 400 km^2 in a non-fragmented forest and 600 km^2 in fragmented forests of Sabah, Malaysia (Alfred et al., 2012).

3.5.3 Conservation implications for large mammals

Despite the predictions of increased range shift rates, human domination of the Earth’s ecosystems is an important factor that currently restricts large mammal distributions. Habitat loss and fragmentation from human activities such as urbanisation, logging and cultivation can prevent the accessibility to new suitable habitats. Hence, species may need to rely on micro-evolution and phenotypic plasticity for adaptation to local conditions in order to survive (Boutin and Lane, 2014; Hetem et al., 2014; Huey et al., 2012). However, generation times of species play a crucial role in determining how fast species can evolve to occupy changing environmental niches (Boutin and Lane, 2014; Gienapp et al., 2012; Meester et al., 2018; Réale et al., 2003). Small mammal taxa with a short generation time have been found to have a high capability of evolution. Rapid morphological changes, which are suggested to be partly associated with climate change, have occurred frequently in rodents over the past 100 years (Pergams and Lawler, 2009). On the contrary, genetic adaptation in large mammals with long generation times occurs slowly and may not be able to keep track with a rapidly increasing rate of climate change (Hetem et al., 2014).

Phenotypic plasticity is another mechanism allowing species to respond to changing environments; it can result in phenological shifts and behavioural flexibility of species (Donnelly et al., 2012). It is essential for large mammals with long gestation and lactation periods to have synchronicity in timing of reproduction at the peak of resource availability (Boutin and Lane, 2014). Short-lived mammals such as small rodents are predicted to be able to adjust reproductive events to match with food availability easily, but longer-lived mammals may struggle to do so (Bronson, 2009). Previous studies have already shown that a phenological mismatch has led to population declines in several large-bodied mammals (Burthe et al., 2011; Plard et al., 2014; Post and Forchhammer, 2008).

Our predictions of increasing rates of range shifts in the next few decades and the aforementioned characteristics of large mammals may imply that the species assessed here are particularly vulnerable to climate changes and may face a higher chance of extinction in the near future. Many species have taken 100,000 years from the last interglacial until now to reach the point of losing at least 50% of their ranges but the future climate change (RCP8.5) could potentially cause this loss to happen in the next few decades. This finding supports the notion that future climate change is one of the major threats to biodiversity and as such it is vital to integrate predictions regarding species responses to climate change into conservation planning, management and policy. The impacts of future climate change are likely to worsen the current situation of biodiversity loss in Southeast Asia and are expected to be more severe for large mammals compared to other taxa, suggesting that these species should be prioritised for conservation (Cooper et al., 2011; Khaliq et al., 2014). The protection of large mammals will also benefit other species cohabiting the same areas. The analyses also show that the species richness of large mammals could potentially be recovered under strong policy implementation aiming to mitigate the effects of climate change, i.e. a small rise in the mean species richness predicted under RCP2.6.

3.5.4 Limitations and future research

Predicting distribution of species requires a firm understanding of relationships between species' ecological attributes such as biotic interactions, abiotic tolerances, habitat history, and dispersal ability (Graham et al., 2006; Wisz et al., 2013). However, in this study, some of these important factors which influence species distribution were not taken into account when determining the rates of species range shifts due to limited data availability. Therefore, the estimated rates presented here for species in the future may be overestimated and should be interpreted with some caution. Biotic interactions have been suggested to influence species geographic distribution at all spatial extents across and within trophic levels (Wisz et al., 2013). They have been found to shape species' spatial patterns by the operation of multiple mechanisms; notable examples are competition, predation and host-parasite (Álvarez-Loayza et al., 2011; Bellingham et al., 2010; Bertolino, 2008). The tigers, for example, are highly threatened by poaching for bones and body parts, habitat loss, and prey depletion. A previous study has indicated a significant negative correlation between tigers’ home range size and their prey abundance (Goodrich et al., 2015; Simcharoen et al., 2014). Dispersal ability also affects the magnitude of range shifts and the survival of species (Williams and Blois, 2018). To my knowledge, predictive models of future land use and human population density for Southeast Asia that are compatible with the WorldClim climate data remain unavailable. The development of these environmental data over large spatial extents and the addition of these factors into the models will improve the robustness of the predictions of SDMs.

Furthermore, future studies at the finer temporal scales with other significant variables may provide a better understanding of large mammal distributions and range shifts in response to changes during the fluctuations of the past climatic states. Using historical species data from archive databases may allow predictions of species distributions during the time when there was a far less anthropogenic impact on the environment.

Chapter 4: The roles of fossil records in examining the hypothesis of niche conservatism and changes in large mammal distributions over a long time scale

4.1 Abstract

1) Predictions of species responses to future climate change rely on the principle of niche conservatism, suggesting that ecological niches of species remain constant over time and shifts in species distribution may reflect species tracking of suitable climate conditions. Although this hypothesis has been tested across various taxa and habitats, studies of niche conservatism are currently lacking for Southeast Asia. The fossil record is a potentially powerful data source for investigating species niche shifts over a longer time scale and determining the impact of environmental change on species distribution.

2) Species data for 15 large mammal species in Southeast Asia were used for the analyses. Modern records were used to construct the distributions for all species under current environmental conditions and hindcast their last interglacial ranges. Niche models were also projected with fossil records under the last interglacial conditions and forecast to the current period. Statistical analyses were used to evaluate model predictive ability.

3) The results showed that fossil records accurately forecast the current distributions for 7 species (*Bubalus bubalis, Capricornis sumatraensis*, *Macaca mulatta*, *Macaca nemestrina*, *Muntiacus muntjak, Nomascus concolor* and *Tapirus indicus*), while modern records accurately hindcast the last glacial distributions of only two primate species (*M. mulatta* and *N. concolor*). There were 5 species (*Cuon alpinus*, *Panthera pardus*, *Panthera tigris*, *Rusa unicolor* and *Sus scrosa*) for which predictions between time intervals were statistically significant for observed occurrence predicted absence.

4) Evidence of niche conservatism was found in the two primate species, *M. mulatta* and *N. concolor.* Climatic niches of the species are suggested to remain stable over time, potentially due to the species' wide tolerance to climatic conditions and limited genetic variation and dispersal. Models that lacked intertemporal predictivity may indicate evidence of climatic niche shifts amongst large mammal species, which may be influenced by both anthropogenic factors and changes in environmental conditions.

4.2 Introduction

An ecological niche is defined as a suite of abiotic and biotic conditions required for species persistence (Hutchinson, 1957). Under changing environments, niches of species are likely to respond in either one of these two directions: (a) niche conservatism, which suggests that the niche remains constant over evolutionary time scales and shifting in species geographical ranges may occur to track niches and prevent extinction; or (b) niche evolution, which is the alteration of species niche through adaptive responses (Malizia and Stigall, 2011; Martínez-Meyer et al., 2004; Wiens et al., 2010). Many studies have reported evidence of both phenomena across taxa within a period of 100 years, but studies over longer geological time scales are relatively few and often require further testing for the validity of methods (Pearman et al., 2008; Peterson, 2011).

The principle of niche conservatism is invoked in many ecological and evolutionary questions; therefore, a variety of approaches have been proposed to test these hypotheses. One of the most frequently used approaches is based on the Ecological Niche Model (ENM), which is also known as the Species Distribution Model. The ENM can be used to study the relationship between niche conservatism, environment and species distribution with the key concept suggesting that when a species tends to retain ecological niche characteristics, unfavourable conditions can restrict its geographical ranges (Wiens et al., 2010). This idea is an important underlying assumption in the study of modern biogeography such as species responses to climate changes (Araújo et al., 2006; Harris et al., 2012; Levinsky et al., 2007) and emergence of non-native species (Ficetola et al., 2007; Jiménez-Valverde et al., 2011; Peterson et al., 2003). However, the accuracy of these predictions for species distributions in the future is difficult to measure because predicted events have not yet occurred. To examine the stability of ecological niches and the accuracy of model predictivity, fossil records can be used as independent dataset for ancestral niche reconstruction, allowing the comparison of species niches across multiple time periods and model evaluation (Malizia and Stigall, 2011).

Even though the hypotheses of niche conservatism have been widely studied in various taxa, research attempts were predominantly focused on the United States and Europe (Broennimann et al., 2012; Cooper et al., 2011; Martínez-Méndez et al., 2019; Petitpierre et al., 2012; Stigall, 2012; Strubbe et al., 2013). Studies of niche conservatism in Southeast Asia, which is one of the world’s biodiversity hotspots with a high level of endemism, are relatively scarce. Previous studies have supported the tropical conservatism hypothesis, suggesting that tropical species with specialised characteristics and small ranges are expected to show a high level of niche conservatism in order to maintain their distribution within a particular region (Cooper et al., 2011; Wiens and Donoghue, 2004). Nevertheless, this hypothesis has yet to be tested rigorously in Southeast Asia, which is possibly due to the limited availability of data from species endemic to this region. Therefore, in this study, we used fossil records and modern data from large mammal species distributed across Southeast Asia to reconstruct the species' climatic niches and predict their distributions across two time intervals: the last interglacial, which lasted from about 120,000-140,000 years before present (using fossil occurrence data in conjunction with environmental data for the last interglacial period), and present (using modern occurrence and current environmental conditions). We also hindcast present niche models to estimate past distributions and forecast past models for the present distributions to test for niche shifts in the species under drastic climate change between the two time periods.

4.2.1 Chapter aims and objectives

1. To use fossil records for investigating the hypothesis of long-term stability in climatic niches of large mammals in Southeast Asia since the Late Quaternary.
2. To determine the impact of climatic change on large mammal distributions in Southeast Asia.

4.3 Materials and methods

The analyses of niche conservatism followed the three steps advocated by Martínez-Meyer et al. (2004): (a) modelling ENMs based on species occurrences and the chosen climatic variables at one time interval; (b) projecting ENMs to a second time interval; and (c) assessing the model ability to predict known species occurrences in the second time interval.

4.3.1 Input data

A dataset of species occurrences of large mammal species in Southeast Asia and 6 climatic variables used in the analyses of this study was the same dataset used in Chapter 3. It was obtained by data collection and processing as described in Chapter 2. Only 15 species with more than 10 localities in both the present and the Pleistocene (about 120,000 – 140,000 years BP) were included for modelling. A specific time period during the Pleistocene was chosen for fossil data collection in order to match it to a period of environmental data provided by WorldClim (Last interglacial; ~120,000 – 140,000 years BP). In total, the dataset contained 556 fossil and 4,243 modern occurrence records.

The environmental data (WorldClim version 1.4) for the present and the Last interglacial (LIG) were summarised in a set of global climate layers, including aspects of temperature and precipitation. They are available for download with various spatial resolutions at http://www.worldclim.com/version1. A dataset for LIG was resampled to 2.5 arc-minute resolution. Six climatic variables together with species occurrences were then used to generate ecological niche models.

4.3.2 Ecological niche modelling (ENM)

The maximum entropy approach implemented in Maxent was used to project the distributions of species potential niches. Modern records were used to construct the niche distributions for all species under the current environmental conditions and hindcast the distributions during the last interglacial. The modelling processes were repeated using fossil records, which are classed as an independent dataset. Niche models were projected with fossil records under the LIG conditions and forecast to the current period to estimate the distributions of large mammal species. Statistical analyses were then used to evaluate model prediction performance (See section 3.3.3 in Chapter 3 for a detailed description of modelling processes).

4.3.2 Evaluating model predictivity

The hindcast and forecast ENMs were evaluated by overlaying species occurrences onto the predicted binary maps of species distribution. Statistical tests were performed to assess the accuracy of niche models in predicting known species occurrences, i.e. determining whether the coincidence between occurrence points and predicted suitable regions for the species occurs by chance. Due to varied sample sizes, different statistical methods were used for each species depending on the number of species records. In the study of Martínez-Meyer et al. (2004), species with sample sizes < 10 were evaluated with the binomial test, while species with occurrences > 10 were assessed with the χ^2 goodness-of-fit test. However, we elevated the boundary of sample size to 30 occurrences according to the central limit theorem, which is based on the sample size $n \geq 30$.

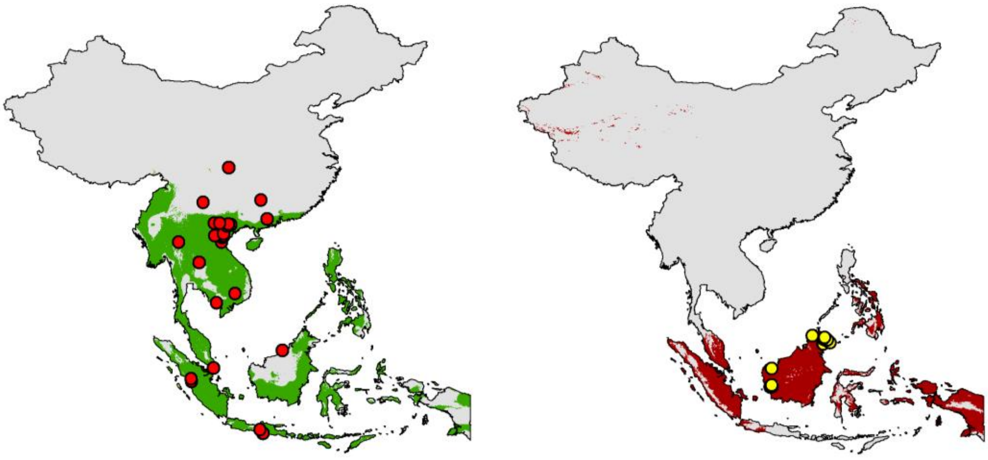
Furthermore, for each species, a percentage accuracy of predicted species distributions between time intervals (Present models hindcasted Quaternary distributions, and Quaternary models forecasted present distributions) was calculated as follows:

$$\text{Percentage accuracy} = \frac{Number\ of\ obseved\ occurrence\ points\ predicted\ as\ present}{Total\ number\ of\ species\ observed\ occurrences}\ x\ 100$$

4.4 Results

4.4.1 Generating models of ENMs

For the analyses of 15 species, there were model predictions that were not statistically significant within time periods (See Appendix 3 for all model predictions for each species). The analyses of the binomial and χ^2 goodness-of-fit tests to evaluate the model predictive ability showed that when using fossil occurrences to estimate the species distributions during the Quaternary period, the coincidence between fossil points and predicted distributions of 10 species was more statistically significant than expected by chance (all p-values < 0.05). When using the modern occurrences to predict the current distributions, the predicted distributions of 7 species were statistically and significantly coincident with known occurrence points (all p-values < 0.05). However, the predicted distributions of only 4 species including *Cuon alpinus*, *Pongo pygmaeus*, *Rusa unicolor* and *Ursus thibetanus* were statistically significant at both time intervals (Table 4.1). In particular, the model predictions for the current distribution of the Bornean orangutan (*Pongo pygmaeus*) coincided with all known current occurrences of the species (binomial test, n = 14, p-value < 0.001), while predictions for the Quaternary distribution covered approximately 78% of fossil occurrences (22 out of 28 known occurrences; binomial test, n = 28, p-value < 0.05) (Figure 4.1).



(a) **(b)**

Figure 4.1. Predicted distributions of the Bornean orangutan (*P. pygmaeus*) that were highly statistically significant at both time intervals (p-value < 0.001). Red and yellow dots indicate fossil and modern occurrences, respectively. (a) The predicted Quaternary distribution coincided with 78% of known fossil occurrences. (b) The predicted current distribution coincided with all known modern occurrences.

Table 4.1. Summary statistics of predicting known species occurrences using species records to generate the niche models.

Species	Fossil data + LIG			Modern data + Current		
	Total points	Predicted known presence	p-value	Total points	Predicted known presence	p-value
Bubalus bubalis	14	13	0.002*	15	11	0.119
Capricornis sumatraensis	12	10	0.039*	212	107	0.891
Cuon alpinus	26	21	0.002*	124	73	0.048*
Elephas maximus	41	18	0.435	495	292	< 0.001*
Macaca mulatta	49	42	< 0.001*	81	32	0.059
Macaca nemestrina	14	10	0.180	46	32	0.008*
Muntiacus muntjak	34	23	0.040*	796	21	< 0.001*
Nomascus concolor	43	35	< 0.001*	31	12	0.209
Panthera pardus	19	11	0.648	155	19	< 0.001**
Panthera tigris	67	19	< 0.001**	107	29	< 0.001**
Pongo pygmaeus	28	22	0.004*	14	14	< 0.001*
Rusa unicolor	52	38	< 0.001*	364	245	< 0.001*
Sus scrofa	94	61	0.004*	1316	639	0.295
Tapirus indicus	16	10	0.455	214	170	< 0.001*
Ursus thibetanus	47	42	< 0.001*	273	163	0.001*

*Significance level at $p < 0.05$ for accurately predicted known species occurrences
**Significance level at $p < 0.05$ for inaccurately predicted known species occurrences

4.4.2 Forecasting and hindcasting niche models

The analyses of the binomial and χ^2 goodness-of-fit tests showed that when forecasting or hindcasting the distributions of potential niches, models were found to perform well at a single time interval in many species (Table 4.2). For example, the niche model of the Malayan tapir (*Tapirus indicus*) was not significant in predictions for the present model hindcasting the Quaternary distribution (binomial test, $n = 16$, p-value > 0.05), but it was highly significant for the Quaternary model forecasting the present distribution ($\chi^2 = 138.24$, d.f. = 1, p-value < 0.001) (Figure 4.2).

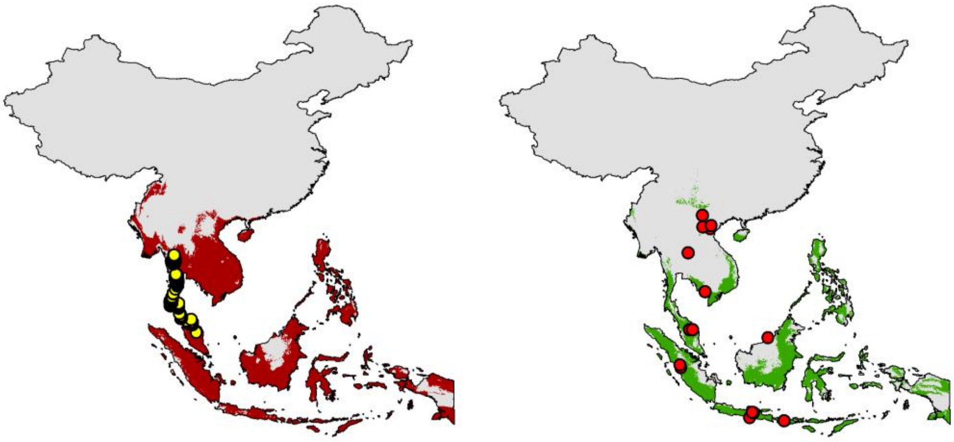
Forecasting the Quaternary niche model to the current environmental conditions to estimate the present distributions of the species was found to accurately predict the known modern occurrences of many large mammal species; model predictions for 7 species (*Bubalus bubalis*, *Capricornis sumatraensis*, *Macaca mulatta*, *Macaca nemestrina*, *Muntiacus muntjak, Nomascus concolor* and *Tapirus indicus*) were highly statistically significant (all p-values < 0.001).

The predicted distributions generated from hindcasting the present niche model to the last interglacial conditions were rarely found to accurately predict the known fossil occurrences; the coincidence between the predicted distributions and known fossil occurrences were statistically significant (all p-values < 0.05) in only two primate species (*M. mulatta* and *N. concolor*). The rhesus macaque (*M. mulatta*) and the black crested gibbon (*N. concolor*) were also the only two species for which model predictions were significant in both directions (Figure 4.3). These results suggest that the distributions of these two primate species have been influenced by similar climatic niches and followed similar climate regime shifts since the Quaternary period.

Table 4.2. Summary statistics for predicting known species occurrences using species records to hindcast and forecast the niche models.

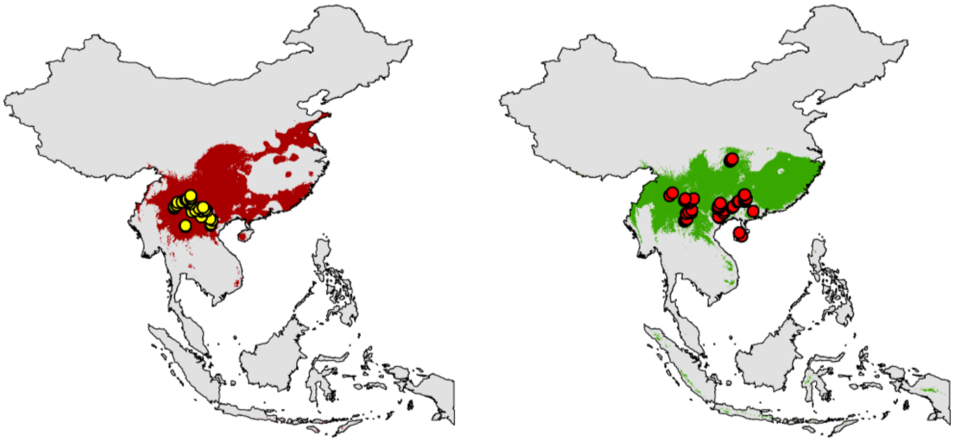
Species	Modern data + LIG (Hindcasting)			Fossil data + Current (Forecasting)		
	Total points	Predicted known presence	p-value	Total points	Predicted known presence	p-value
Bubalus bubalis	14	3	0.057	15	15	< 0.001*
Capricornis sumatraensis	12	9	0.146	212	211	< 0.001*
Cuon alpinus	26	1	< 0.001**	124	0	< 0.001**
Elephas maximus	41	1	< 0.001**	495	265	0.116
Macaca mulatta	49	49	< 0.001*	81	63	< 0.001*
Macaca nemestrina	14	6	0.791	46	46	< 0.001*
Muntiacus muntjak	34	8	0.002**	796	794	< 0.001*
Nomascus concolor	43	30	0.010*	31	31	< 0.001*
Panthera pardus	19	1	< 0.001**	155	15	< 0.001**
Panthera tigris	67	9	< 0.001**	107	9	< 0.001**
Pongo pygmaeus	28	1	< 0.001**	14	10	0.180
Rusa unicolor	52	3	< 0.001**	364	6	< 0.001**
Sus scrofa	94	14	< 0.001**	1316	0	< 0.001**
Tapirus indicus	16	11	0.210	214	193	< 0.001*
Ursusthibetanus	47	22	0.662	273	0	< 0.001

*Significance level at $p < 0.05$ for accurately predicted known species occurrences
**Significance level at $p < 0.05$ for inaccurately predicted known species occurrences



(a) **(b)**

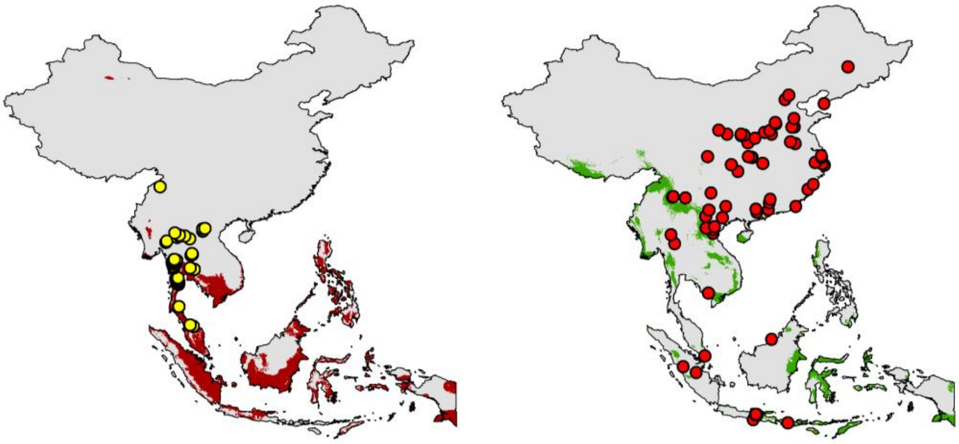
Figure 4.2. Projected distributions of the Malayan tapir (*T. indicus*) between time intervals that were highly statistically significant in one direction. Red and yellow dots indicate fossil and modern occurrences, respectively. (a) Quaternary niche model forecast to the current conditions (p-value < 0.001). (b) Current niche model hindcast to the last interglacial climatic conditions (not significant, 69% accuracy in predicting known occurrences).



(a) **(b)**

Figure 4.3. Predicted distributions of the black crested gibbon (*N. concolor*) between time intervals that were highly statistically significant in both directions (p-value < 0.05). Red and yellow dots indicate fossil and modern occurrences, respectively. (a) Quaternary niche model forecast to the current conditions ($\chi^2 = 30$, d.f. = 1, p-value < 0.001). (b) Current niche model hindcast to the last interglacial climatic conditions ($\chi^2 = 42$, d.f. = 1, p-value < 0.05).

In addition, there were 5 species of large mammals (*Cuon alpinus*, *Panthera pardus*, *Panthera tigris*, *Rusa unicolor* and *Sus scrosa*) for which the probability of the coincidence between known occurrences and predicted unsuitable habitats for the species were higher than expected by chance (all p-values < 0.001). The current distribution of the tiger (*P. tigris*) forecast by the species' Quaternary niche model accurately predicted about 8% of known modern occurrences of the species (9/107 occurrences), while the Quaternary distribution hindcast by the species' current niche model correctly predicted approximately 13% of known fossil occurrences (9/67 occurrences) (Figure 4.4).



(a) **(b)**

Figure 4.4. Projected distributions of the tiger (*P. tigris*) between time intervals that the coincidence between known species occurrences and predicted unsuitable habitats were highly statistically significant in both directions (p-value < 0.001). Red and yellow dots indicate fossil and modern occurrences, respectively. (a) Quaternary niche model forecast to the current conditions (8% accuracy in predicting known occurrences). (b) Current niche model hindcast to the last interglacial climatic conditions (13% accuracy in predicting known occurrence).

In addition, Figure 4.5 illustrates the summary of percentage accuracy of predicted niche models for all large mammals in the study and statistical significance level.

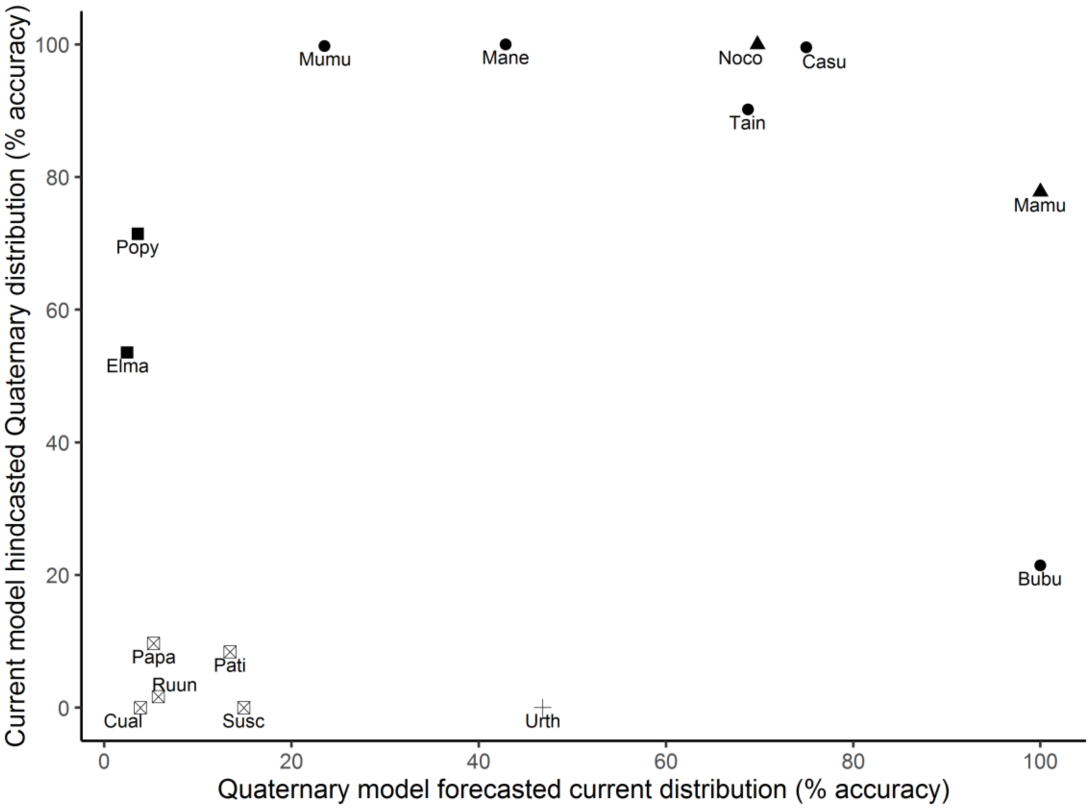


Figure 4.5. Percentage accuracy of niche models in predicting species distributions between time intervals (Present models hindcasting the Quaternary distributions and Quaternary models forecasting the present distributions). ▲ indicates species that the coincidence between known occurrences and predicted suitable habitats for species was statistically significant in both directions (p-value < 0.05). ● represents species that predictions of the Quaternary niche models for present distributions were statistically significant (p-value < 0.05). ☒ represents species that the coincidence between known occurrences and predicted unsuitable region for species were statistically significant in both directions (p-value < 0.05). + species that predictions of occurrences and unsuitable habitats were significant for the Quaternary model forecasting the present distributions (p-value < 0.05). ■ species that predictions of occurrences and unsuitable habitats were significant for Present hindcasting the Quaternary distributions (p-value < 0.05). Abbreviations are the first two letters of the species genus and epithet.

4.5 Discussion

4.5.1 Model prediction

When projecting the niche distributions within time periods, model predictions of some large mammal species that were not statistically significant may result from a spatial bias in data collection and the effect of small sample size. Spatially biased data can result in an environmental bias of the species because the small number of sites where species occur may be unable to capture all the environmental variations that the species require and narrow species niches. This can then lead to inaccurate model predictions, i.e. predicted small species distributions because of the relative difficulty in identifying a specific suite of favourable environmental conditions over the area (Levinsky et al., 2007; Phillips et al., 2009).

4.5.2 Conservatism of climatic niches in large mammals of Southeast Asia

When using fossil records to forecast modern species distributions, the statistical significance in the analyses of 7 species indicates that there is evidence of niche conservatism amongst large mammal taxa from Southeast Asia. The predictive ability of the Quaternary niche models may imply that climatic niches of these species remain stable over the past 100,000 years. Particularly, for the two primate species, *M. mulatta* and *N. concolor*, intertemporal predictivity was significant in both directions, indicating that climatic niches of these species have been highly conserved. Niche conservatism may be influenced by several factors that can prevent the evolution of new niches, including a wide tolerance to climatic conditions, limited genetic variation, biotic interaction and dispersal ability (Kamilar and Cooper, 2013; Wiens et al., 2010). The rhesus macaque (*M. mulatta*) is considered a generalist species. It has the widest geographical range among non-human primates and is found in a broad range of habitats throughout Asia (Brandon-Jones et al., 2004). This geographic range and characteristics of the species indicate the ability to cope with wide-ranging conditions. *M. mulatta* is also characterised by the flexibility in several traits including diet, home range and group size that may promote its ability to tolerate disturbance and remain in the same habitat (Albert et al., 2014). In contrast, the black crested gibbon (*N. concolor*) is listed as one of the critically endangered species by the IUCN. It currently occupies a discontinuous distribution in parts of China, Laos and Vietnam (Bleisch et al., 2008). The isolated distribution of the gibbon may permit little gene flow between populations, which in turn leads to low genetic variation and restricted evolutionary processes (Leimu et al., 2010). Furthermore, the prediction of current species distribution suggests that there is a large area in China where a suitable habitat for the gibbon is predicted for, but the species now occupies a rather restricted area in the central part of the region. These results indicate that other factors unrelated to climatic conditions such as habitat loss and fragmentation may limit the present distribution of *N. concolor*.

Using modern records to hindcast the Quaternary distribution rarely accurately predicted known fossil records. The low success in hindcasting models may result from the shifts in ecological niches of the species and the effects of disturbance on species modern distributions, including environmental changes and anthropogenically driven constraints. The palaeontological records of the Malayan tapir (*T. indicus*) indicate that the species was present from China to the islands of Java and Borneo in the past but its modern distribution has become restricted and highly isolated by discontinuous forest fragments (Cranbrook and Piper, 2009). The current populations of the species have been found only in parts of Myanmar, Thailand, Peninsular Malaysia and the island of Sumatra (Cranbrook and Piper, 2009; Traeholt et al., 2016). During the middle Pleistocene, the tapir was suggested to adapt to the open savannah woodland. Hence, the expansion of tropical rainforests caused by the Holocene climate change was found to be unfavourable for the species and subsequently led to a population decline (Cranbrook and Piper, 2009). A previous study on the influence of environmental variation and human disturbance on tapir occurrence in Thailand, where the climates experience a more marked dry season, suggested that at the present, the species populations observed at a wide range of altitudes in the past were found to be restricted to steep slopes at higher elevation where a high level of humidity is recorded (Lynam et al., 2012; Steinmetz et al., 2008; Traeholt et al., 2016). Species occurrence has been found to be positively associated with evergreen tropical rainforests and annual rainfall, and the tapir is now likely to occur in more closed forest habitats (Lynam et al., 2012). Evidence from this study strongly supports a climatic limitation of the species because the tapir populations in Thailand are less sensitive to human disturbance and relatively more stable than populations in other parts of their global range because rates of forest loss in their Thai ranges have declined by more than 40% over the past 20 years. Furthermore, the tapirs are mostly active at night, and typically not targeted for hunting and trade (Lynam et al., 2012; Traeholt et al., 2016). These recent changes in species preferences and ranges may render modern niche models incapable of accurately hindcasting the Quaternary distribution of the species.

In addition, niche models of several species in the study were shown to lack predictive ability, i.e. not significant in predicting known species occurrences. For several species, the coincidence between known species occurrences and predicted unsuitable habitats was also shown to be statistically significant. This finding most likely resulted from the effect of other non-climatic factors rather than the shifts in species niches. The tiger (*P. tigris*), for example, was once widely distributed across Asia (Nowell and Jackson, 1996). However, over the past century, it has experienced a severe population decline and gone extinct from more than 90% of its historical range, mainly due to overhunting and prey depletion (Goodrich et al., 2015; Sanderson et al., 2010). Tigers are illegally killed and poached for high-value products from their body parts (Goodrich et al., 2015). Tiger bones have been used in traditional Asian medicine for over thousands of years, while the skin is used as a symbol of power and authority (Nowell, 2000). Another important factor determining tiger occurrence is biotic interaction. Prey species and availability are crucial for the species' successful reproduction and survival. Tigers primarily prey on large ungulate species, including sambar deer (*R. unicolor*) and wild pigs (*S. scrofa*) (Hayward et al., 2012). In Southeast Asia, over 80% of its prey species are also threatened with decreasing population trends (Wolf and Ripple, 2016). During the late Pleistocene, the mass extinction of large-bodied predators in the genera *Crocuta*, *Hyaena* and *Panthera* in the region may have reduced competitive interactions among carnivores and increased the opportunity of surviving species to disperse and occupy new habitats (Louys et al., 2007). These studies indicate that significant driving factors for changes in tiger distributions might have been biotic factors such as anthropogenic pressure, dispersal ability and prey abundance (Martínez-Meyer et al., 2004).

4.5.3 Insight from the fossil record on the impact of climate change on large mammal distributions in Southeast Asia

It is crucial for conservation planning to understand species responses to past environmental changes and factors previously contributing to species extinction in order to prevent further biodiversity loss (Louys, 2012). Well-documented fossil records with species names and locality provide valuable resources for investigating these ecological and evolutionary questions. In this study, using fossil data to project current distributions of large mammal species can enhance the understandings of species plasticity, ecological niche requirements and drivers of species range shifts. The analyses presented here highlight that many large mammal taxa in Southeast Asia were able to withstand a number of extreme climatic events from the late Quaternary to present. For the species whose niches are likely to remain constant through time, this may indicate the ability to keep track with climate change. Alternatively, species may have sufficient genetic variability and ecological plasticity to adapt to fluctuating environments (Parmesan, 2006; Woodruff, 2010). Such an adaptive ability may imply that these species will likely be less sensitive to future climate change (Woodruff, 2010). However, the species that survived past environmental changes may not be able to cope with the ongoing climate changes in conjunction with severe anthropogenic impacts such as habitat loss, habitat fragmentation and overhunting. Several species have been found to already respond to recent environmental constraints by shifting their ecological niches and species ranges. Hence, future climate change may exacerbate the extinction risk of these taxa. Particularly, species that have shown to have dramatic range contractions from the historical time and currently occupy restricted geographical ranges. The findings highlight the need for increased conservation efforts in the region to protect these species. It is suggested that without a higher level of conservation activity, Southeast Asia may experience the next megafauna extinction event by the end of this century (Louys, 2012; Sodhi et al., 2010).

4.5.4 Limitations and further studies

Spatial biases and the small number of the occurrence data are likely to be a limitation of this study even though the models with target group background were suggested to provide better predictions when compared to distribution maps generated by using random background points (Phillips et al., 2009). However, species occurrences of some common species in the study (i.e. *M. muntjak* and *S. scrofa*) were merely from a relatively small area of the entire species range as suggested by the IUCN. Therefore, additional data across the species ranges may improve the model performance and lead to more accurate predictions. Furthermore, several other approaches, including computational software, have been developed to facilitate tests for niche similarity (Oksanen, 2015; Warren et al., 2010) The uses of these additional methods may provide useful information for obtaining a more precise interpretation.

Chapter 5: Assessing the agreement between SDMs based on point locality and range map data for predicting species responses to climate change

5.1 Abstract

1) Species range maps have been increasingly used in the study of species distribution in relation to environmental conditions due to limited availability of species occurrence data. However, the issue has been raised regarding the reliability of using this type of data because they are not produced for macroecological research. In this study, predicted species distributions derived from using point locality and range map data were compared and used to determine the consequences of using different data types for SDMs.

2) Point locality data of 8 primate species across Southeast Asia were collected from existing publications and databases. Range maps of these species were provided by the IUCN. An ensemble of 7 frequently used modelling methods were implemented in the package Biomod2 in R to predict potential distributions of the species at the present and in the future.

3) Ensemble models for each data type of all primate species obtained high AUC values, indicating that model predictions were robust with respect to different data sources. Although point locality data predicted a higher value of maximum species richness (6 species) compared to IUCN (4 species), the patterns of species richness predicted by both data types were found to be relatively similar at a broad scale.

4) Under the RCP2.6 scenario, predicted species responses from point and range map data agreed for only 3 species. The agreement in model predictions was found in more species under RCP8.5 (6 species).

5) Relying on a single data source to predict species responses to climate change may lead to a misunderstanding of the true threatened status of the species and subsequently misguide conservation decisions. Thus, it is recommended to integrate all information of known species occurrences to obtain more robust analyses of species-environment relationships. However, incomplete species data may still provide a useful insight into the pattern of species richness.

5.2 Introduction

Species distribution modelling (SDM) has been increasingly used during the past few decades to investigate the impact of environmental changes on species distributions. Species point locality data, which are a major requirement of input into SDMs, are often limited in many parts of the world, particularly in tropical regions, where not only are the number of species poorly sampled and under-recorded, but there is also a lack of commitment to biodiversity data sharing at national and international levels (Jenkins et al., 2013; Meyer et al., 2015). Newbold (2010) highlights that in the online database resource for biodiversity occurrences, the Global Biodiversity Information Facility (GBIF), the density of species records is biased towards more developed countries. The majority of species records that are georeferenced on the GBIF database are from countries such as the United States, Sweden, Australia and the United Kingdom. Species occurrences from Southeast Asian countries account for only about 0.7% of the database (GBIF, 2019). The lack of robust data in the tropics may pose dangers to species that urgently require assessments for designing protection plans and conservation strategies. Ideally, extensive surveys throughout study areas or species ranges should be carried out to collect complete species datasets, but this is a time- and budget-consuming process. Many studies, therefore, have been using polygon range maps to study the relationship between species occurrences and environmental variables, and investigate the impact of environmental changes on biodiversity (Belmaker and Jetz, 2015; Gouveia et al., 2014; Newbold, 2018; Pineda and Lobo, 2012; Pompa et al., 2011).

The International Union for Conservation of Nature (IUCN) has provided species range maps to support Red List assessments. These maps are created by integrating currently known distributions of species with knowledge of the areas of remaining suitable habitats, and expert knowledge of species ranges (IUCN, 2018). IUCN species range maps have been increasingly used in research during the past decade because they are often the only resource available for studying species occurrences (Herkt et al., 2017). The issue has been raised concerning the use of this data type because IUCN range maps have been produced with the initial objectives to assess species status and provide guidance for conservation actions, but not for the purpose of macroecological research (Herkt et al., 2017). Furthermore, range maps have been suggested to frequently underestimate the species complete geographical range, even in well-studied taxa, due to the currently limited knowledge (Ficetola et al., 2013). Ineffective or lack of information sharing between researchers is another key factor for incomplete range maps of true species distributions. For example, the Sumatran serow (*Capricornis sumatraensis*) occurs in national parks across Thailand and has been classified as near threatened (NT) according to the assessment of Thailand Red List of mammals (Nabhitabhata and Chan-ard, 2005; Wildlife Research Division, 2010). However, the IUCN range map may have underestimated the distribution of this species by suggesting that it is found in Indonesia, Malaysia and southern Thailand (Duckworth et al., 2008).

Using polygon range maps instead of point locality data to model species distribution could potentially be a useful approach for assisting biodiversity conservation; nevertheless, the discrepancy between these two approaches has not been widely examined. Herkt et al. (2017) compared the disagreement between IUCN maps and species complete geographical ranges predicted by SDM in bats of Africa. The results showed that these maps have varied greatly, potentially due to a higher sensitivity to sampling bias of the range maps. The IUCN range maps are likely created by restricting species ranges to areas where species are known to occur in order to prioritise conservation efforts, because false prediction of species occurrence generally costs more than false absence (Herkt et al., 2017; IUCN Standards and Petitions Subcommittee, 2017; Schipper et al., 2008). Therefore, range maps may not reflect the complete range of species and provide insufficient information for macroecological research purposes (Herkt et al., 2017). Vasconcelos et al. (2012) also investigated discrepancies between species richness patterns of amphibians in North and South America obtained by range maps and SDM. They found that although SDM tended to overestimate species richness in comparison to range maps, richness gradients derived from both data sources were similar at a broad scale; the species richness of North American amphibians was found to be higher in the south-eastern part of the region.

In this study, we compare species richness patterns and distributions of non-human primates in Southeast Asia, which are derived from IUCN range maps and point locality data. Southeast Asia is one of the world’s biodiversity hotspots due to high species richness and endemism (Myers et al., 2000). Even though the region holds the highest mean proportion of the country’s endemic mammal species (11%), it also has the highest rates of deforestation among the tropics and the highest proportion of threatened mammals (Sodhi et al., 2010). Southeast Asia is home to 97 non-human primates, including 19 prosimians, 58 Old World monkeys, 20 gibbons and 2 great apes. About 78% of these recognised primate taxa are currently threatened (IUCN/SSC Primate Specialist Group, 2018; Roos et al., 2014). Primates play a crucial role in seed dispersal of many plant species (Chapman, 1995; McConkey et al., 2002; Russo et al., 2006). Hence, a trend of continuous decline in global primate populations may have a significant impact on the community and ecosystem (Estrada et al., 2017).

Since climate change is recognised as one of the major threats to biodiversity, primates have been predicted to respond negatively by experiencing more than 50% reductions in species ecological traits and properties such as population size, geographic range size and survival rate (Pacifici et al., 2017). The study of primate distribution in response to climate change is important for helping to design effective protected areas and planning conservation strategies to protect species of conservation concern. The aim of this study was also to determine the consequences of using the IUCN range maps and species occurrences for assessing the potential impacts of climate change on primate distribution.

5.2.1 Chapter aims and objectives

1. To compile occurrences of primate species in Southeast Asia.
2. To investigate species richness patterns derived from IUCN range maps and point data predictions.
3. To compare predicted species distributions derived from IUCN range maps versus point data predictions.
4. To determine the consequences of using point locality data and IUCN range maps for modelling species distributions.

5.3 Materials and methods

5.3.1 Input data

Species point locality data of primates between AD 1945 to present in Southeast Asia were compiled from published literature, official reports, museum collection records and online databases of biodiversity data. Species records with inaccurate GPS coordinates were excluded from the analyses. Out of 97 primate species in Southeast Asia, there were 8 species from 4 families that had a sufficient number of records for producing useful models (>10 records) (Stockwell and Peterson, 2002). A total of 286 records collected in this study are shown in Table 5.1.

Table 5.1. Species records and data used in the modelling processes.

Family	**Species**	**IUCN Status**[1]	**No. of presence sites**	**Elevation limits**[2] **(metres)**	
				Lower	**Upper**
Cercopithecidae	*Macaca mulatta*	LC	81	NA	4000
Cercopithecidae	*Macaca nemestrina*	VU	46	NA	NA
Cercopithecidae	*Trachypithecus cristatus*	NT[3]	27	NA	NA
Cercopithecidae	*Trachypithecus phayrei*	EN	32	NA	NA
Homonidae	*Pongo pygmaeus*	CR	14	NA	500
Hylobatidae	*Hylobates pileatus*	EN	16	NA	1500
Hylobatidae	*Nomascus concolor*	CR	31	500	2500
Lorisidae	*Nycticebus pygmaeus*	VU[3]	39	NA	1500

[1] IUCN status categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern.

[2] NA in Elevation limits indicates that information is not available on the website of the IUCN Red List of Threatened Species due to lack of data.

[3] In 2020, the threatened status *of T. cristatus* was reclassified to VU and EN for *N. pygmaeus*. Note that these reclassifications were published after the first submission of this thesis.

Each polygon of the IUCN species range maps contained the codes of presence ranking from 1 to 6 (Table 5.2). Only polygons with Presence = 1 (Extant) were selected for the modelling process. The selected polygon range maps were converted to raster grid cells with the same resolution as other environmental layers (2.5 arc-minute resolution) and then cropped to the extent of Southeast Asia. Elevation data (GTOPO30) provided by the United States Geological Survey (USGS) (available for download at https://lta.cr.usgs.gov/GTOPO30), were also resampled to 2.5 arc-minute using ArcGIS version 10.3. They were then used to extract the elevation value for each grid cell of species range maps. Grid cells that had elevation values exceeding species limits in Table 5.1 were removed from the analyses. The centre points of remaining grid cells with suitable elevation for species were later used as species occurrences for the model input. The numbers of data points of each species derived from the IUCN range maps after the data preparation processes are shown in Table 5.3.

Current and future projections of climate were downloaded from WorldClim. Six climatic variables related to temperature and precipitation were used for modelling species distributions. Two future climate scenarios were selected for the analyses to investigate variations in species responses to climate change.

Table 5.2. IUCN codes for recording the Presence of a taxon within a polygon (IUCN Red List Technical Working Group, 2019).

Code	Presence	Definition
1	Extant	The species is known or thought very likely to occur currently in the area, which encompasses localities with current or recent (last 20-30 years) records where suitable habitat at appropriate altitudes remains. Extant polygons can include inferred or spatially projected sites of present occurrence.
2	Probably Extant	This code value has been discontinued for reasons of ambiguity. It may exist in the spatial data but will gradually be phased out.
3	Possibly Extant	There is no record of the species in the area, but the species may possibly occur, based on the distribution of potentially suitable habitat at appropriate altitudes, although the area is beyond where the species is Extant (i.e., beyond the limits of known or likely records), and the degree of probability of the species occurring is lower (e.g., because the area is beyond a geographic barrier, or because the area represents a considerable extension beyond areas of known or probable occurrence).
4	Possibly Extinct	The species was formerly known or thought very likely to occur in the area (post 1500 AD), but it is most likely now extirpated from the area because habitat loss and/or other threats are thought likely to have extirpated the species, and there have been no confirmed recent records despite searches.
5	Extinct	The species was formerly known or thought very likely to occur in the area (post 1500 AD), but it has been confirmed that the species no longer occurs because exhaustive searches have failed to produce recent records, and the intensity and timing of threats could plausibly have extirpated the taxon.
6	Presence Uncertain	A record exists of the species' presence in the area, but this record requires verification or is rendered questionable owing to uncertainty over the identity or authenticity of the record, or the accuracy of the location.

Table 5.3. Species data points derived from IUCN range maps that were used for modelling.

Species	No. of data points derived from IUCN range maps
Macaca mulatta	182,288
Macaca nemestrina	63,239
Trachypithecus cristatus	56,120
Trachypithecus phayrei	53,153
Pongo pygmaeus	5,269
Hylobates pileatus	5,840
Nomascus concolor	846
Nycticebus pygmaeus	22,748

5.3.2 Modelling methods

The modelling method used in this chapter was different from the two previous chapters due to the size of datasets. A large IUCN dataset was difficult to handle in the Maxent software. Thus, the Biomod2 package implemented in R was used to run the models of species distributions in this chapter. The novel method of using ensemble models has been increasingly used and suggested to have more advantages than the use of a single forecasting model by providing more robust decision-making under uncertainty (Araujo and New, 2007). Therefore, a combination of 7 modelling methods (regression, classification and machine leaning techniques), that are commonly employed in the study of species distribution modelling, was attempted to use here. These 7 models included Generalised Linear Model (GLM), Generalised Additive Model (GAM), Classification Tree Analysis (CTA), Surface Range Envelope (SRE, also known as BIOCLIM), Multiple Adaptive Regression Splines (MARS), Random Forest (RF) and Maxent.

Species occurrences of each primate were split for model training (70%) and evaluation (30%). The use of a large number (e.g. 10,000) of pseudo-absence/ background data, and a minimum of 10 model replicates were suggested to return the best results (Barbet-Massin et al., 2012). Hence, 10,000 points of background data were randomly chosen from the entire study area, representing the environmental conditions available in the region. Species distribution models were input with locality data and point data derived from IUCN range maps, and run with 10 replicates to find the average probability of species occurrences. The models were repeated only 10 times in order to optimise model performance because the complete modelling process is generally time-consuming and requires a high performance computer. In this study, it took approximately 5 hours to model each data type of each species.

Models with AUC value > 0.70 were accepted to produce probability maps of species potential distribution for further analysis. Current distribution models were then projected to RCP2.6 and RCP8.5 future climate scenarios with the same environmental variables to examine how future projections vary based on point locality and range map data. Probability maps of species occurrences generated by ensemble models were converted to binary Presence/Absence maps using the maximum sum of sensitivity and specificity (maxSSS).

5.3.3 Comparison of species richness patterns and species ranges

In this study, species richness refers to the number of species present in each grid cell of the study area. To compare the patterns of species richness predicted by different data sources and how they may change under future scenarios of climate change, maps of species richness were created by overlaying binary distributional maps of primate species at each time interval; current and future (RCP2.6 and RCP8.5). For each species, binary maps of predicted species distributions from both data types were overlaid to calculate the percentage of prediction agreement. Percentage changes in the number of cells classified as suitable habitats from the current to future time periods were calculated to determine the agreement of model predictions.

5.4 Results

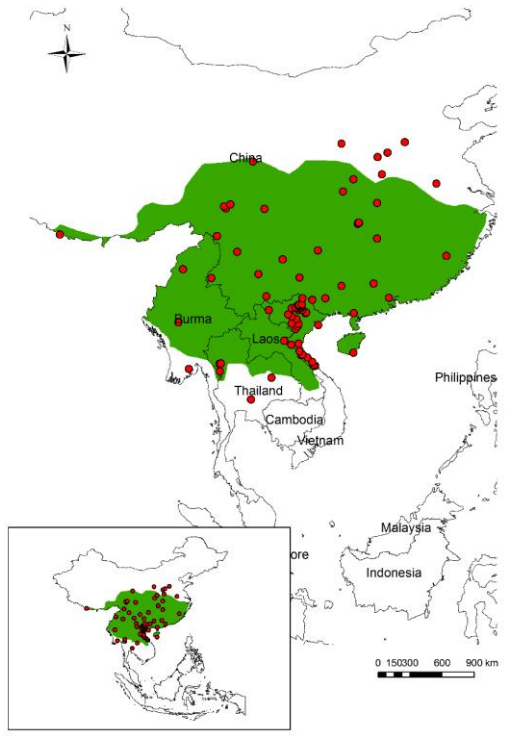
5.4.1 Species records

In total, the dataset contained 286 occurrences of primates. About 65% of species records were from the family Cercopithecidae. *Macaca mulatta* had the highest number of records and was present at 81 sites across the study area. The species can occupy a wide range of habitats and has been listed as a least concern species by the IUCN (Timmins et al., 2008). The primate species with the smallest number of presence sites was *Pongo pygmaeus*, which has been classified as one of the world’s critically endangered species. The Bornean orangutan is native to Indonesia and Malaysia (Ancrenaz et al., 2016). In this study, 14 presence sites were collected from its entire range.

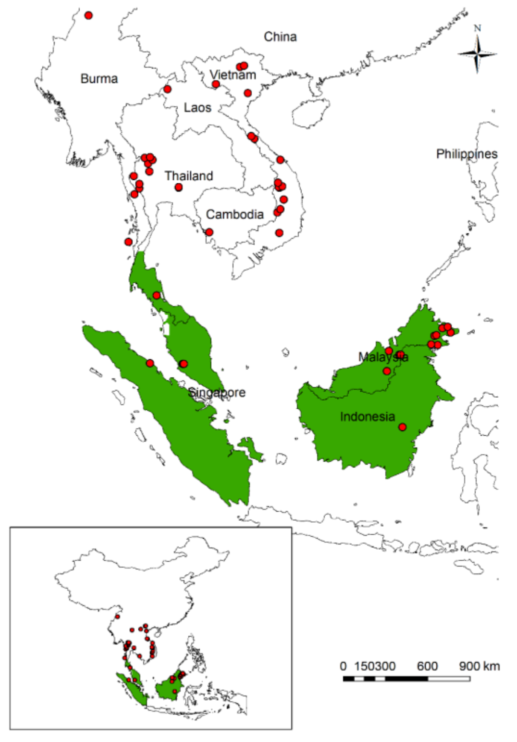
According to the IUCN range maps, *Nomascus concolor* or black crested gibbon was suggested to be a species with the smallest distribution range. After excluding the area beyond the species elevation limits, 846 grid cells were found to be a suitable habitat for the black gibbon. *N. concolor* is another primate species listed as Critically Endangered by the IUCN due to its 80% population decline in the last 45 years. The species now has an estimated population of 2,000 individuals, occurring in small and isolated populations in China, Laos and Vietnam (Pengfei et al., 2020). The rhesus macaque (*M. mulatta*) was found to have the largest IUCN range. It could occupy 182,288 grid cells across China and Southeast Asia.

The majority of point locality data obtained were within the species range maps provided by the IUCN. However, there were a few primate species whose species point data were outside the IUCN range maps (Figure 5.1). This indicates that these species data may have been under-recorded by the IUCN or it may imply that such species no longer occupy those areas today.

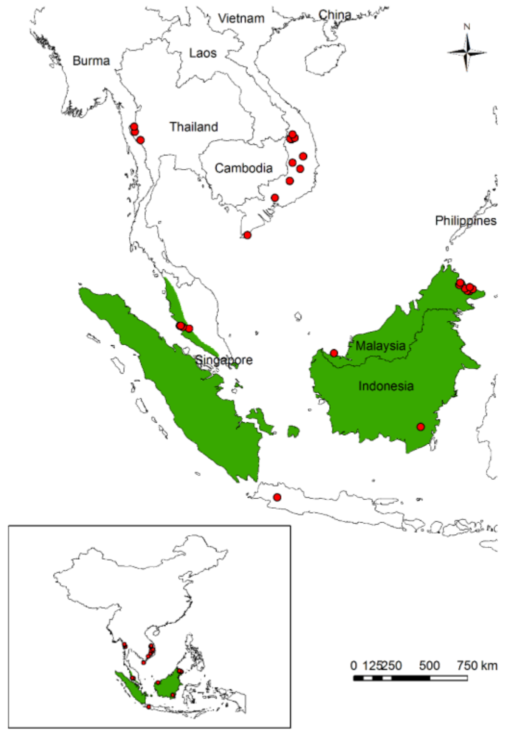
Macaca mulatta



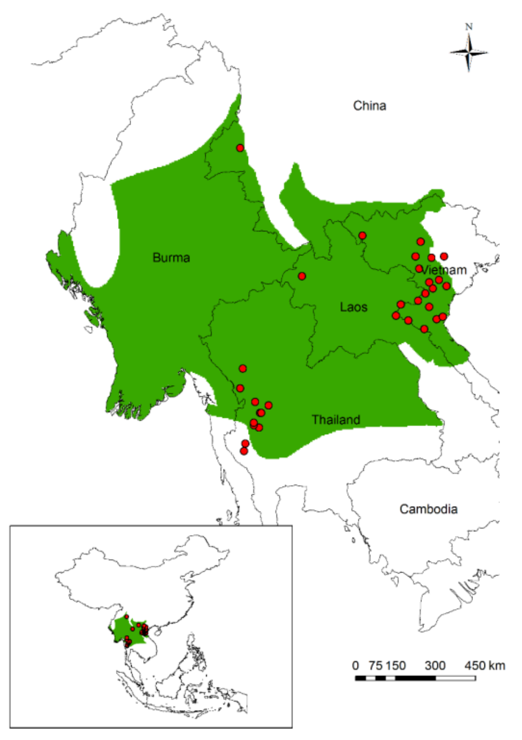
Macaca nemestrina



Trachypithecus cristatus



Trachypithecus phayrei



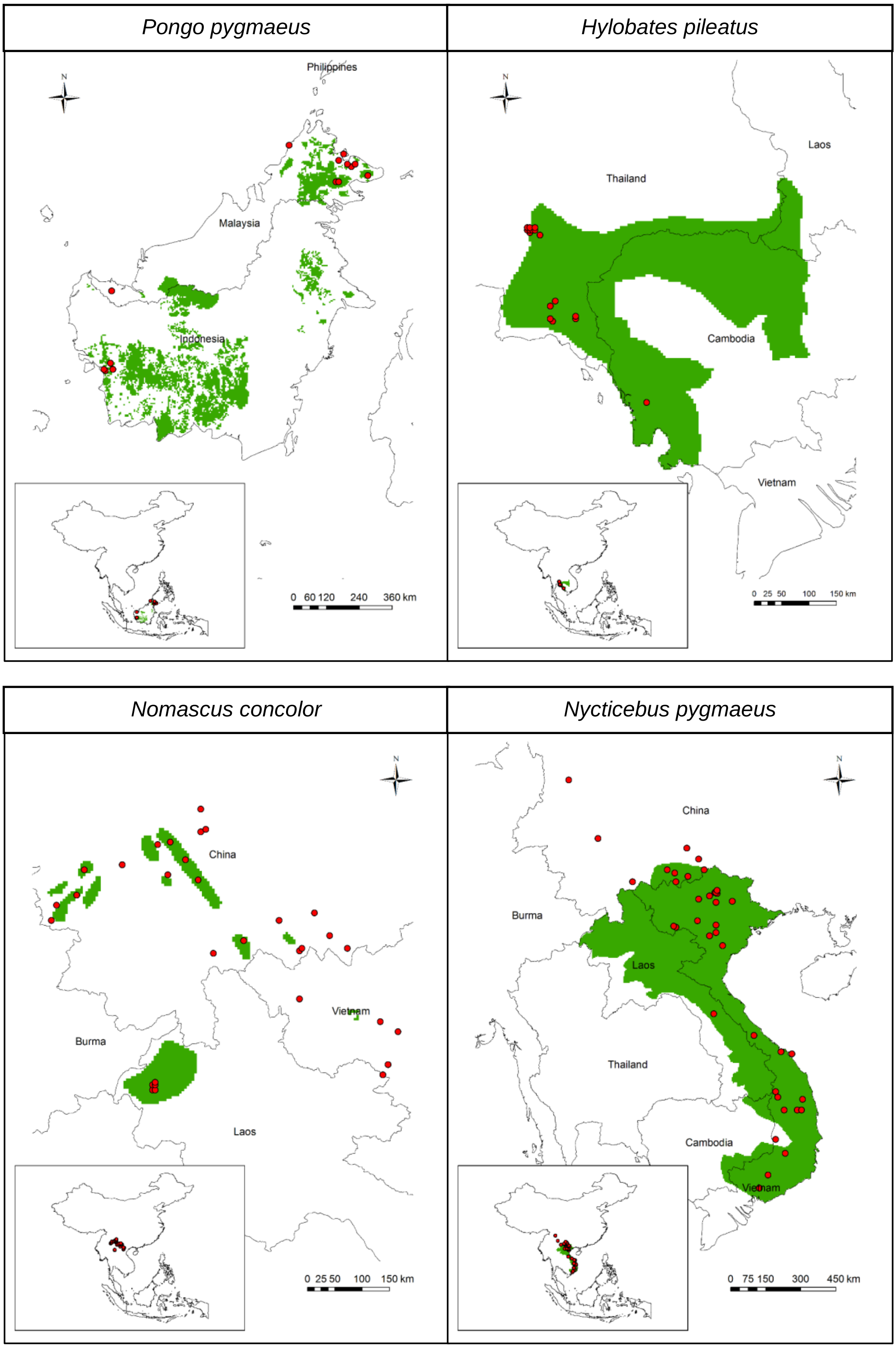


Figure 5.1. Maps showing occurrence sites of the 8 primate species during AD 1945 to present and its geographical range. The green area indicates the species range map as provided by the IUCN, while red is point localities where species have been reported.

5.4.2 Model performances

Overall, the mean AUC values of ensemble models for each primate species were > 0.9, showing a high predictive ability in discriminating species occurrences and background sites, and indicating that the models were robust in providing predictions of habitat suitability for species (Table 5.4).

Table 5.4. Average AUC values of ensemble models showing predictive ability when using different types of data.

Species	**Mean AUC_{PT}**	**Mean AUC_{IUCN}**
Macaca mulatta	0.939	0.997
Macaca nemestrina	0.965	0.992
Trachypithecus cristatus	0.982	0.994
Trachypithecus phayrei	0.990	0.996
Pongo pygmaeus	0.995	0.995
Hylobates pileatus	1	0.998
Nomascus concolor	0.994	0.998
Nycticebus pygmaeus	0.984	0.995

For each species, AUC_{PT} is the area under the receiver operating characteristic curve (AUC) when using point locality data as input of the models. AUC_{IUCN} is the AUC of the models using data derived from the IUCN range map.

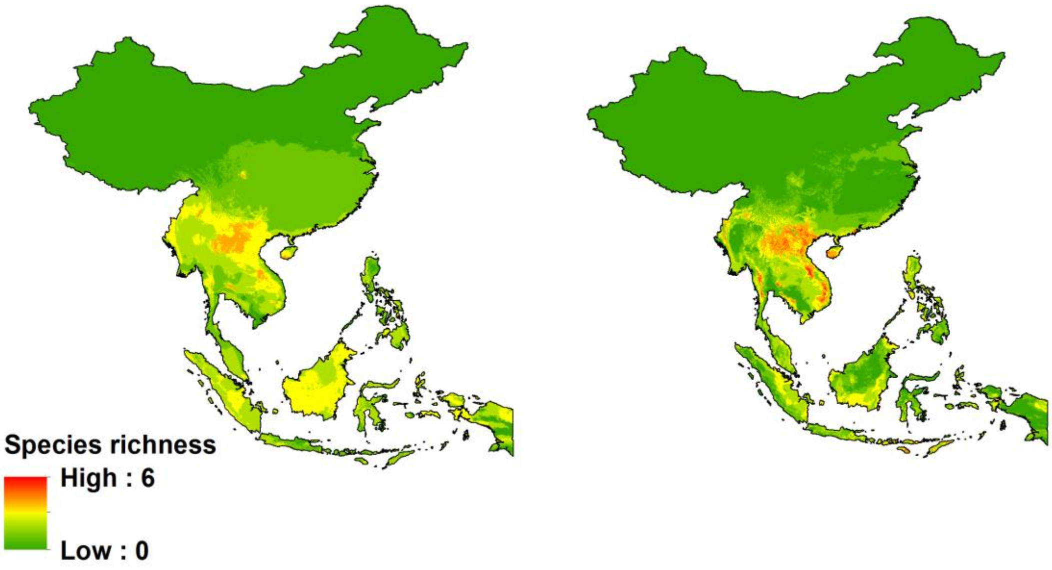
5.4.3 Discrepancies in species richness patterns

Maps of current species richness were generated by overlaying predicted binary distributions of 8 primate species. The mean species richness was calculated and compared for model predictions from using point and IUCN input data. It was found that the models with IUCN data predicted significantly higher mean species richness than the models using point data under all climate scenarios (Mann-Whitney U test, all p-values < 0.001). The models with point locality input showed a trend of reducing species richness in the study area as the climate change scenarios became more extreme, whereas the predictions of IUCN data input fluctuated from scenario to scenario. However, for both types of input data the standard deviations (SD) were similar between the two groups of predictions. The SD values also tended to decrease under all climate projections (Table 5.5).

Table 5.5. Summary of statistics of model predictions generated by using point locality data and point data derived from IUCN range maps.

Statistic	**Scenario**	**Data types**		**Mann-Whitney U test**
		Point locality	IUCN points	
Mean species richness	Current	0.58	0.82	All p-values < 0.001
	RCP 2.6	0.57	0.79	
	RCP 8.5	0.44	0.85	
SD	Current	1.05	1.07	NA
	RCP 2.6	1.01	1.01	
	RCP 8.5	0.80	0.94	

For all scenarios, predicted species richness by point data ranged from 0 to 6 species per grid cell, while it ranged from 0 to 4 species when using IUCN data. Although the maximum richness was different based on the data type, the species richness patterns predicted by range maps and point data were found to be relatively similar at a broad scale. Both types of data suggested that the central part of Southeast Asia was likely to support the highest numbers of species. The southern part of Borneo was estimated to have high species richness. However, some discrepancies were still found in the richness patterns at a smaller scale. One of the notable disagreements between predictions of the two data types was in the northern part of Borneo (Figure 5.2).



(a) **(b)**

Figure 5.2. Current species richness patterns of primates in Southeast Asia (a) predicted by IUCN range maps and (b) predicted by species point occurrences.

Under future climate change, the patterns of species richness predicted by two types of data remained similar at a broad scale for both climate scenarios. Under RCP2.6, it was expected that the central part of the region would still provide suitable habitats for most primate species. However, it was shown that areas with low species richness were likely to increase under RCP.8.5. The predicted richness patterns of two data types were also most similar across the southern part of the region under this climate scenario (Figure 5.3).

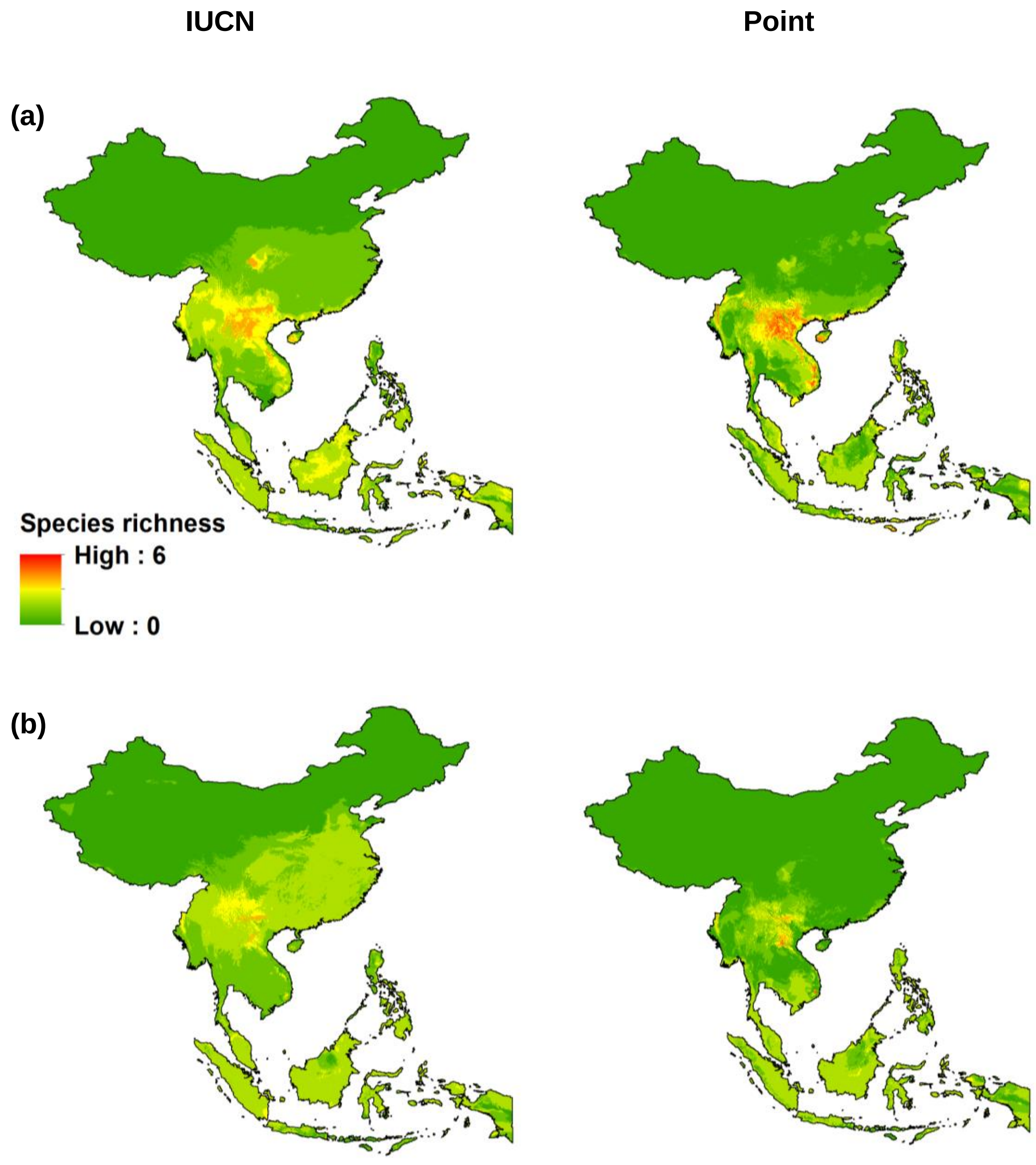


Figure 5.3. Predicted patterns of species richness by IUCN range maps (left) and SDM with species occurrences (right) under future climate scenarios (a) RCP2.6 and (b) RCP8.5.

5.4.4 Discrepancies in species ranges

For each primate species, the agreement in ranges was measured as a percentage of overlapping location areas predicted to be suitable habitats by both data types. Predicted species ranges by the IUCN range maps and point data varied substantially across species (see Appendix 4 for predictions of all species). Under the current environmental conditions, only two species had overlapping areas of more than 50% (*Nomascus concolor*, 65%; *Nycticebus pygmaeus*, 60%). *Hylobates pileatus* had the least area of agreement between the IUCN and point predictions (7%) (Figure 5.4).

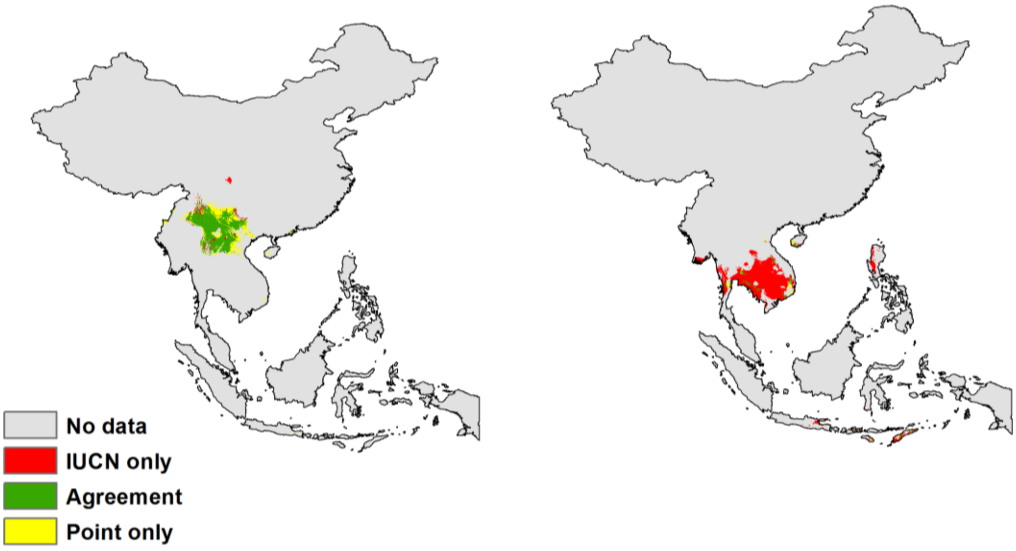


Figure 5.4. Example of predicted species ranges by two data types under the current climate conditions for *N. concolor,* which had the most overlapping areas of predicted habitat suitability (left) and for *H. pileatus* which had the smallest overlapping areas (right). Red shows suitable habitats for the species predicted only by the IUCN range map. Yellow shows suitable habitats predicted only by species occurrences. Suitable habitats predicted by both data types are shown in green. No data refers to the area predicted to be unsuitable for the species.

Under future climate scenarios, the agreements in species ranges predicted by both data types were expected to get smaller for nearly all species, except for *H. pileatus* and *T. cristatus*. *H. pileatus* showed a variable pattern of percentage changes in areas of agreement depending on the climate scenario. Under RCP2.6, overlapping areas of suitable habitats were predicted to slightly increase from the current 7% to 8%, whereas they were likely to decrease to 1% under RCP8.5. *T. cristatatus* was the only species whose overlapping areas were predicted to increase under all future climate scenarios (Figure 5.5).

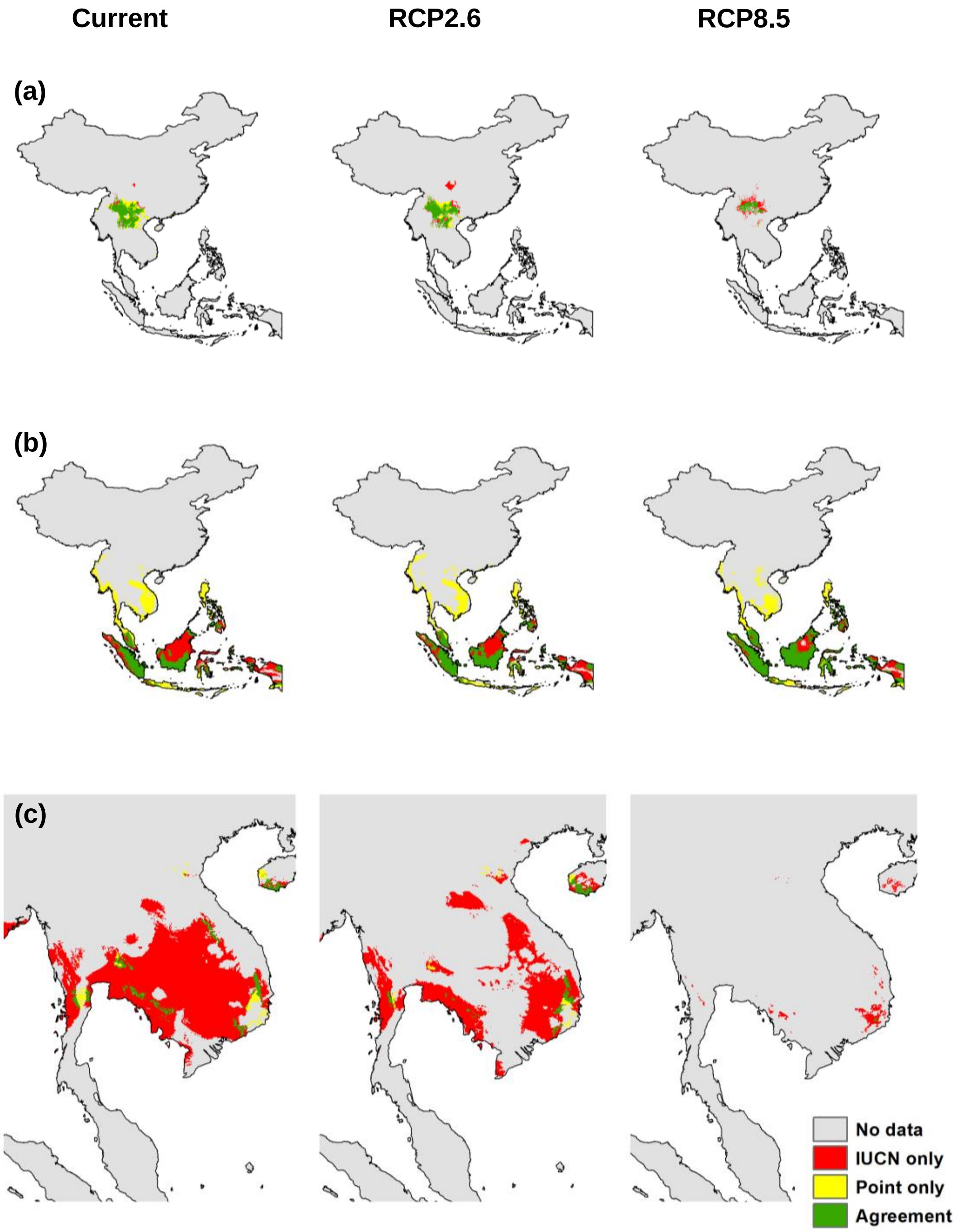


Figure 5.5. Maps of suitable habitats for primate species predicted by the IUCN range maps and species point localities under the current (left), RCP2.6 (middle) and RCP8.5 (right) conditions. Under future climate change, sample species show variable patterns of predictions (a) *N. concolor* shows a smaller agreement in areas predicted to be suitable habitats by both data types, (b) *T. cristatus* shows larger overlapping areas, and (c) *H. pileatus* shows an inconsistent pattern depending on the climate scenario.

Furthermore, the predicted percentage changes in the size of species' potential distribution from the present indicated that under the mild climate change scenario (RCP2.6), predictions of the IUCN range maps and species occurrences agreed for only three primate species. *H. pileatus* and *N. pygmaeus* were expected to experience a decrease in the distributional area in the near future, while suitable habitats of *T. cristatus* were predicted to increase (Figure 5.6). However, it was found that predictions by both types of data were in the same direction for more species under the extreme climate change scenario (RCP8.5). There were only two species, *T. phayrei* and *P. pygmaeus*, whose range maps and point data predicted opposite patterns of response (Figure 5.7). Particularly for *P. pygmaeus*, both types of data predicted completely different outcomes with the largest percentage changes under two future scenarios. For species with a predicted agreement, point data were more likely to predict a greater magnitude of change than range maps.

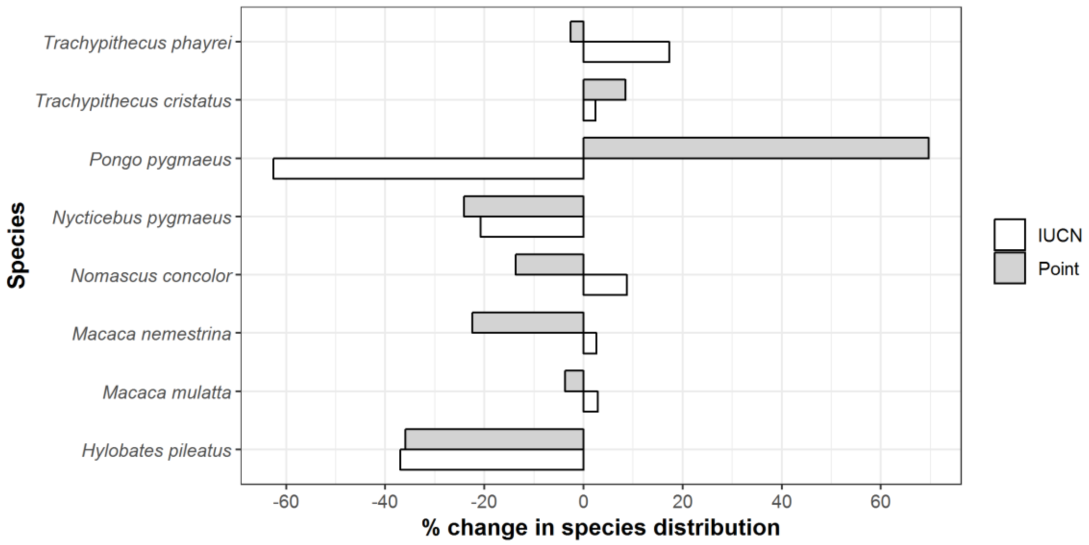


Figure 5.6. Predicted percentage change of species distributional areas from the present to future for 8 primates under the RCP2.6 scenario by the data derived from IUCN range maps and species occurrences.

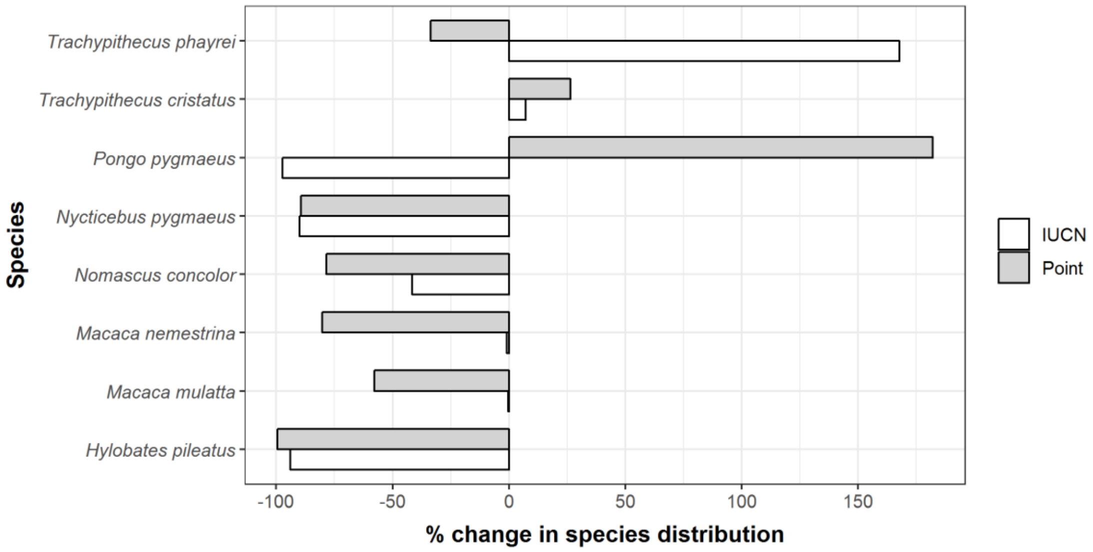


Figure 5.7. Predicted percentage change of species distributional area from the present to future for 8 primates under the RCP8.5 scenario by data from the IUCN range maps and species occurrences.

5.5 Discussion

5.5.1 Database of species records

This study identified 8 primate species that had an appropriate number of species point occurrences for species distribution modelling (> 10 localities); it represents about 8% of all recognised primate species in Southeast Asia, supporting the assertion that a lack of species point locality data is still a major problem in this part of the world. Many more species could potentially be modelled if we relied only on the IUCN range maps. Poor availability of data records may be caused by several reasons. Firstly, although many research studies about primates have been conducted extensively throughout the region, there is still a lack of systematic collation of primate records in Southeast Asia. One of the main obstacles could be because different languages are used in different countries. Language barriers may lead to the difficulty in gaining access to local databases and prevent effective communication in exchanging data and sharing information. Therefore, a higher level of collaboration between scientific researchers and local authorities is required to overcome this challenge. Secondly, the particularly low number of compiled records for several primate species may be explained by the characteristics of the species. *P. pygmaeus* and *H. pileatus*, for example, have been classified as endangered species by the IUCN due to an on-going decline in the populations over their past three generations (Ancrenaz et al., 2016). The threatened status of the two species together with fragmented habitats may result in low encounters of the species; this corroborates our assertion of the importance of integrating historical records into Species Distribution Models (see Chapter 3 and 4). Lastly, severe human pressure in the region has led to an unwillingness to make precise location information of species available, for fear of increasing the risk of hunting and poaching, especially for critically endangered species. It was found that in GBIF, there was an attempt to protect the threatened primate species by the intentional provision of GPS coordinate information of species observations with uncertainty of more than 5,000 metres. These locality points with inaccurate coordinate data were excluded from our database for the analyses and therefore reduced the number of species records in the study even further.

5.5.2 The reliability of SDMs

Overall, high AUC scores (≥ 0.93) of all models generated by both types of data indicate that SDMs derived from using either point locality data or the IUCN range maps are robust and can provide useful information for the study of species habitat suitability. The maximum AUC score of 1.0 achieved by using point data of the pileated gibbon (*H. pileatus*) indicates the ability of model performance in perfectly distinguishing species presence records from background data, or it may imply that the distribution of this species is restricted by environmental variables used for modelling (Hernandez et al., 2006; Levinsky et al., 2007). The pileated gibbon is generally found in moist, seasonal evergreen and mixed deciduous-evergreen forests. Its main diet relies on fruits, shoots, immature leaves and insects (Brockelman et al., 2020). Thus, temperature and precipitation are environmental factors that are certainly important for the occurrence and survival of the species.

However, caution is required when interpreting the findings of models with a small number of species records. The sample size may affect the reliability of the predicted range size. 16 localities of *H. pileatus* occurrence were observed from its entire range. This small number of presence sites may not be able to capture all the environmental conditions that the species prefers and narrow species niches. Consequently, the models with point data may predict small range sizes for *H. pileatus* because the very specific combinations of environmental variables were rarely found over the region (Levinsky et al., 2007).

5.5.3 Discrepancies in estimates of species richness and ranges

Species ranges generated by distribution models are generally likely to be overestimated due to the difficulty to include all range-determining factors such as species' dispersal ability and biotic interactions (Pineda and Lobo, 2009; Vasconcelos et al., 2012). SDMs with point occurrence data are often found to overestimate species ranges even more than range maps, which can in turn lead to higher species richness estimates (Herkt et al., 2017; Vasconcelos et al., 2012). In this study, there were point occurrences of primate species that were collected beyond the range maps. Species occurrences in the database were compiled from 1945 to the present, while the IUCN range maps were created more recently in the later 2000s and tended to reflect the current species ranges. It could be that the species may now be extirpated in locations where they were previously reported, and such records have been rejected when building the IUCN range maps. SDMs with point occurrences may therefore provide insight into the historical ranges of the species (Graham and Hijmans, 2006). Hence, the predictions of larger species ranges and higher species richness derived from point occurrence-based models here are not unexpected.

The number of species occurrences is likely to explain the discrepancies between richness maps generated by SDMs with point and range map data (Graham and Hijmans, 2006). Under the current environmental conditions, SDMs-based range map data generally predict higher species richness in central Borneo than the prediction of point occurrence data. A small number of occurrences relative to the range map area collected on the Borneo island for a few primate species (Figure 1) may lead to this prediction of SDMs. At the area with no species occurrences, climate variables that were dissimilar to the area with species occurrences might be considered unsuitable habitats for the species by distribution models generated using point occurrence data (Graham and Hijmans, 2006; Kadmon et al., 2004).

Furthermore, sample size and bias in point occurrences may influence the disagreement in species range size estimates. Discrepancies in locations of predicted species ranges were commonly found among all primate species in our study. The least agreement between predictions under the current climate conditions was for *H. pileatus*. A small number of occurrences of this species were collected along the western part of the range map, leaving a large geographical sampling gap in the east (Figure 1; *H. pileatus*). In contrast, for *N. concolor* and *N. pygmaeus*, who had prediction agreements of >50%, species occurrences of these species were collected from sites throughout their range maps (Figure 1; *N. concolor* and *N. pygmaeus*). However, a strong disagreement in range sizes (>70%) was still found in species with a relatively large sample size (>80 localities i.e. *M. mulatta*). This suggests that species with large geographical ranges may require more point occurrences to predict small discrepancies (Herkt et al., 2017).

5.5.4 Implications for macroecological research and future study

In this study, the important point raised is that although SDMs provide a powerful tool for assessing the potential impacts of climate change on species distribution, using different types of input data can result in completely different conclusions. The opposite direction of predicted species responses to future climate change for several primate species such as *P. pygmaeus* can potentially lead to a misunderstanding of the true threatened status of the species and possibly mislead conservation planning.

However, it did not identify here which data type is the best for modelling species distribution; therefore, it is not possible to recommend the use of one data type over another. A further layer of analysis with more species and environmental variables such as elevation is required to potentially justify the use of these data types towards more reliable predictions. What can be recommended to macroecological researchers from this study is the use of multiple data sources to integrate all aspects of information of a known species occurrence to obtain more robust analyses of species-environment relationships. Point locality and range map data can be used to cross-check the reliability and validity of the information regarding species occurrence. Caution should be exercised when relying solely on a single source of data for macroecological analyses, especially for endangered or rare species with small numbers of occurrences. Nevertheless, in some parts of the world where there is incomplete species information, the use of any species data available to generate SDMs may still provide valuable information for a broad macroecological perspective; indeed, with the aim of understanding the pattern of species richness here, point occurrence data and range maps have revealed a useful insight.

Chapter 6: The effectiveness of protected areas in Thailand in the conservation of large mammal species under future climate change

6.1 Abstract

1) In the face of climate change, protected areas (PAs) have been expected to facilitate migration and preserve more spaces for species ecological adaptation. Hence, it is important to include species responses to environmental changes when assessing the effectiveness of PAs. The ‘Zonation’ reserve design software can be used to examine the conservation values of PAs and identify areas of high priority in order to ensure the achievement of long-term conservation objectives.

2) Species data for 16 large mammal species in Thailand were obtained from the surveys of PAs across the country between 2004 to 2007. Maxent was used to generated species distribution maps under current and future climate conditions. Zonation with the ABF model and land cover data was then used to calculate the conservation value of each grid cell across the country. Changes in the conservation values of PAs and non-PAs under changing environments were examined.

3) It was predicted that the current species richness of large mammals in Thailand (1.89 species per grid cell) will decline under two future climate scenarios (0.97 species under RCP2.6 and 0.57 species under RCP8.5). Under the current climate conditions, 58.2% of high priority cells were located within PAs. The mean ranking score of PAs (0.83, SD = 0.15) was significantly higher than those of non-PAs (0.41, SD = 0.25). In the future, these rankings were expected to remain relatively similar whereas the percentage of high priority cells in PAs would slightly reduce to 58.0% and 57.4% under RCP2.6 and RCP8.5, respectively.

4) The results from Zonation suggest that the current PAs in Thailand are likely to be effective in supporting large mammal species under future climate warming. However, the gradual decrease in high priority cells in PAs indicate that PAs will continuously require deliberate conservation planning to maintain these sites. The remaining 41.8% of high priority cells outside PAs also deserve higher levels of protection.

6.2 Introduction

Over the past few decades, protected land areas have been constantly expanding. In 2016, there were more than 100,000 sites under legal protection worldwide, covering 14.8% of the world's terrestrial area (WDPA, 2016). Although protected areas (PAs) were primarily established for the long-term conservation of biodiversity habitat and the maintenance of ecosystem functions, they are now expected to contribute to the mitigation and adaptation challenges under the current conditions of rapid population growth and environmental changes (Dudley, 2008; Watson et al., 2014). In the face of climate change, the expansion and the increase of natural protected area coverages are believed to play an important role in providing corridors for facilitating species migration and preserving more spaces for species ecological adaptation (Dudley, 2008; Mansourian et al., 2009). However, it is often unclear whether PAs can achieve these fundamental objectives since they are also vulnerable to future climate change (Chape et al., 2005; Mansourian et al., 2009).

Climate change can have a direct impact on PAs by altering environmental conditions of microhabitats, which in turn result in changes of species composition within the PAs (Hannah, 2008). Under climate change, the temperature within PAs of Thailand was estimated to be approximately 2°C cooler than the areas outside PAs. Even though the annual precipitation was expected to increase in both PAs and non-PAs of Thailand, higher levels of precipitation inside the PAs were anticipated (Klorvuttimontara et al., 2011). Variations in environmental conditions of PAs and non-PAs may force some species to move beyond PA boundaries for favourable habitats, while others that are currently outside the PAs may move in when suitable conditions become available. Shifts in species distributions may no longer allow PAs to support biodiversity, for which they were initially planned (Hole et al., 2009). It is therefore important to include species responses to environmental changes when measuring the effectiveness of the current PAs and planning the establishment of new PAs. Especially in the tropics, where there are high levels of biodiversity, understanding the changes in PA values may enhance the achievement of long-term conservation objectives and assist in the decision-making process for better conservation plans and management of PAs in the future.

6.2.1 Spatial conservation prioritisation approach to evaluate the effectiveness of PAs

The effectiveness of PAs can be assessed by using many approaches including spatial conservation prioritisation. This approach is a technical stage within the broader concept of systematic conservation planning (SCP) which comprises a set of operational models focusing on planning, implementing and monitoring conservation actions (Lehtomäki and Moilanen, 2013; Margules and Sarkar, 2007). Spatial conservation prioritisation is traditionally used to support decision making in the design and expansion of reserve networks (Moilanen, 2013). This technique uses spatial analysis of quantitative data to prioritise areas for conservation action and investment (Wilson et al., 2009). Kukkala and Moilanen (2013) have suggested the 12 key concepts of spatial conservation prioritisation as “to create a system of protected areas that conserve as much of a region’s biodiversity, species, and habitats (representation) while covering different spatial scales and compositional and hierarchical levels (comprehensiveness, representativeness) and also taking these principles into account in the long term (adequacy and persistence). In the real world, not all biodiversity and ecosystems can be protected and, consequently, we must apply the complementarity principle and economic objectives (efficiency and cost effectiveness) so that we can achieve effective solutions. We should ensure that critical biodiversity is adequately protected (irreplaceability and replacement cost), but in a flexible (flexibility) manner that allows for implementation and integration with the future needs of competing land uses (vulnerability and threat)”.

Moreover, biodiversity processes are dynamic and take place both in time and space (Pressey et al., 2007). These factors together with human impact on the environment demand the protection of habitats to find the optimal balance between conserving the present sites of high conservation values and the most cost-effective sites to minimise biodiversity losses in the future (Moilanen et al., 2011). The quantitative technique of spatial conservation prioritisation has integrated computational tools for analyses of various data types to identify the best areas for protection and conservation investment (Lehtomäki and Moilanen, 2013; Minin et al., 2014). This approach has been developed to be compatible with GIS data such as current and future distributions of biodiversity features across a large geographic extent, and connectivity of habitats, allowing the evaluation of PA effectiveness under changing environments over time (Minin et al., 2014).

6.2.2 The Zonation framework and software for conservation prioritisation

The design of planning tools for spatial conservation prioritisation is based on the following three key concepts: complementarity, irreplaceability and vulnerability (Sarkar et al., 2006). The principle of complementarity is to minimise the cost of conservation action and ensure that all biodiversity features, e.g. species persistence and habitat types, receive some level of conservation investment (Wilson et al., 2009). The complementarity value of the site is measured from its quantitative contribution to the representation of unrepresented biodiversity features in the existing set of prioritised sites (Sarkar et al., 2006). The concept of complementarity is essential because the conservation priority of planning areas is dynamic. It can change according to the establishment or expansion of a network of priority areas, and changes in the distribution of biodiversity features (Wilson et al., 2009). The second key concept is irreplaceability. It concerns the importance of the planning site inclusion in the network of priority areas to achieve conservation goals. The sites considered irreplaceable include, for example, those experiencing a rare occurrence of a biodiversity feature or containing the only cost-effective example of a feature (Wilson et al., 2009). Vulnerability is the third crucial concept for designing planning tools because the aim of identifying priority conservation areas is to maintain species persistence by mitigating threats to biodiversity and minimising future loss (Sarkar et al., 2006; Wilson et al., 2009).

Zonation is a freely available software programme that has been increasingly used for various conservation purposes in both marine and terrestrial systems of many countries including Finland, Madagascar, New Zealand and UK (Kareksela et al., 2013; Kremen et al., 2008; Lehtomäki et al., 2009; Moilanen et al., 2011, 2005; Sirkiä et al., 2012). It has adopted the key principles to focus on the identification of the most important areas that support high connectivity for long-term biodiversity persistence (Lehtomäki and Moilanen, 2013). The Zonation software includes a set of analytical features, allowing for the evaluation of existing or proposed reserve networks, the identification of ecologically low-value areas for economic use, and many prioritisation purposes. Analysis by Zonation operates on raster grids of predicted species distribution and other relevant features across the landscape. The process starts by assuming that protecting all species is the best way for conservation. It produces a hierarchical prioritisation of an area by removing cells that lead to the smallest aggregation marginal loss in biodiversity. The removal process also takes into account the connectivity of habitats and priority over biodiversity (Moilanen et al., 2014). The least valuable cells for biodiversity receive the lowest rank (close to 0) and the most useful cells obtain the highest rank (close to 1). The cells with the highest rank are generally those with high species richness or high occurrence patterns of rare species (Lehtomäki and Moilanen, 2013; Minin et al., 2014). The main outputs of Zonation consist of a priority-rank map and performance curves that illustrate the conservation level of each biodiversity feature at each removal step (Moilanen, 2013).

There are several ways to measure conservation values of areas depending on cell removal rules in Zonation. The additive-benefit function (ABF) focuses on species richness. It calculates the conservation value of cells based on values of all species. ABF is appropriate when species are believed to be a representative of species pools (Moilanen, 2007). The core-area zonation (CAZ) relies on the presence of rare species. It calculates conservation values based on the occurrence of the most important species in the cell (Minin et al., 2014). Therefore, the cells with low species richness could be ranked as high priority if there is a high occurrence rate of a single rare species (Lehtomäki and Moilanen, 2013; Minin et al., 2014; Moilanen, 2007). CAZ is used to ensure that all of the important species are protected (Moilanen et al., 2014). Target-based planning aims to achieve a specified target representation of each species (Moilanen, 2007).

6.2.3 Chapter aims and objectives

1. To use Maxent models to examine how large mammal species richness in Thailand may change under future climate change (RCP2.6 and RCP8.5).
2. To use Zonation software to calculate the conservation values of areas across Thailand.
3. To compare the conservation values of PAs and non-PAs.
4. To determine the effectiveness of PAs under future climate scenarios.

6.3 Materials and methods

6.3.1 Input data

Species records of 16 large mammal species were derived from the surveys in Thailand conducted by the Wildlife Research Division between 2004 and 2007 (Table 6.1). These species were selected based on their current conservation status and importance to the ecosystems (i.e. umbrella, indicator and keystone species). The surveys initially aimed to assess the status of large mammals in PAs of Thailand and were carried out to cover 56 wildlife sanctuaries and 95 national parks across the country. Prior to the fieldwork, park officials were trained to use field equipment and record data systematically. The survey routes were designed to cover PAs. Evidence of species presence including sighting, footprints, dropping and marking signs on trees along each survey track, was recorded with GPS coordinates (Wildlife Research Division, 2010). Point locality data of species were thinned out to a one point per 1-km resolution grid cell to reduce recording errors and match with the resolution of existing environmental data.

Maps of projected species occurrences were generated by Maxent version 3.4 using species records and six climatic variables (available from http://www.worldclim.org/version1), including annual mean temperature (BIO1), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual mean precipitation (BIO12), precipitation of the wettest month (BIO13) and precipitation of the driest month (BIO14), at 30 arc-second under the current conditions and future climate scenarios (RCP2.6 and RCP8.5). This chapter uses finer resolution species data and environmental variables than those in other chapters because prioritisation results are sensitive to the resolution used in the analysis. Input data of low resolution can lead to less reliable outcomes (Arponen et al., 2012).

The total area of Thailand consists of 620,614 grid cells. The land use map of the country was built by the Royal Forest Department in 2000 based on the remote sensing data from Landsat 5-TM. In this study, it was classified into four major land use types: forest, natural non-forest, agricultural and urban areas (Klorvuttimontara et al., 2011). Each land use type accounted for 33.0%, 1.6%, 64.5% and 0.9% of the total land area of Thailand, respectively (Figure 6.1). Locations and boundaries of PAs were obtained from the World Database of Protected Areas (WDPA; available at https://www.protectedplanet.net/) (Figure 6.2). PAs of Thailand consist of 128,657 grid cells, approximately 20.7% of the country’s total area.

Table 6.1. Large mammal records used in the analyses

Species	Common name	IUCN Status[1]	No. of presence sites
Bos gaurus	Gaur	VU	1187
Bos javanicus	Banteng	EN	142
Bubalus bulalis	Water buffalo	EN	33
Canis aureus	Golden jackal	LC	512
Capricornis sumatraensis	Sumatran serow	VU	351
Cuon alpinus	Dhole	EN	211
Elephas maximus	Asian elephant	EN	1850
Helarctos malayanus	Malayan sun bear	VU	705
Muntiacus muntjak	Barking deer	LC	1893
Naemorhedus caudatus	Long-tailed goral	VU	36
Panthera pardus	Leopard	VU	271
Panthera tigris	Tiger	EN	235
Rusa unicolor	Sambar deer	VU	993
Sus scrofa	Wild boar	LC	3935
Tapirus indicus	Malay tapir	EN	475
Ursus thibetanus	Asiatic black bear	VU	543

[1] IUCN status categories: EN, Endangered; VU, Vulnerable; LC, Least Concern.

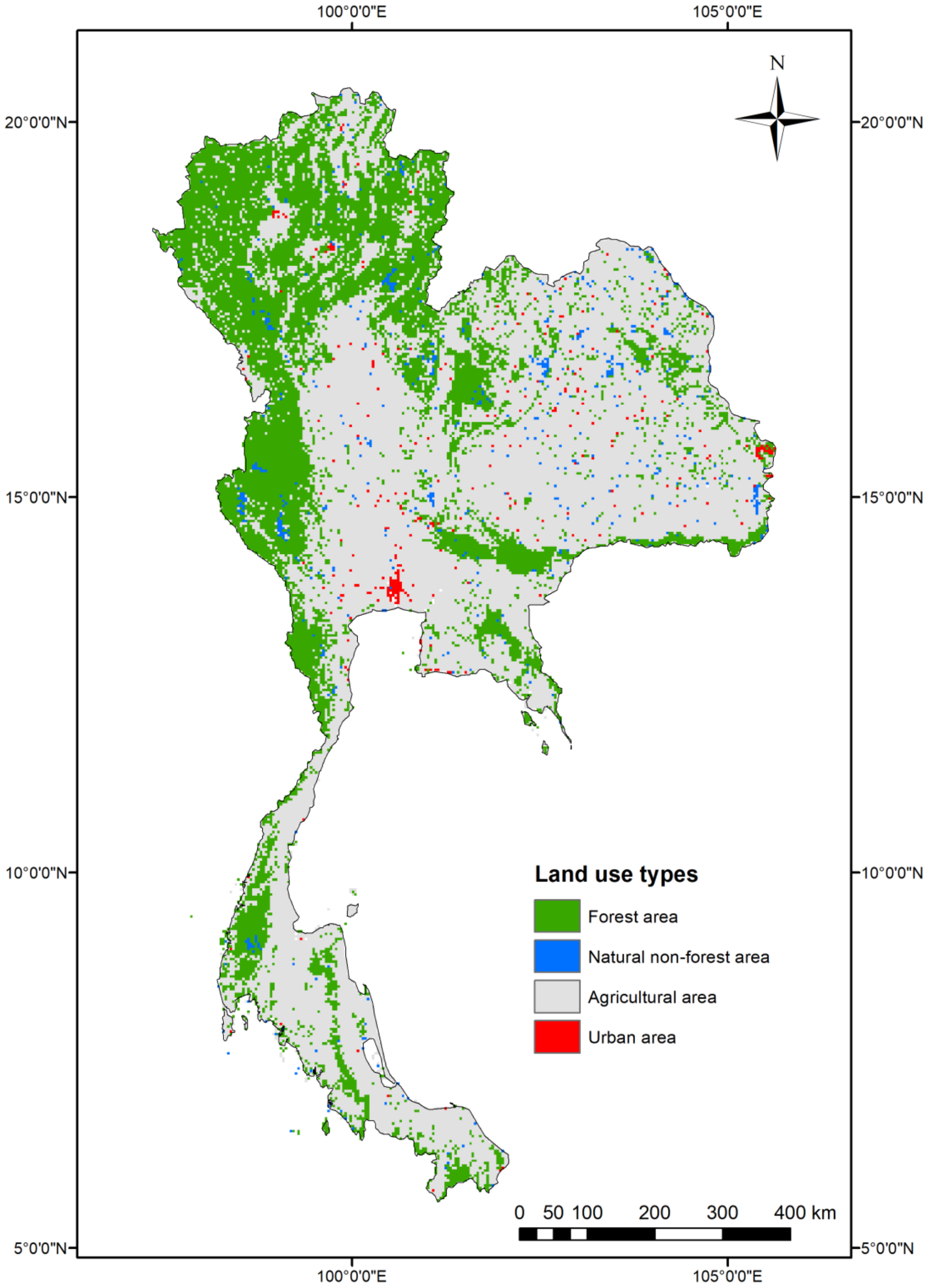


Figure 6.1. Land use map of Thailand

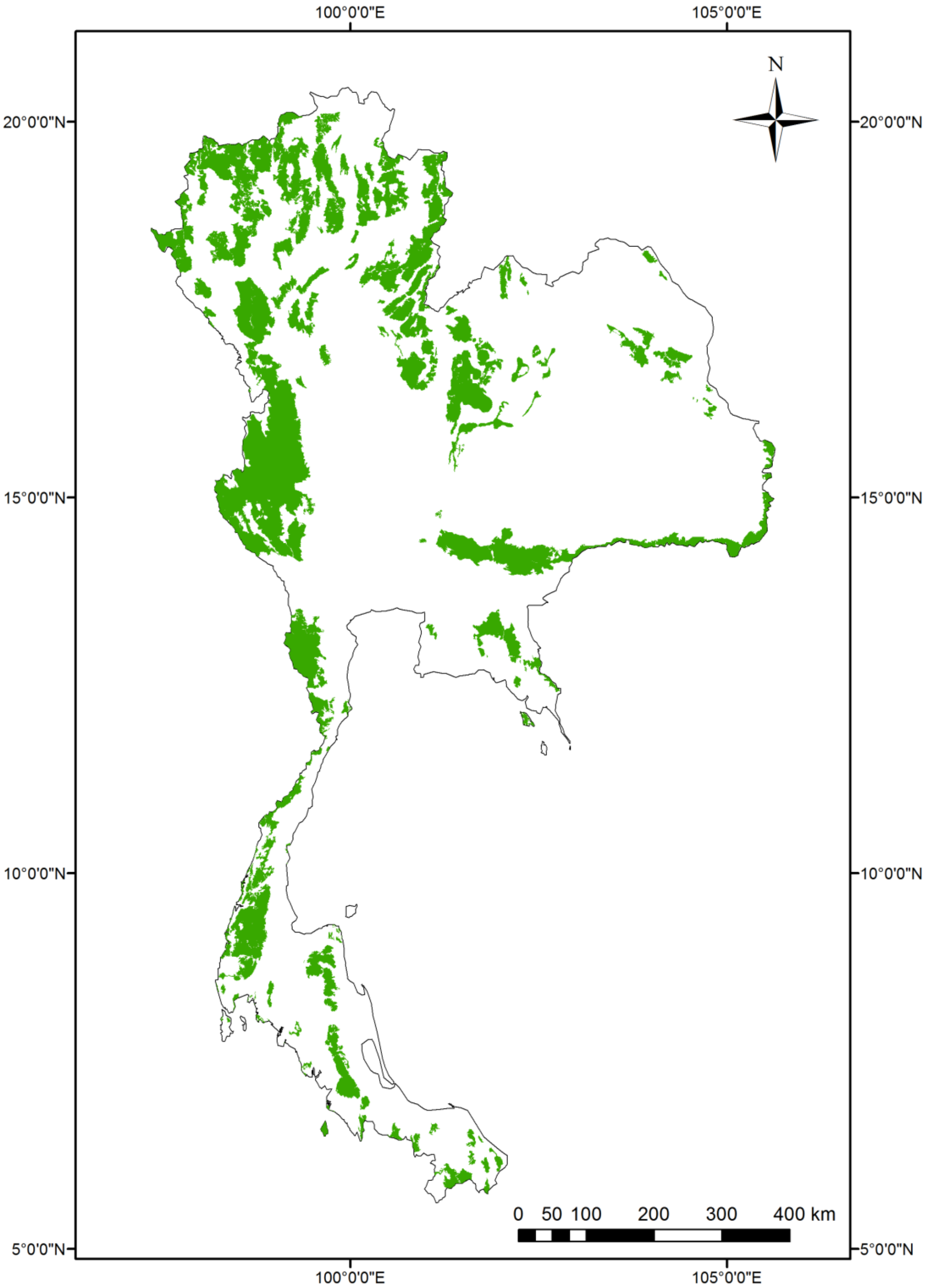


Figure 6.2. Map of PAs in Thailand

6.3.2 Identifying the prioritised areas and examining the changes in conservation value of PAs using Zonation software

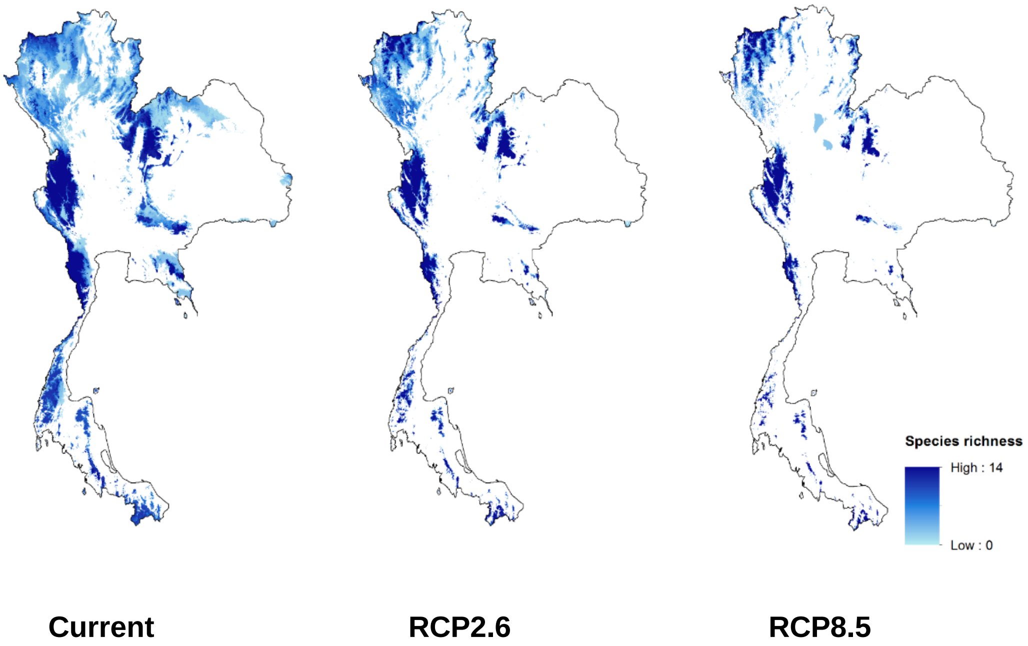
Zonation version 4.0 with the ABF model was used to identify prioritised areas of Thailand to ensure high species richness because all species in the study play a crucial role in the ecosystems, i.e. while tigers are top predators in tropical rainforests, wild boars and sambar deer are important prey species for tiger persistence (Hayward et al., 2012). Although ABF included all large mammal species when calculating the conservation values of each grid cell, each species was assigned a different weight according to its conservation status. The weight was set higher for species with a higher level of conservation concern: 1 (LC), 4 (VU) and 6 (EN) (Pouzols et al., 2014). Other parameters that were set when running Zonation were the warp factor and the hierarchical removal mask. The warp factor is the number of grid cells removed at each stage of the removal process (Minin et al., 2014); this was set as 10 to achieve the best performance of the computational tool while obtaining reliable results (Klorvuttimontara et al., 2011). The land use map of Thailand was used as the removal mask to specify the removing order of cells. This feature divided cells into three categories: 1 (remove first), 2 (normal) and 3 (remove last). Cells in remove first category were from agricultural and urban areas, which are considered as unsuitable habitats for large mammals. Forest areas, which are preferable habitats, were set to remove last.

Zonation was run using the distribution data of large mammals under three different scenarios (current, RCP2.6 and RCP8.5) that were derived from Maxent. It produced the value of cells ranging from 0 to 1. Cells with value > 0.7 were considered as high priority (Klorvuttimontara et al., 2011). To examine the impact of climate change on the conservation value of sites, the changes in the ranked scores of each cell under three scenarios were calculated. A Mann-Whitney U was used to compare the difference in mean rank scores of grid cells between PAs and non-PAs.

6.4 Results

6.4.1 Species richness

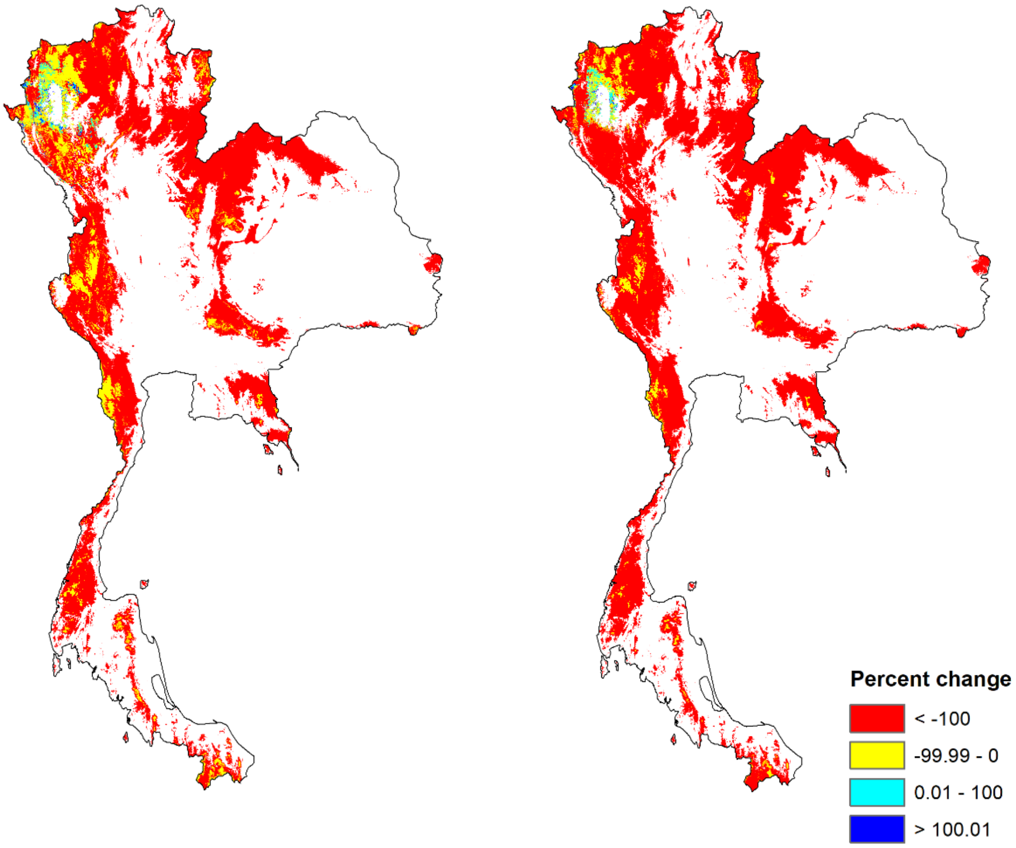
Species richness refers to the number of species present in each grid cell of the study area. Maps of large mammal species richness in Thailand under three climate change events were generated by overlaying predicted species distribution maps of 16 species (Figure 6.3). Under the current climate conditions, the mean species richness across the country was 1.89 species per grid cell (SD = 3.47). In the future, the species richness of large mammal in Thailand is expected to decline under both climate scenarios. Particularly in the southern part of Thailand, species are likely to disappear as temperature and precipitation increase. In the future, the mean species richness was predicted to decrease to 0.97 (SD = 2.65) and 0.57 (SD = 2.10) species per grid cell under RCP2.6 and RCP8.5 scenarios, respectively. However, the results suggest a likelihood of new species migrating to some areas in the northern part of Thailand.



Current **RCP2.6** **RCP8.5**

Figure 6.3. Maps of predicted large mammal species richness in Thailand PAs under the current conditions and two climate scenarios. Background areas in white are where SDM predicted species absence.

Percentage changes in large mammal species richness of Thailand were calculated based on the changes from the current species richness (Figure 6.4). Warm colours indicate areas with a decrease in species richness, whereas cool colours denote areas with an increase in number of species. If the RCP2.6 scenario happened, the mean species richness across the country would be estimated to decline by 81.82% (SD = 45.15). The loss of species was expected to be more severe under RCP8.5 with the prediction of 91.88% decline (SD = 31.83).



RCP2.6 **RCP8.5**

Figure 6.4. Percentage changes in large mammal species richness across Thailand under future climate scenarios

6.4.2 Prioritised areas and conservation values of PAs under changing environments

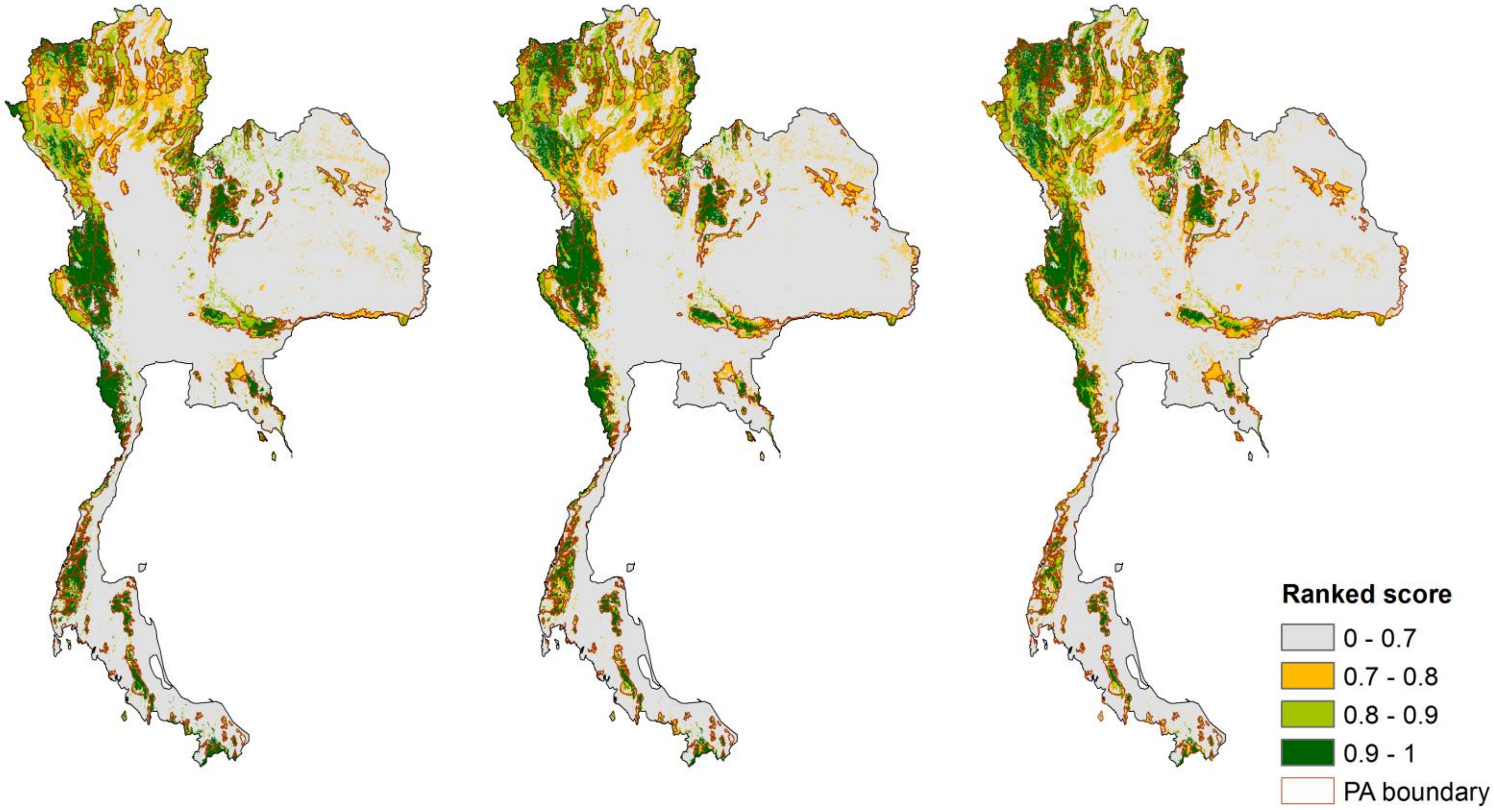
The rank score map of Thailand produced by Zonation is shown in Figure 6.5. At present, there are 186,038 grid cells that have been ranked more than 0.7 and therefore classified as high priority areas for large mammals. These high priority sites account for 30% of the total area of Thailand (434,576 cells of low priority, 70% of Thailand area). However, only 108,343 cells or 58.2% of these high priority sites were located within PAs, while 77,695 cells (41.8%) were not protected. The percentages of high priority areas in PAs were estimated to slightly decrease to 58.0% and 57.4% under RCP2.6 and RCP8.5, respectively.

The mean rank scores of cells were calculated for PAs and non-PAs in Thailand. The values were found to be statistically significantly higher in PAs compared to non-PAs for all climatic conditions (Mann-Whitney U test, all p-values < 0.001). For both types of area, the values of the mean and SD remained relatively similar across the environmental conditions. Under future climate change, the mean scores were likely to decline, whereas the SD values tended to increase. The current mean score of PAs (0.83, SD = 0.15) were higher than that of the areas outside PAs (0.41, SD = 0.25). In the future, it was predicted to be slightly different according to the climate change scenarios. Under RCP2.6, while the mean Zonation score remained at 0.83, the SD rose to 0.16. For RCP8.5, the average score decreased to 0.81 whereas the SD slightly increased to 0.18 (Table 6.2).

Table 6.2. Summary statistics of mean rank scores and SD for PAs and non-PAs

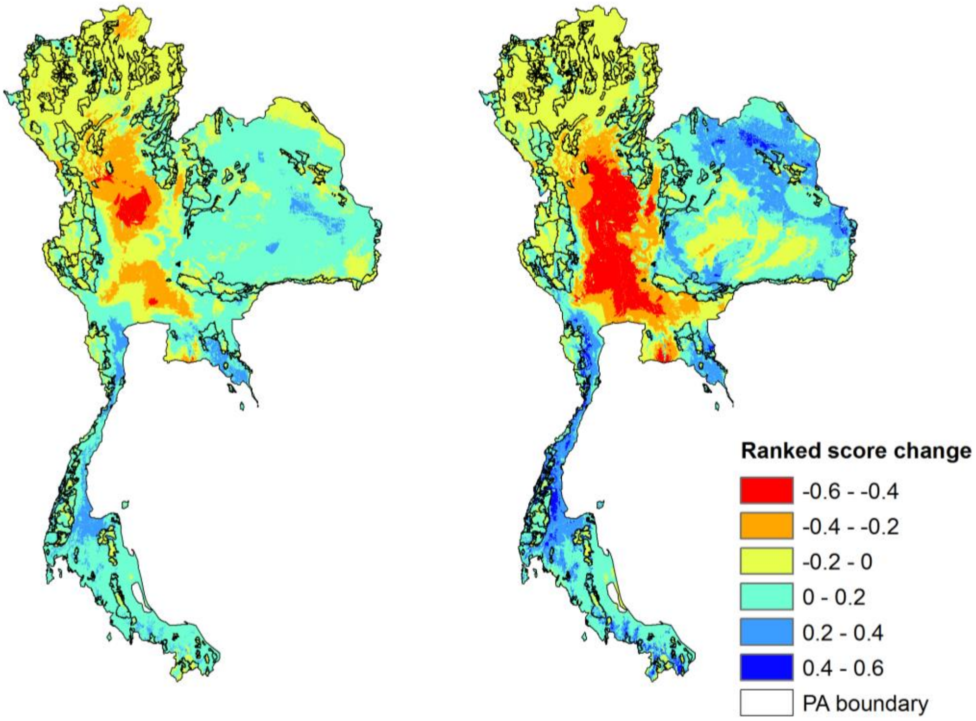
Statistic	**Scenario**	**Area**		**Mann-Whitney U test**
		PAs	Non-PAs	
Mean rank score	Current	0.83	0.41	All p values < 0.001
	RCP 2.6	0.83	0.41	
	RCP 8.5	0.81	0.42	
SD	Current	0.15	0.25	NA
	RCP 2.6	0.16	0.25	
	RCP 8.5	0.18	0.25	

The overall changes in the rank scores of Thailand based on the present conditions are shown in Figure 6.6. A wider range of changes is expected to occur under RCP8.5. The changes in the conservation value under RCP2.6 ranged from -0.6 to 0.4, while they were predicted to range from -0.6 to 0.5 under RCP8.5.



(a) **(b)** **(c)**

Figure 6.5. Ranked score map of Thailand based on the distribution data of large mammals under different climate conditions (a) current (b) RCP2.6 and (c) RCP8.5



RCP2.6 **RCP8.5**

Figure 6.6. Changes in Zonation ranked scores of Thailand under climate change scenarios compared to the present. Warm colours denote a decrease in the conservation value of the area, whereas cool colours indicate an increase. Polygons on the map indicate locations of PAs.

6.5 Discussion

6.5.1 Changes in large mammal species richness in Thailand

Climate change was found to be a potential driver of the range contraction and the extirpation of large mammal species in PAs of Thailand. In the future, dramatic declines in species richness were predicted to occur across the country. The areas with the highest species richness were likely to shift to the north; this may be due to the sensitivity of tropical species to changing climates. Species in the tropics have adapted to cope with a narrow range of temperature and seasonal variation (Wright et al., 2009). Many such species have been suggested to live near their temperature limits before the start of the recent climate change (Deutsch et al., 2008). Therefore, only a small change in temperature may exceed the tolerance level of these species and consequently lead to a shift in species ranges (Wright et al., 2009). Large mammals may respond to warming temperature by moving to cool refuges, which are likely to be in an upslope or poleward direction. However, the distance to cool refuges is likely to be the greatest around the equator. This factor, as well as the shallow latitudinal temperature gradient in the tropics, may limit the species' dispersal ability (Colwell et al., 2008; Wright et al., 2009). The extinction of the species may occur when there is no accessible corridor to facilitate their dispersal to cooler habitats (Colwell et al., 2008).

In addition, PAs in Southern Thailand were expected to have a reduced ability to maintain species richness in the future. PAs in this region may need urgent conservation action to prevent this potential loss. It is also important to ensure that the existing PAs have established networks to provide corridor stepping stones for vulnerable species. The size of PAs in the south tends to be smaller than PAs in the northern part of the country (Wildlife Research Division, 2010). This may be another factor responsible for species loss apart from climate change. Small PAs were found to mismatch the requirement for home range size of large mammal species, as it may be impossible to protect the entire species population within the PAs (Chundawat et al., 2016). Further studies on the relationship between PAs size and species richness and the effects of habitat fragmentation may be beneficial for the assessment of PA effectiveness.

6.5.2 The conservation values of PAs under current and future climate changes

The high conservation values of PAs obtained from the Zonation analyses suggested that PAs are currently effective in supporting large mammal biodiversity. The conservation values of PAs were found to be higher than that of non-PAs because PAs in Thailand commonly cover forest areas, which are favourable habitats for large mammals. The species in the study heavily rely on forest habitats for food and shelter. They generally have large home range sizes and require high quality habitats in the core forest areas (Kinnaird et al., 2003). The order of cell removal in the hierarchical removal mask was also set according to the species' preference. Hence, Zonation generated high ranked scores for forest habitats and adjacent areas. Currently, PAs hold nearly 60% of high priority sites. However, the remaining 40% of the high priority areas are without designation. These sites present potential concern for conserving biodiversity and require increased levels of attention and protection.

Even though there were predictions of only a slight decrease in the conservation values of PAs in the future, the gradual loss of high priority areas in PAs was expected under both future climate change scenarios (0.2% and 0.6% decreases under RCP2.6 and RCP8.5, respectively). The decrease in the mean and the higher variation in SD of the conservation values indicate that PAs will continue to require deliberate conservation management practices to maintain and improve these values. The conservation actions may include strategies to reduce deforestation in PAs and to alleviate human disturbance, which poses severe problems in tropical regions.

It was estimated that 12% of forest cover in Thailand may be lost by 2050 under the current trend of land-use conversion. Forest habitats were predicted to remain mostly in the upper northern and the western parts of the country due to their geographic features of high altitude and low accessibility (Trisurat et al., 2010). The results from the previous study, together with predictions presented here of increased conservation values in the northern areas of Thailand under climate changes (Figure 6.5), suggest that maintaining protection and enhancing connectivity of these areas may produce high return on conservation investment. The focus on reforestation and improving forest habitat quality within PAs are suggested strategies that can contribute to an increase in the conservation values of PAs in the future, while avoiding conflict with local residents over a growing demand for land.

6.5.3 Implications of the study

Thailand has generally expanded the existing PAs and established new PAs based on four major criteria. Firstly, the size of the area must be sufficient for maintaining ecological systems. Secondly, the area must be rich in natural resources or has outstanding natural beauty. Thirdly, the area must be suitable for tourism and education. Lastly, the aims of the establishment must be to conserve natural resources and to use them for research and leisure proposes (DNP, 2017). However, over the past few decades, the country has joined many conservation agreements such as CITES (ratified in 1983), Ramsar Convention (ratified in 1998) and Conservation on Biological Diversity (CBD, ratified in 2004), which require Thailand to develop national strategies to achieve the agreed targets. Several agreements require the management of PAs to enable mitigation and adaptation measures under climate change. The Zonation analyses can provide useful information for stakeholders and decision makers to create effective conservation plans and place conservation efforts on where they are most appropriate. The results presented here suggest that PAs with decreased conservation values should be highlighted and attempts should be directed at the improvement of forest cover and habitat quality. Additionally, it is essential to ensure the ongoing protection and conversation management of the existing PAs, as they are likely to remain high priority areas in the future.

6.5.4 Limitations and future work

In this chapter, Zonation was used to assess the conservation values of existing PAs for large mammal distributions under future climate scenarios. The conservation value of sites in Thailand appeared to be dependent on forest. This is because most of large mammal species in the study are forest-dwelling. Several stages in species life history are associated with this type of habitat; therefore, land cover was used as the removal mask in the Zonation process. The results were greatly influenced by the reliability of the land cover data and the assumption of no changes in land cover over a period of time in the study. However, Thailand is experiencing some of the highest rates of deforestation in the world (Sodhi et al., 2004) so it is predicted that there will be a significant degree of change in land cover in the future. Thus, scenarios involving land cover changes in the future could be integrated into Zonation in future work to obtain a better understanding of changes in conservation values of PAs.

Zonation was implemented using the outputs from species distribution models of large mammals. However, species data obtained from surveys in Thailand is biased towards specific areas, PAs. Thus, the results from SDM may contain inaccuracies in the predictions. In order to improve the predictive ability of the distribution models, species data from the areas outside PAs should be included in the modelling process or corrective approaches to data bias should be used in future work.

Chapter 7: General discussion

7.1 Summary of findings

This thesis investigates the impacts of environmental changes on large mammal distributions in Southeast Asia from the past to present, and predicts species responses to future climate change. Chapter 1 provides a review of the geological history and environmental changes of the region, showing that Southeast Asia has been a highly dynamic area where environmental change has occurred persistently over many thousands of years and that this has had significant effects on species diversity and community structure. Climate change has recently become a serious threat to biodiversity because it currently occurs at a rate much faster than previous changes the world has experienced. This rapid change has put a number of species at a high risk of extinction. Effective conservation planning is urgently required to prevent biodiversity loss. Species distribution modelling (SDM) has been increasingly used in macroecological research to investigate a relationship between species occurrence and environmental conditions and facilitate conservation planning and management. An introduction of the SDM framework is also provided in this chapter.

Chapter 2 provides a detailed description of all materials and methods used in the thesis. Species occurrence records had been compiled from published literature, archival and historical records, museum collections and online biodiversity databases before the processes of data manipulation was conducted. In total, the species dataset consisted of 556 fossil and 6,939 modern records from 24 large mammal species. Environmental data were derived from WorldClim version 1.4. Six climatic variables were selected for modelling processes. Overall, 7 SDM techniques implemented in two platforms were used for the analyses.

In Chapter 3, the impacts of climate change on large mammal distributions were examined using SDMs to project species distributions and predict how species may change under future climate scenarios. Fossil and modern occurrence data were used to investigate how species diversity may have changed over time by analysing changes in species richness and distribution. The rates of species range shifts spanning three time intervals: the last interglacial (~120,000 – 140,000 years BP), present (AD 1945 to present) and future (2050) were determined. The results showed that the species richness and distributions of large mammals in Southeast Asia have changed considerably since the Quaternary Period. The mean species richness was found to decline from 4.14 species per grid cell during the last interglacial to 2.46 in the present, while model predictions suggested that it would slightly drop further to 2.41 under the RCP8.5 scenario. The patterns and rates of range shifts were found to vary among and within species. In the future, large mammals are expected to shift their distributions 33 - 105 times faster than they did in the past period depending on future climate scenarios. However, large mammal species in the tropics with long generation times and generally narrow thermal tolerance ranges may not be able to increase range shift rates to keep up with future environmental change. The findings indicate that these species are particularly vulnerable to climate changes and face a high risk of extinction. Thus, they should be prioritised for conservation. Protection of large mammals and their habitats will also benefit many other species occupying the same area since large mammals play a crucial role in maintaining ecosystem functions and commonly have large home ranges.

In Chapter 4, fossil data were used to examine climatic niche conservatism in large mammals of Southeast Asia. The results showed evidence of niche conservatism among some of the focal taxa. Climatic niches for two primate species, *M. mulatta* and *N. concolor*, were found to remain stable over the past 100,000 years. This stability is likely due to factors including the ability of the species to cope with a wide range of climatic conditions and geographical barriers to dispersal, and gene flow that may prevent the evolution of new niches. Nevertheless, several species were found to shift their climatic niches and species distributions in response to changes. Current distributions of many species were likely to be influenced by recent climatic changes and anthropogenic activities. Tigers (*P. tigirs*), for example, have experienced high hunting pressure in Asia. This has led to a severe population decline and the disappearance of tigers from more than 90% of their historical range. At present, it is estimated that there are only 3,200 tigers remaining in the wild. Therefore, it is indicated that a combination of climate change and anthropogenic factors may lead to the extinction of the species that withstood numerous environmental changes in the past, especially critically endangered species that have experienced extreme range reduction and currently occupy restricted geographical ranges. The findings also highlight the need to step up conservation efforts for these species in order to prevent further biodiversity loss and the next megafauna extinction predicted to occur in Southeast Asia by the end of this century.

In Chapter 5, the discrepancies between the use of the IUCN polygon range map and point locality data for the examination of the patterns of primate species richness and species distributions in Southeast Asia were compared. Although the high AUC values produced by the SDMs with the two aforementioned data types are indicative of the predictive ability of both polygon range map-based and point locality-based models, the disparities between predicted species ranges derived from the different types of data were large enough to cause the inconsistency in the classification of the conservation status of the species and, subsequently, their conservation planning. Generally, the point occurrence data may predict larger species ranges and higher species richness than the IUCN range maps because they tend to produce the historical ranges of the species. These results indicate that caution is required when relying exclusively on a single source of species data to predict species responses to climate change. For this reason, the integration of multiple species data sources is recommended to generate more robust model predictions. Point locality and range map data can be used to cross-check the reliability and validity of the information regarding species occurrence. However, in some parts of the world where there is incomplete species information, the use of any species data available to generate SDMs may still provide valuable information for a broad macroecological perspective such as the pattern of species richness.

In Chapter 6, the Zonation software was used to examine the changes in conservation values of different areas across Thailand under future climate change and to assess the effectiveness of PAs in the future. The results showed that future climate change is likely to cause range contraction in large mammals of Thailand, engendering a decrease in species richness across the country. Currently, nearly 60% of the areas with high conservation values in Thailand are located within the PAs. This percentage is predicted to slightly decrease in the future, indicating that the PAs require continual conservation management to maintain their conservation values. In addition, the remaining 40% of the high priority areas outside the PAs are shown to have the potential to conserve biodiversity and deserve some degree of protection. Therefore, in order to achieve conservation objectives more effectively, information on species responses to future climate change should be taken into consideration in the process of establishing new or expanding existing PAs.

7.2 Limitations of the study

The findings of this study depend critically on the limited availability of data and the reliability of SDMs. Data on many large mammal species in Southeast Asia are scarce; this possibly reflects the rarity of the species throughout the study areas. However, data on many species are not made publicly available despite the attempts to protect their exact locations from high hunting pressure in the region; findings from this study indicate that other data sources should be explored to augment occurrence records. Species occurrence data in this study were biased towards China and Thailand, where I was able to access unpublished archival and records of historical large mammals. China has vast collections of flora and fauna archives spanning centuries, but in-depth historical research is required to exploit these data. Other Southeast Asian countries also have extensive archives, but language barriers and time availability have impeded the progress of historical research. This bias in the collection of data inevitably caused sampling bias. Although I used specialised modelling approaches to nullify the effects of bias and the small sample size, more data collected from different parts of the species' ranges may improve the reliability of model predictions and provide a better understanding of species responses to climate change. Furthermore, the uncertainty in model prediction may result from the challenge of the taxonomic classification of fossil records. New evidence based on genetic data analysis has supported the separations of many species into other genera (Brandon-Jones et al., 2004).

The uncertainty in the model predictions may arise from multiple causes. Currently, a number of modelling techniques and climate scenarios have been developed to assess impacts of climate change. The global climate models (GCMs) have been created by many modelling groups worldwide to project future climate. Using different GCMs may lead to uncertainties in model predictions due to their structural differences and variations in incorporated elements (Semenov and Stratonovitch, 2010). Therefore, in an attempt to reduce the uncertainty for the predictions in this study, I applied mean GCM scenarios to the projection (Hannah, 2012). Furthermore, the predictions of species distributions in the future did not consider factors such as dispersal ability, biotic interactions and human activity that may restrict species range shifts. Occurrences of many large mammal species are strongly influenced by human disturbance and prey availability. For example, high concentrations of tigers were found in areas with low human population density and living a long distance from villages (Johnson et al., 2006). The abundance of large ungulate prey taxa was also found to be crucial to the sustenance of tiger populations (Hayward et al., 2012). As a consequence, the models in this study that generally assumed unlimited dispersal were likely to overestimate species distribution under future climate change.

7.3 Conclusions

The findings of this study indicate that large mammal species in Southeast Asia are highly vulnerable to environmental change and now face an elevated risk of extinction. Large mammals are expected to shift at a faster rate than they previously experienced. Range contraction is predicted for many species, leading potentially to decreased species richness in many parts of the region. Hence, this region is in urgent need of trans-boundary conservation planning to prevent further biodiversity loss. Prioritising large mammal species for conservation will benefit a number of species co-existing in the same habitats. The findings may also apply to other tropical ecosystems, where future climate change will have a prominent impact on tropical biodiversity.

Using fossil and species data from museum collections and archival/historical records was shown to shed light on species responses to environmental changes. However, these records are likely to be poorly documented and tend to be under-reported in Southeast Asia compared to countries in Europe and the US (Newbold, 2010). Relatively small numbers of records of many species in the study may address this common problem of the tropics which support high biodiversity but lack systematic collation of species data. These findings indicate that Southeast Asia requires a greater level of communication and collaboration among local authorities and international experts to share information and data, which is key to success in protecting biodiversity.

Since climate change has become a significant threat to global biodiversity, various computational tools have been developed to determine its potential impact on biodiversity and mitigate the adverse effects on ecosystems. In this study, SDMs and Zonation were used successfully to investigate changes in species distributions and identify priority areas for conservation. Southeast Asia may benefit from the results of these analyses because they can provide useful information for conservation planning purposes and ensure the implementation of effective conservation actions. Consequently, this study could serve as a basis for further improvement in conservation strategies with the application of SDMs and Zonation by all stakeholders including policymakers. Although the study has shown that the large mammal species richness in Thailand is expected to decline under future climate change, the existing PAs are likely to remain high priority areas for conservation in the future. Increased conservation values predicted for the northern part of Thailand may indicate that ensuring protection of this region and enhancing connectivity of PAs in this part of the country will have the potential to yield the greatest return on conservation investment.

Increased protection for forests of high conservation values outside the PAs may also have a positive effect on biodiversity.

To the best of my knowledge, this study was the first to amass large mammal records of Southeast Asia spanning large time periods to analyse species responses to environmental changes. In this study, novel modelling techniques, including the uses of target group background data and ensemble modelling methods were employed to improve the accuracy in the model predictions of species responses. Thus, the findings concluded from this study will potentially provide valuable information, which will support the improvement of SDMs and the incorporation of prediction models into the decision-making process for our future conservation planning. The use of multiple data sources and the application of ensemble methods are recommended in the study of other taxonomic groups in order to reduce variance and enhance a better predictive performance of a model projection. This study also adds to the knowledge of the effect of climate change on tropical species and can serve to tackle the challenge of global biodiversity loss. It is suggested that large mammal species of Southeast Asia are vulnerable to climate change, especially ones with currently restricted geographical ranges. Remarkably, areas of possible climate change refugia (for example, northern Thailand) are identified in some parts of the region. Furthermore, this study presents a new venue for global collaboration between research scientists and local authorities in Southeast Asia for improved climate actions. Ultimately, it is essential that we, as a collective community, are aware of climate change impacts and embrace scientific recommendations to reduce adverse effects on the ecosystems and the communities.

7.4 Future research

In the face of climate change, it is vital to gain insight into how species may respond to environmental changes in the future and assess the effectiveness of current conservation actions. However, only a relatively small number of large mammal species were investigated in this study compared to the overall high species richness and endemism of Southeast Asia. The findings may merely reflect the responses of a single group of fauna but may not necessarily mirror an ecosystem-wide response across the region. Hence, further investigation into other groups of species is needed to fully understand the effects of climate change. Additional species occurrences of large mammal species analysed in the study may also improve model predictivity and accuracy. Moreover, if integrated into the prediction models, important factors determining species ranges such as biotic interactions, land use, and vegetation types may enhance the reliability of predictions.

Many large mammal species are often surveyed within PAs across countries in Southeast Asia. However, more quality recording during fieldwork and systematic data collation are required in the region. Integrating advanced computational and GIS technology into the digitisation of species data will prove highly beneficial to future ecological studies. Furthermore, historical records of large mammal species in Southeast Asia are rarely exploited in species distribution analyses, but, as this study highlights, they provide valuable insights into the investigation of the impacts of past environmental changes and the prediction of future responses to change. For example, in Thailand, elephants and several albino mammals have cultural importance as they represent prestige and power of the king. These mammal species with their sighting locations have therefore been frequently recorded officially in historical and public documents. The development of methodological frameworks for information extraction from these historical archives could enable the assessment of environmental change and its impact on species distribution during the time when anthropogenic influences were negligible.

Biogeography is a growing field of study as the effects of climate change have become more acute and evident globally. Computational tools to support such research are therefore under rapid development. Many SDM approaches have been introduced to facilitate prediction of species responses to environmental change. However, using different approaches can lead to variation in modelling results. Further research featuring ensemble model methods and target group background data may therefore improve the robustness and accuracy of model predictions. Finally, alternative computational methods such as ENMTools and the package ‘vegan’ in R can also be used to comparatively measure niche similarity in order to obtain a more reliable interpretation of the model output.

Appendix 1

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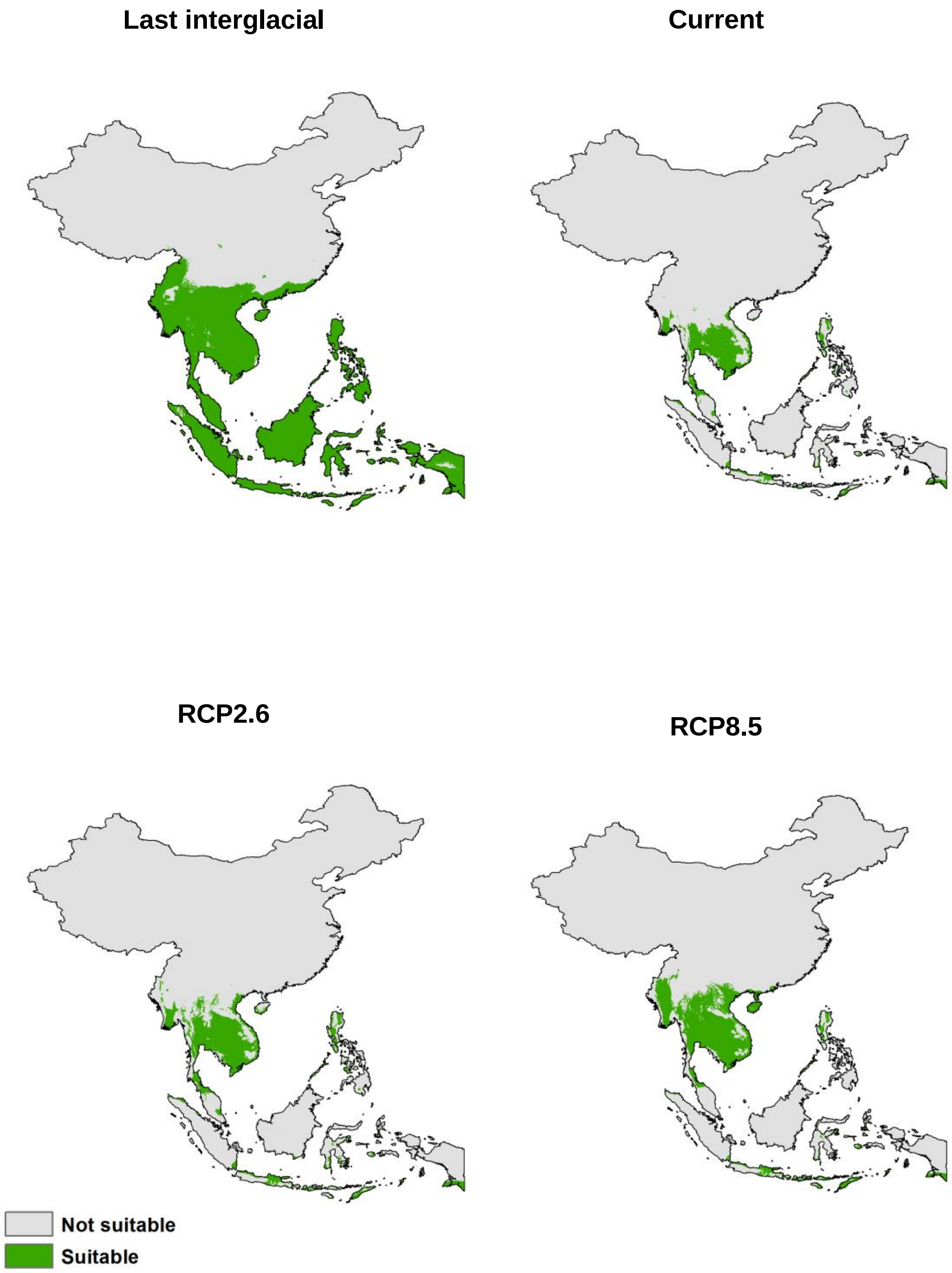
Appendix 2

Appendix 2.1. Data from species distribution modelling in Chapter 2

Map of the predicted distributions of suitable habitats for 15 large mammal species during the last interglacial, the current conditions and future climate scenarios (RCP2.6 and RCP8.5).



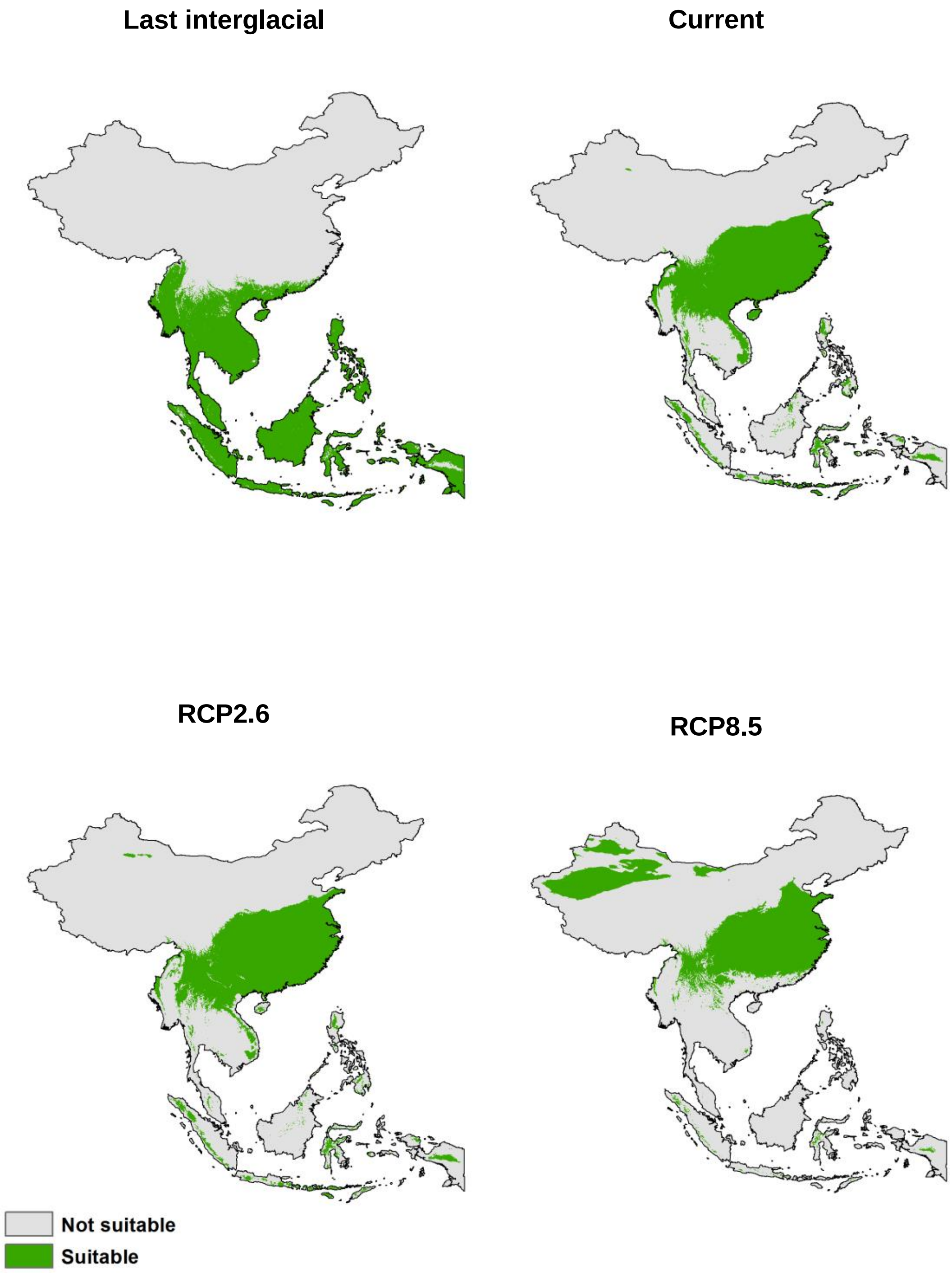
Last interglacial

Current

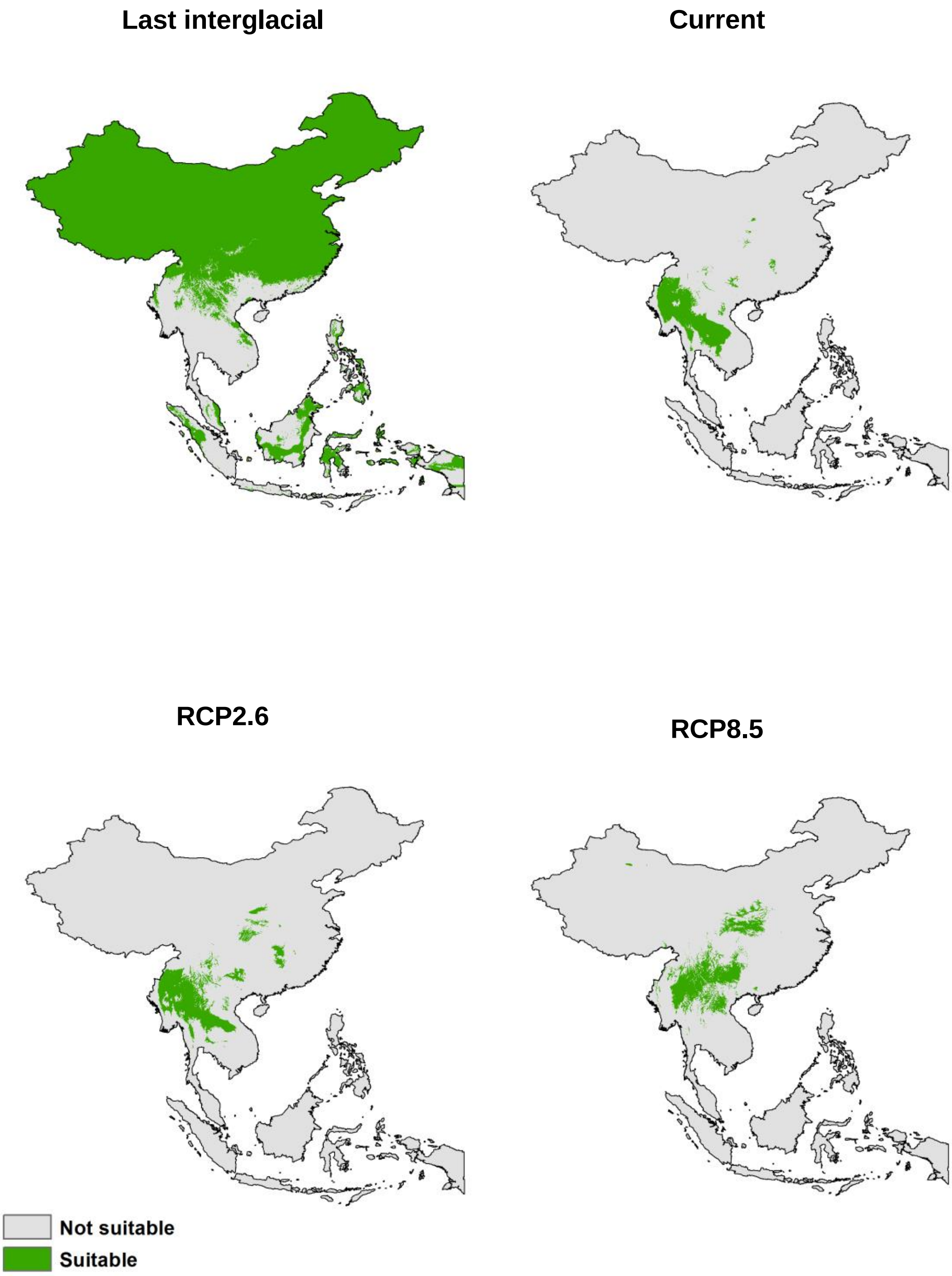
RCP2.6

RCP8.5

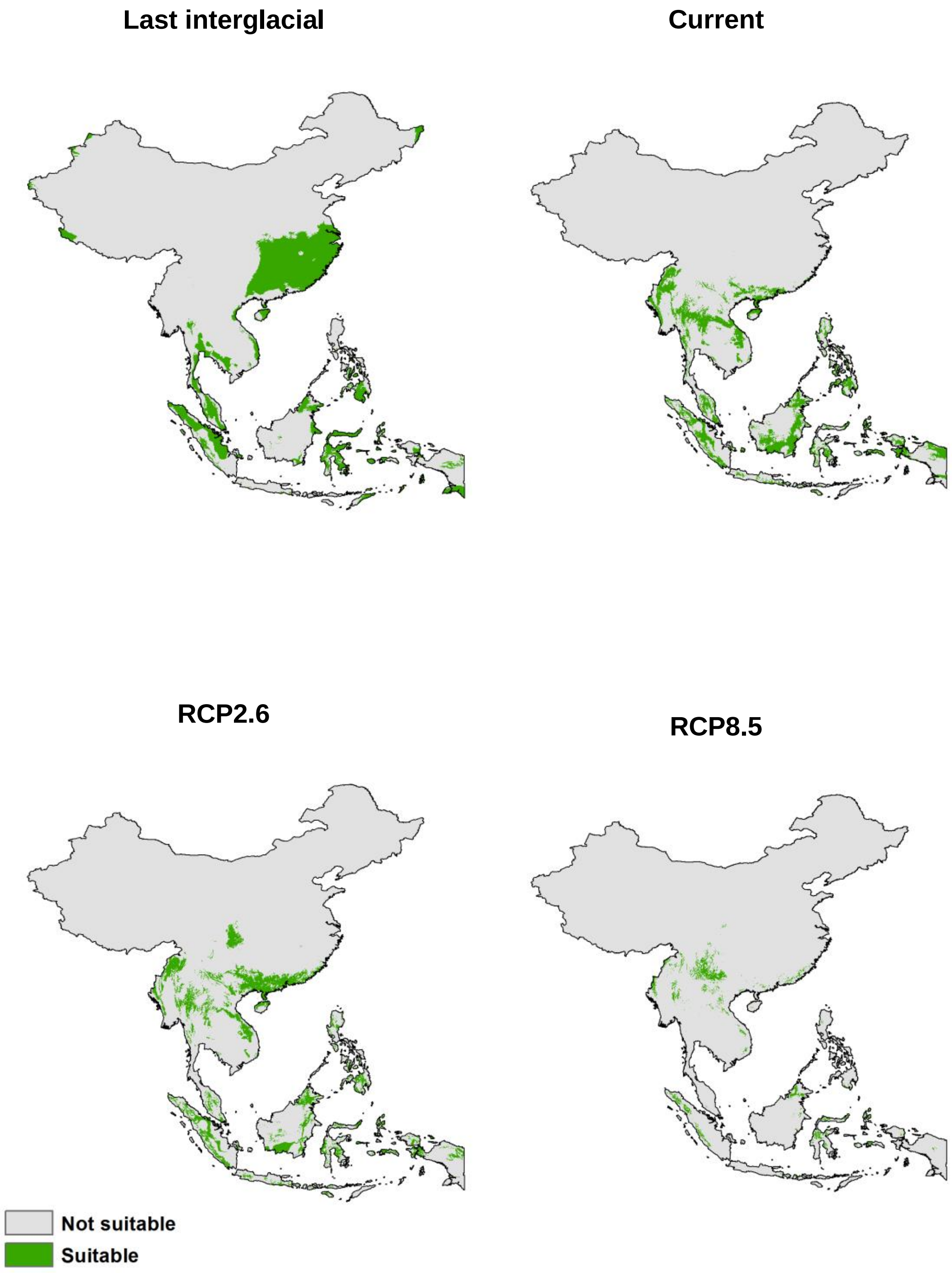
(a) *Bubalus bubalis*



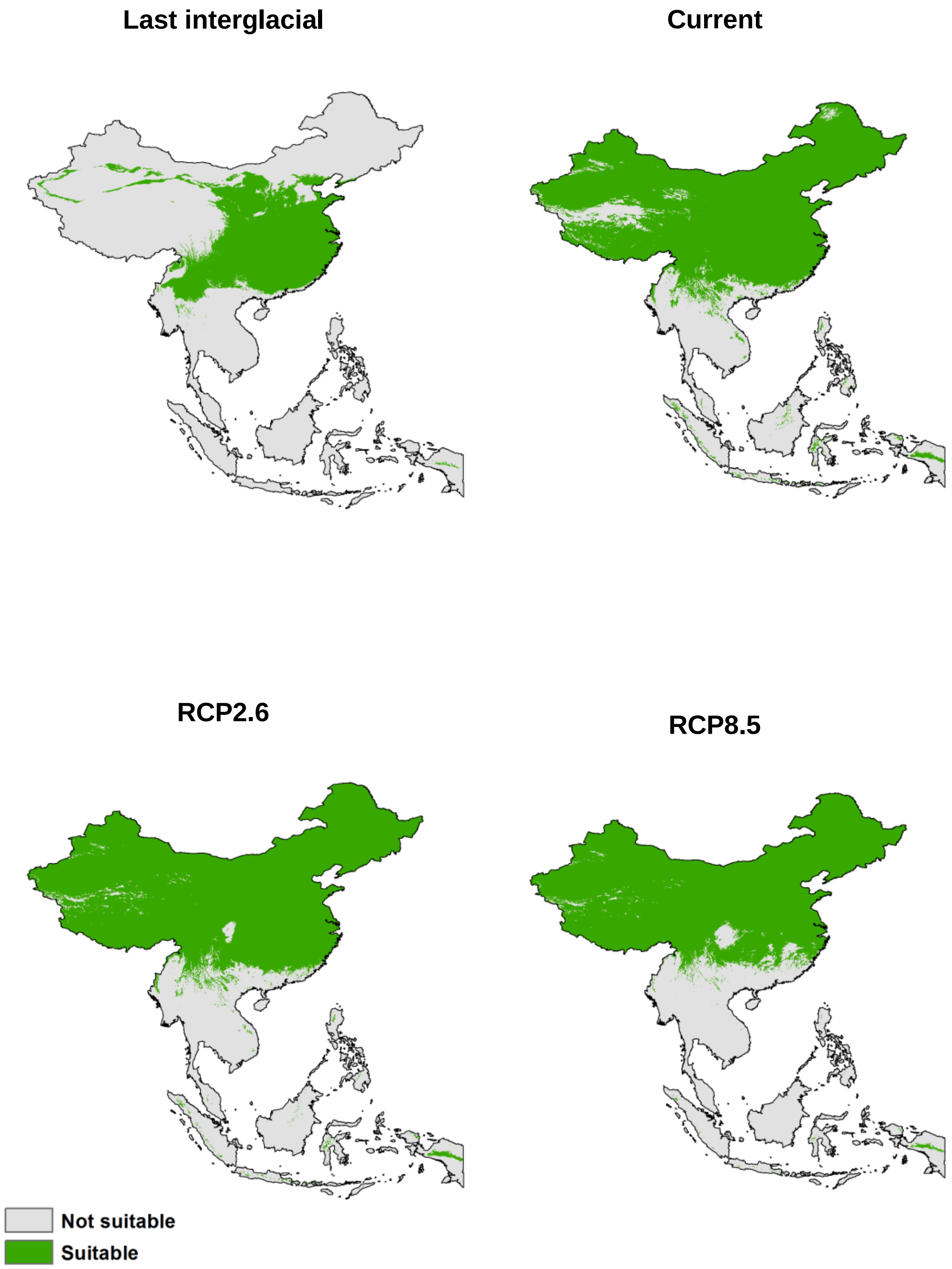
(b) *Capricornis sumatraensis*



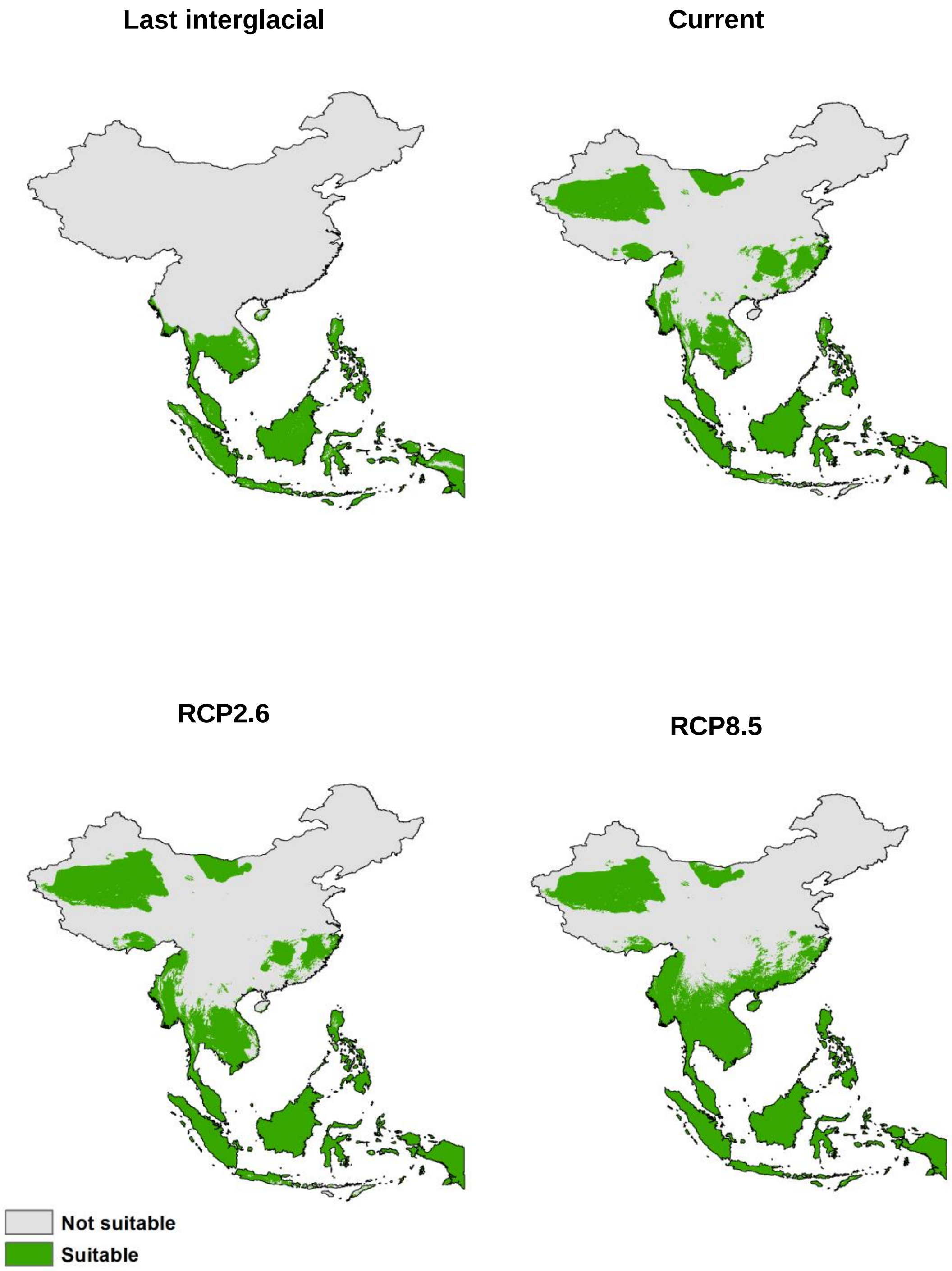
(c) *Cuon alpinus*



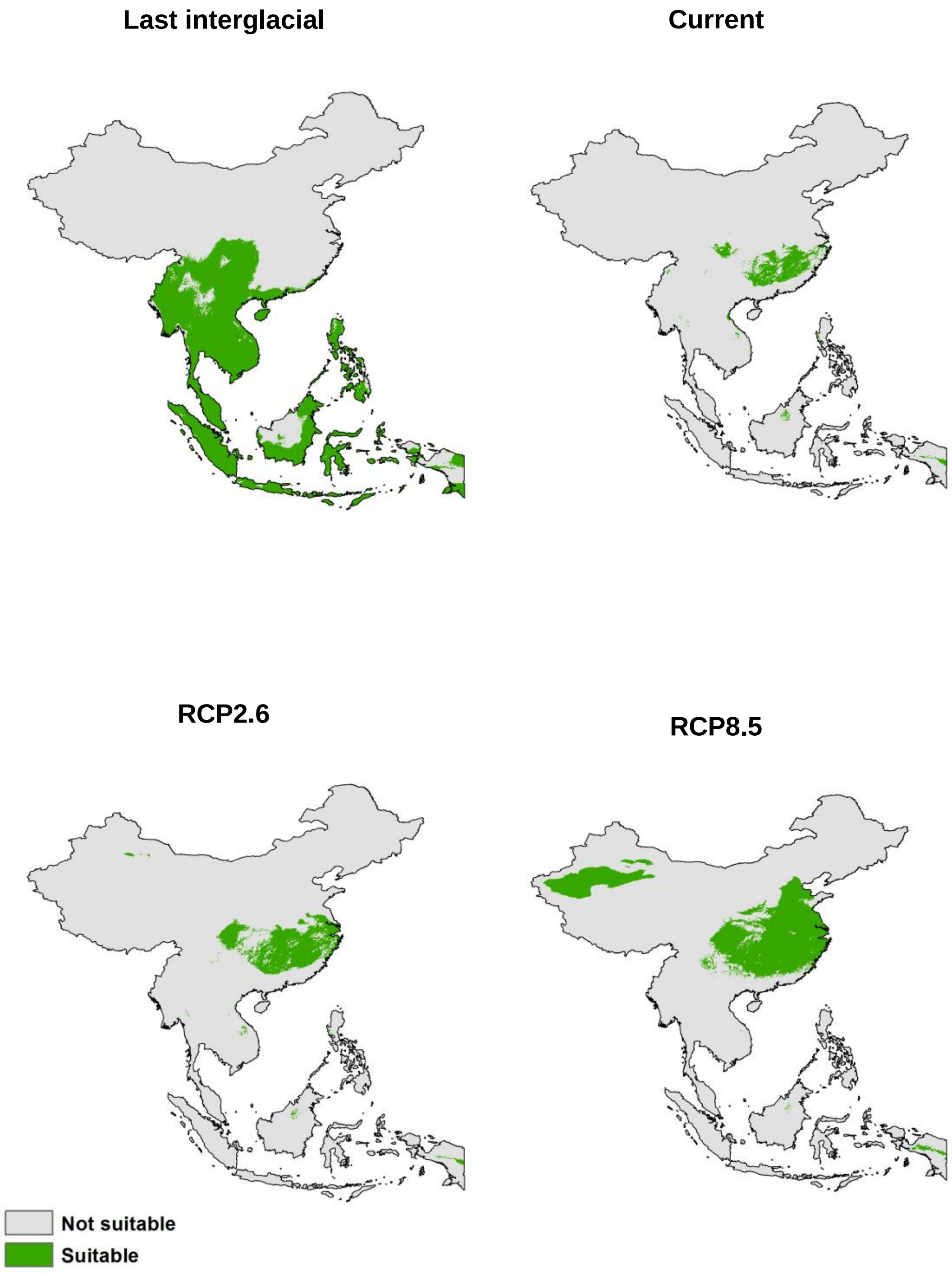
(d) *Elephas maximus*



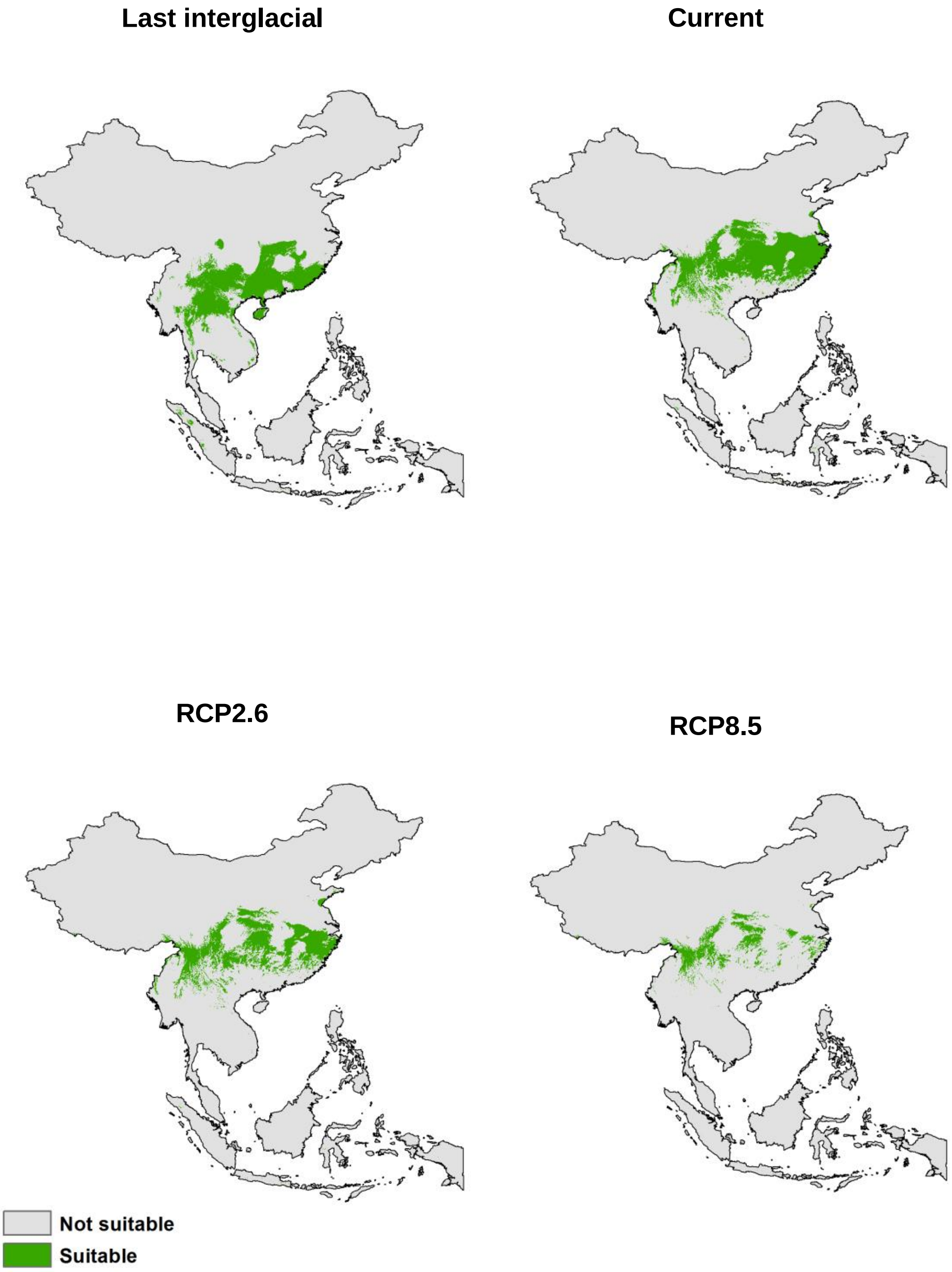
(e) *Macaca mulatta*



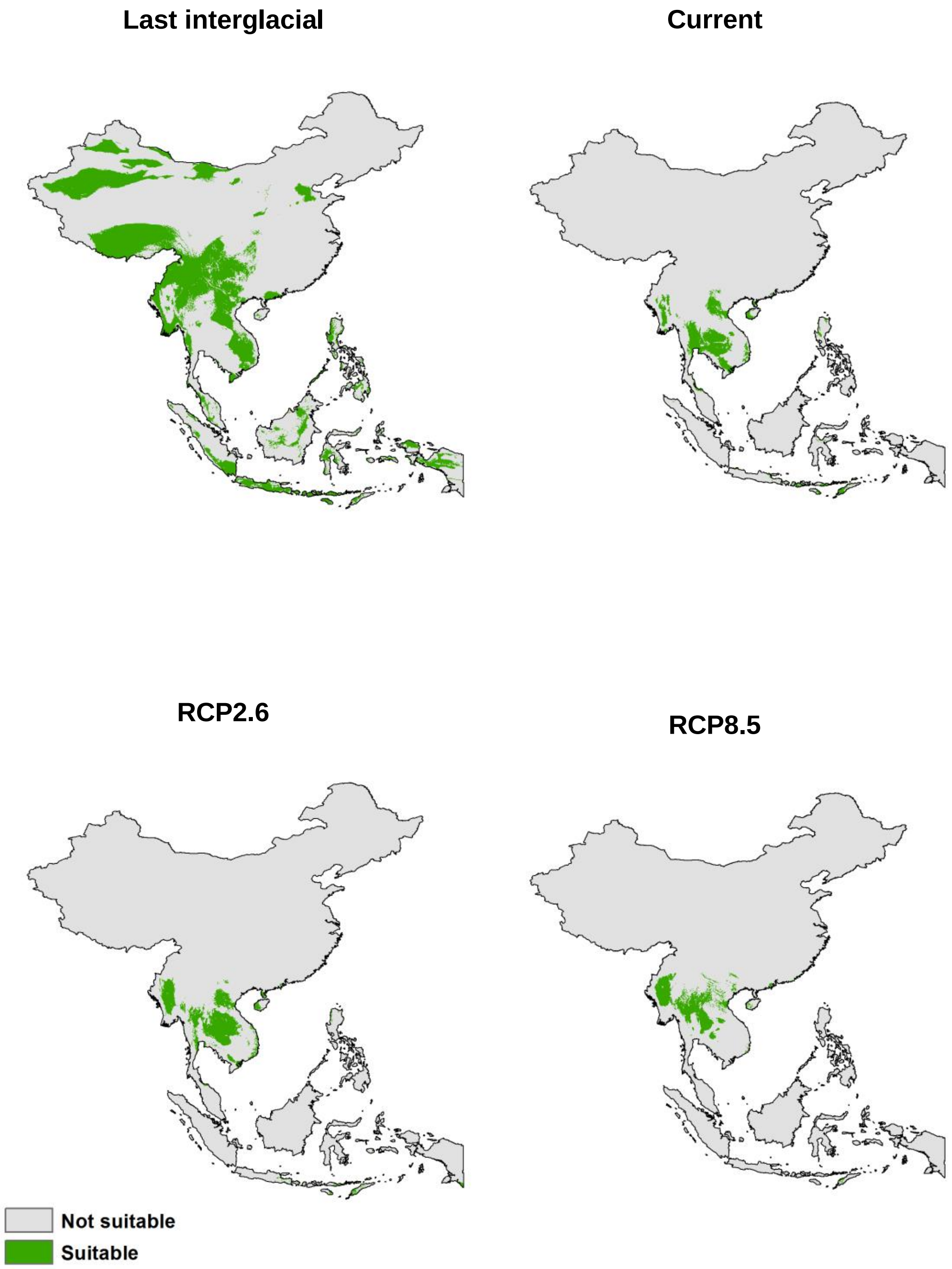
(f) *Macaca nemestrina*



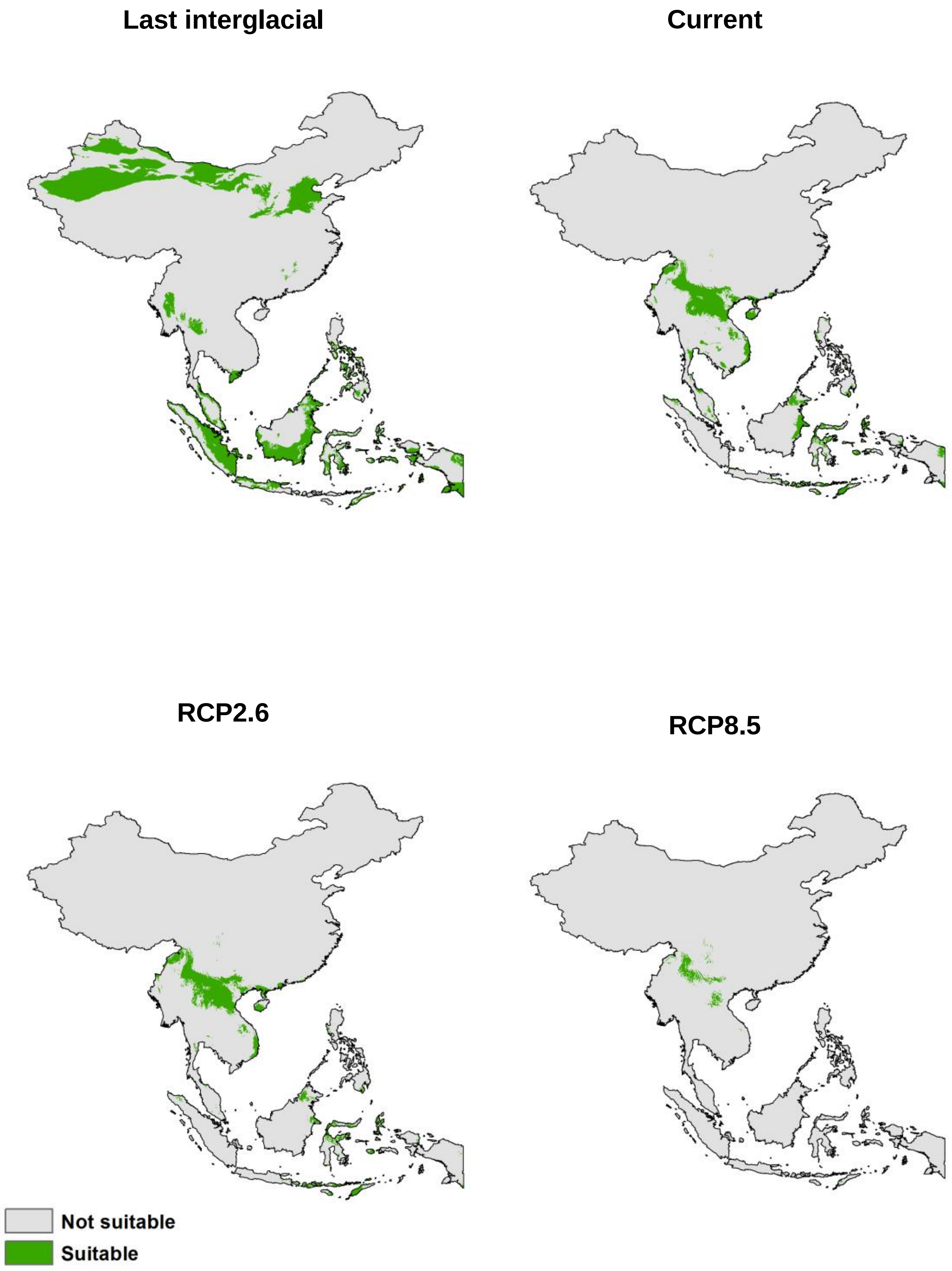
(g) *Muntiacus muntjak*



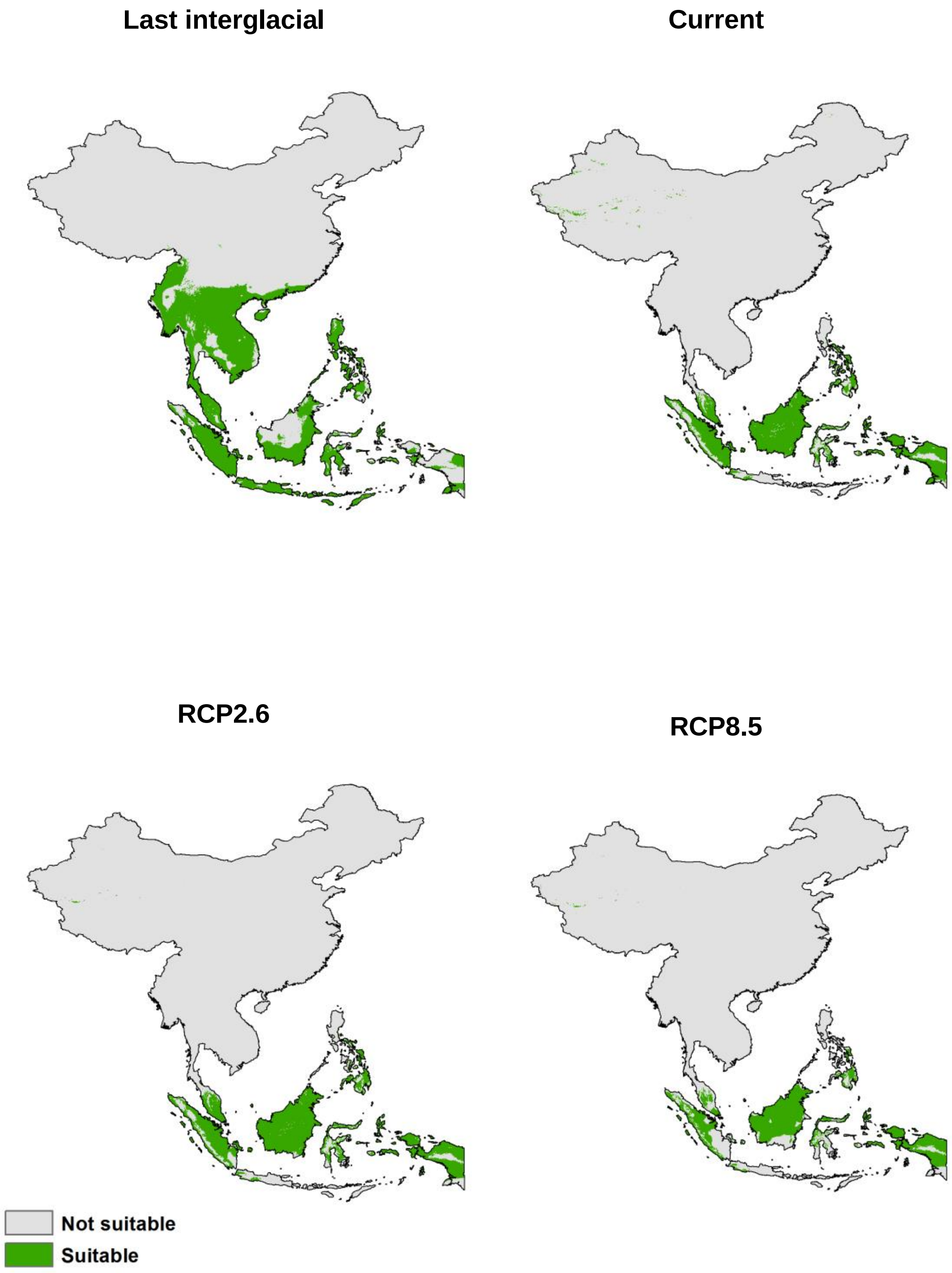
(h) *Nomascus concolor*



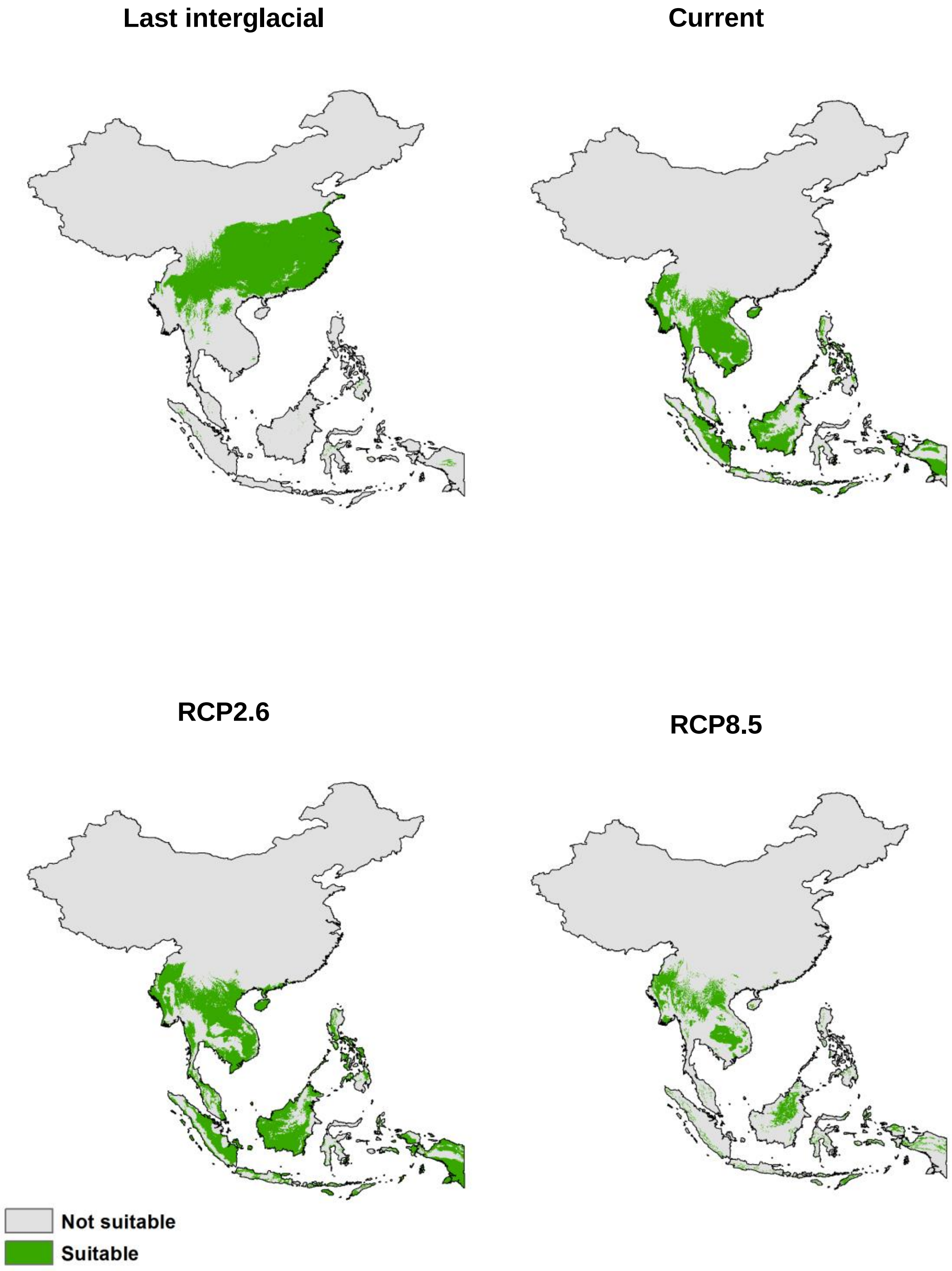
(i) *Panthera pardus*



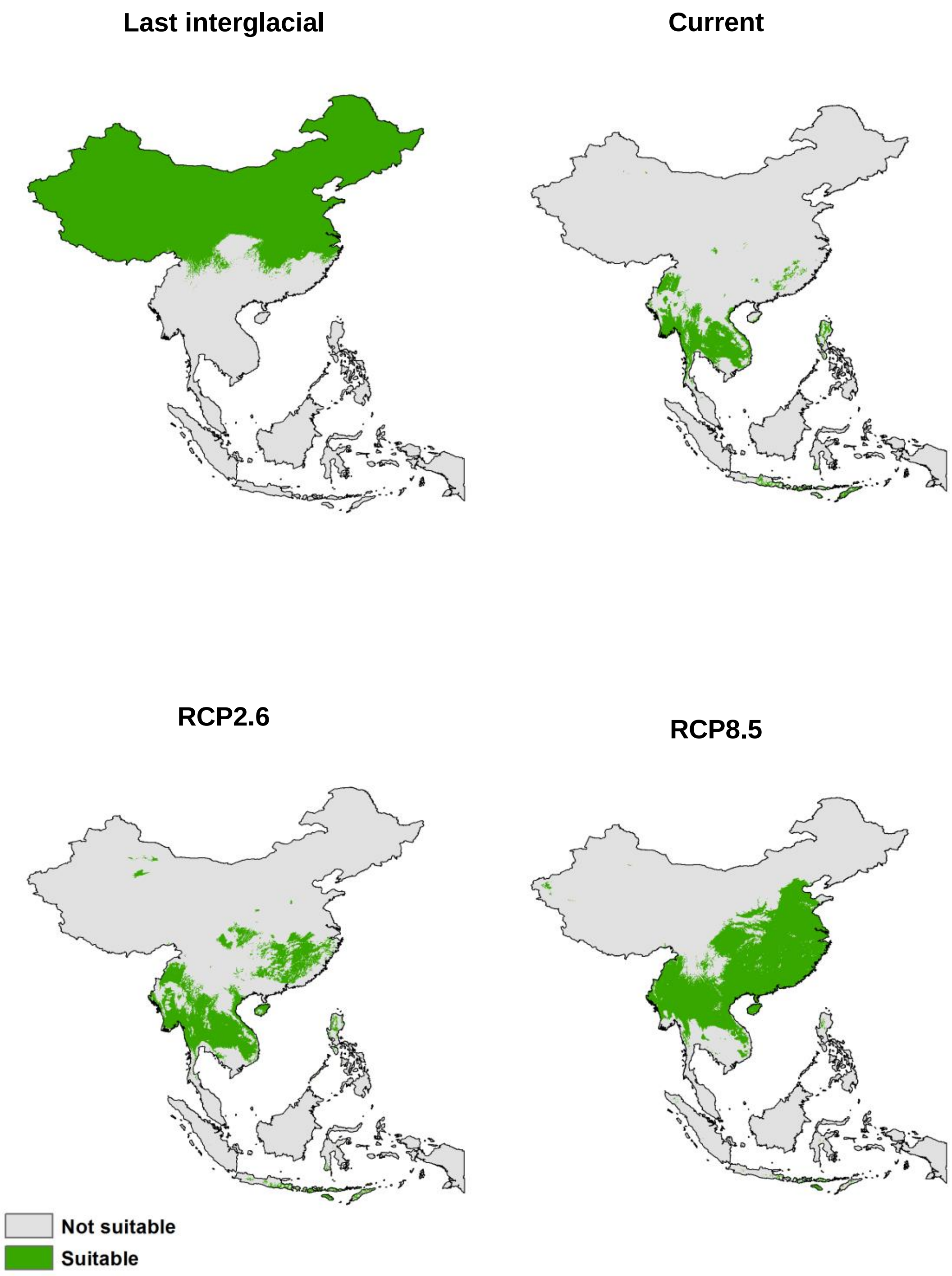
(j) *Panthera tigris*



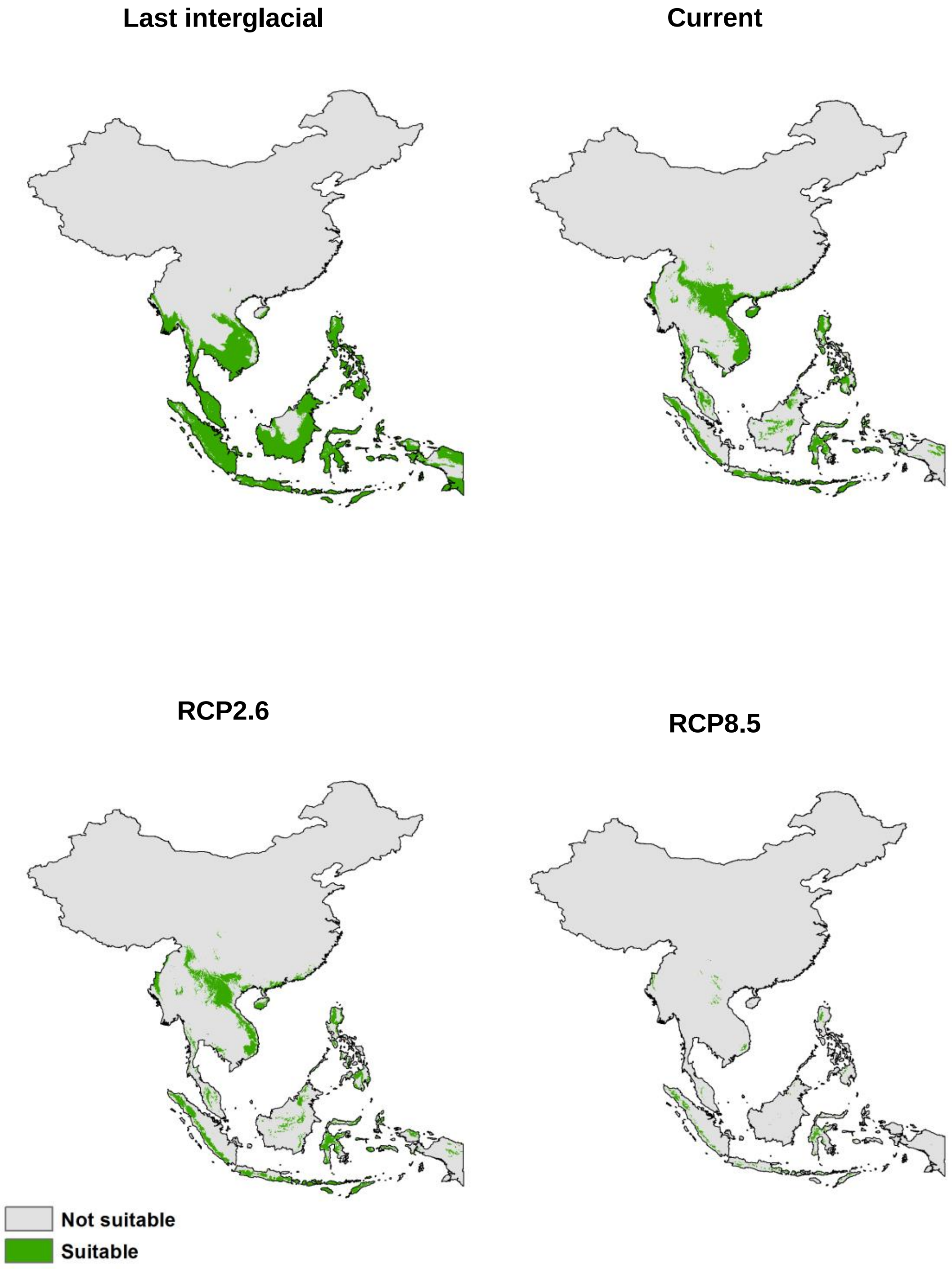
(k) *Pongo pygmaeus*



(l) *Rusa unicolor*


Last interglacial
Current
RCP2.6
RCP8.5
Not suitable
Suitable

(m) *Sus scrofa*



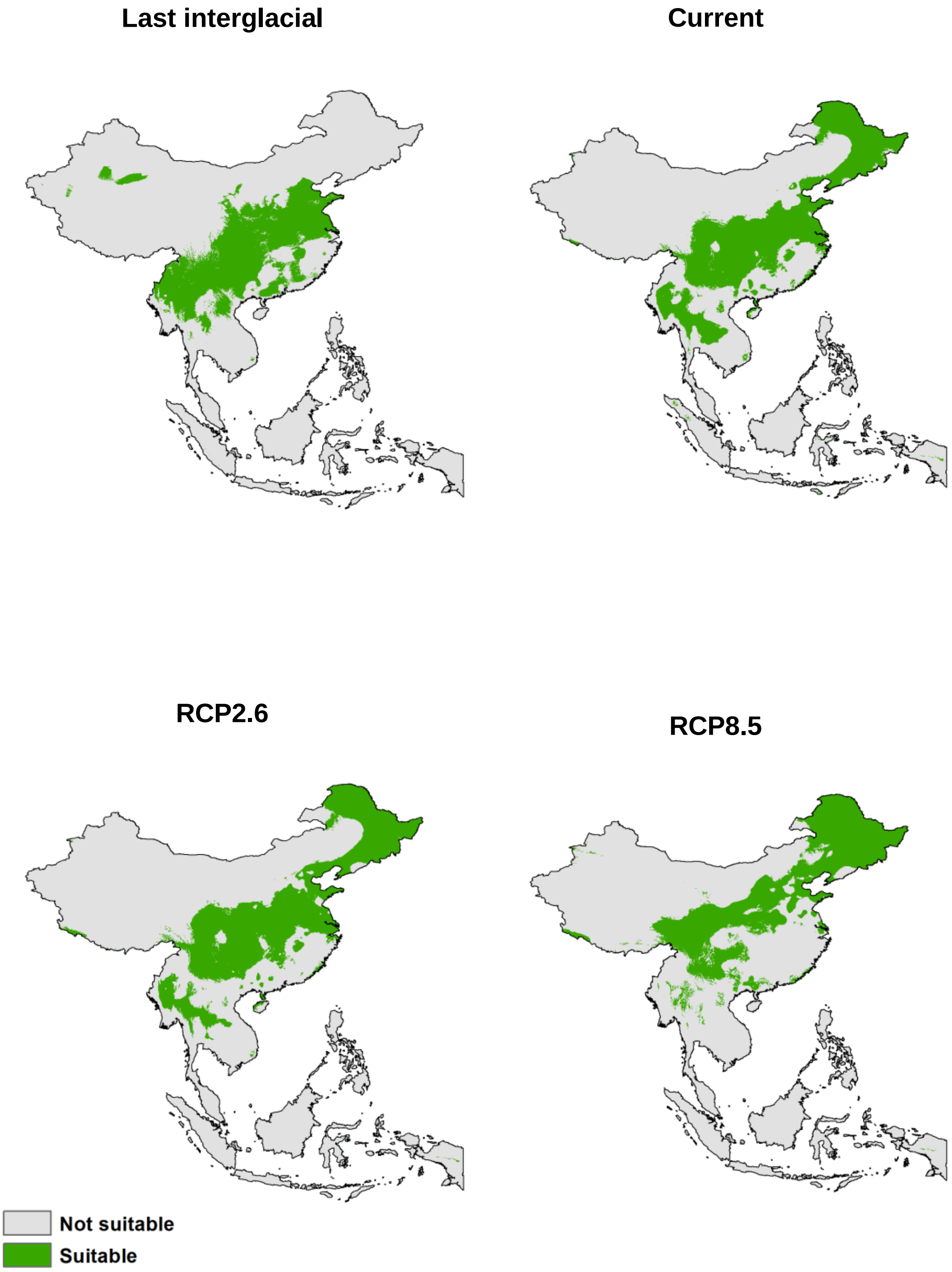
Last interglacial

Current

RCP2.6

RCP8.5

(n) *Tapirus indicus*



Last interglacial

Current

RCP2.6

RCP8.5

(o) *Ursus thibetanus*

Appendix 2.2. Rate of range shift for each species (km/yr)

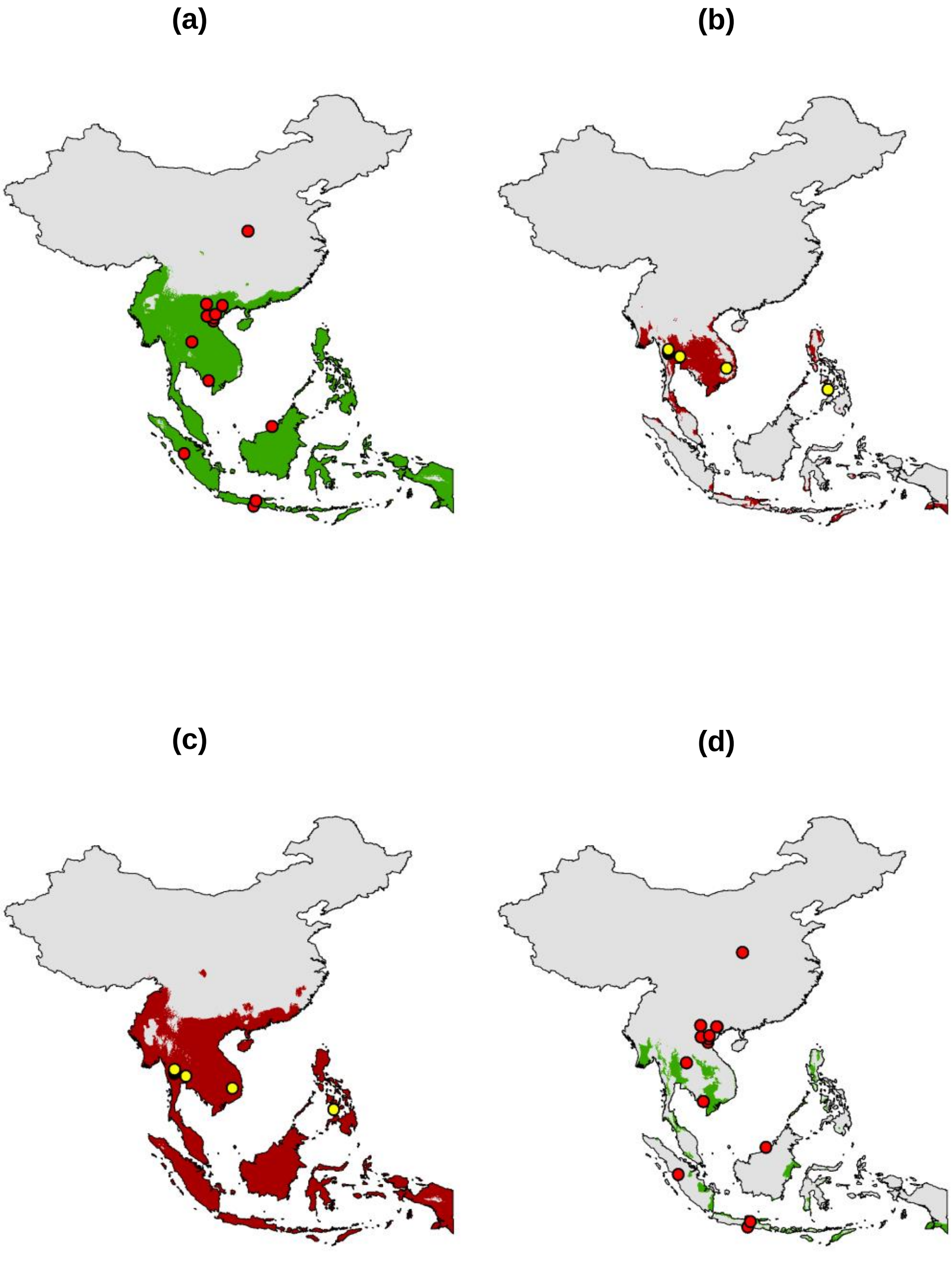
	Time interval		
Species	120,000 -140,000 years BP	1945 – 2050 (RCP2.6)	1945 – 2050 (RCP8.5)
Bubalus bubalis	0.014	0.595	4.513
Capricornis sumatraensis	0.083	1.671	9.787
Cuon alpinus	0.085	2.883	7.053
Elephas maximus	0.051	5.048	9.117
Macaca mulatta	0.037	0.887	1.717
Macaca nemestrina	0.089	0.537	0.479
Muntiacus muntjak	0.079	2.962	9.513
Nomascus concolor	0.025	0.757	3.422
Panthera pardus	0.063	1.643	6.482
Panthera tigris	0.057	3.172	12.707
Pongo pygmaeus	0.068	0.799	1.557
Rusa unicolor	0.099	1.918	4.253
Sus scrofa	0.127	5.459	12.264
Tapirus indicus	0.044	0.320	7.219
Ursus thibetanus	0.035	1.118	4.795

Appendix 3

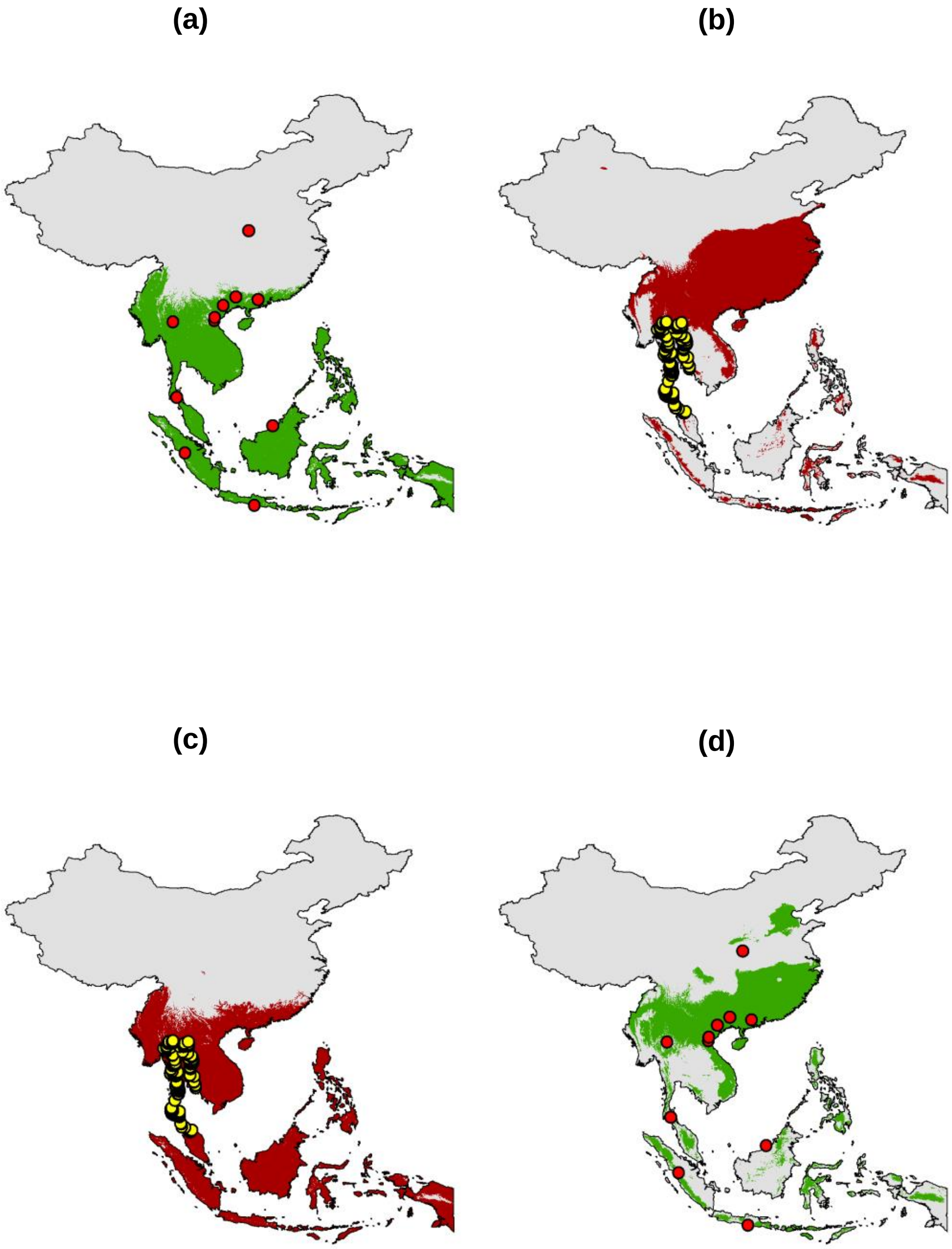
Data from ecological niche modelling in Chapter 3

Maps of the predicted distributions of 15 large mammal species between time intervals: (a) The Quaternary niche model predicted the distribution of the species during the last interglacial; (b) The current niche model predicted the distribution at present; (c) The Quaternary model forecasted the current distribution; and (d) The current model hindcasted the Quaternary distribution.

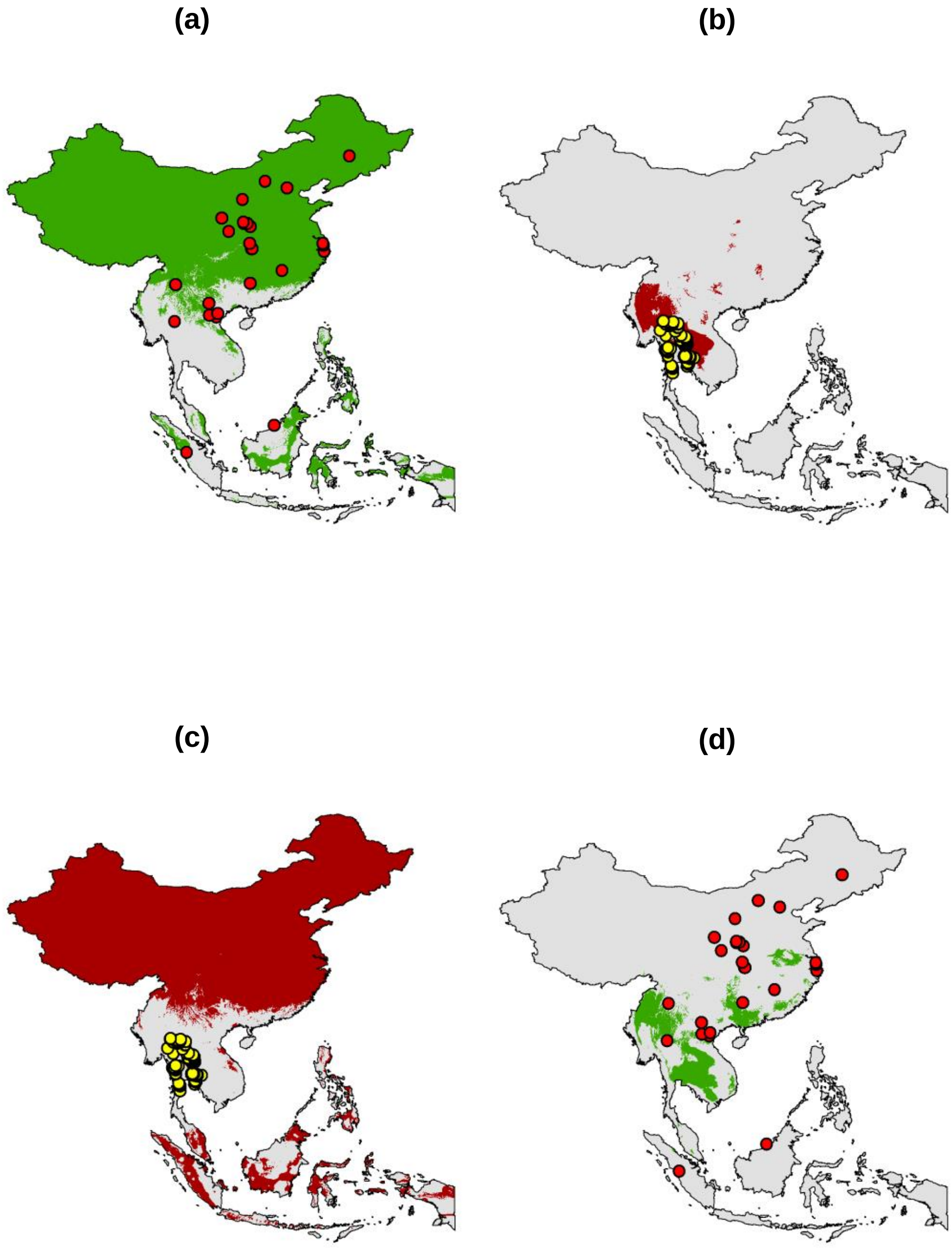
Bubalus bubalis



Capricornis sumatraensis



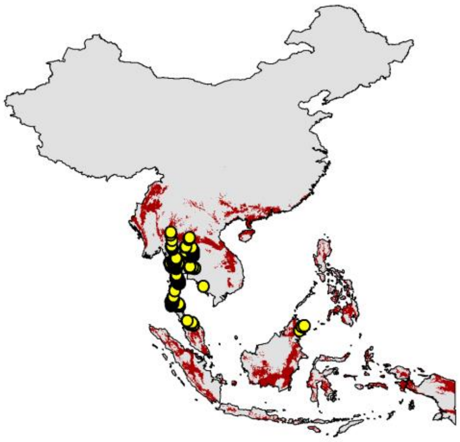
Cuon alpinus



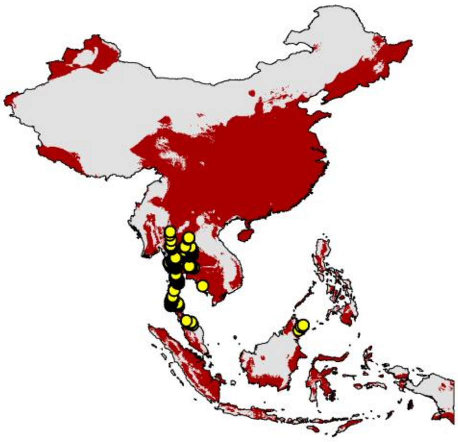
Elephas maximus

(a)

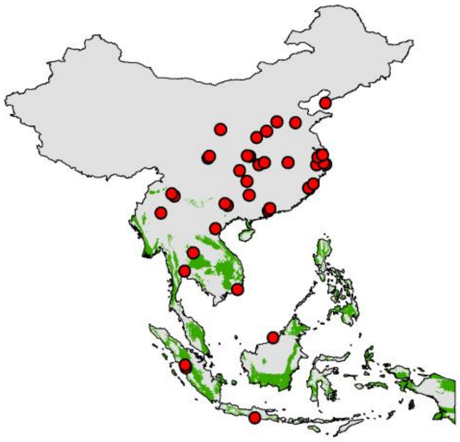
(b)



(c)

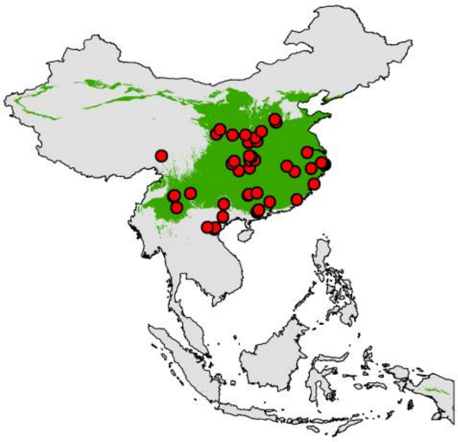


(d)

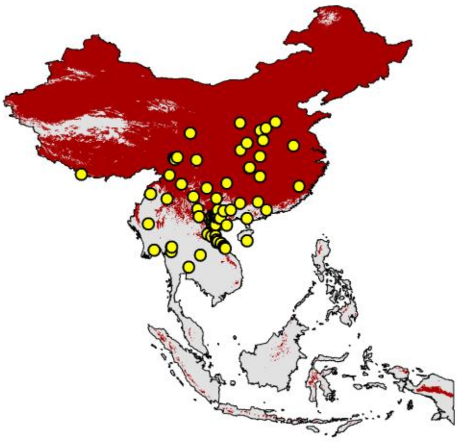


Macaca mulatta

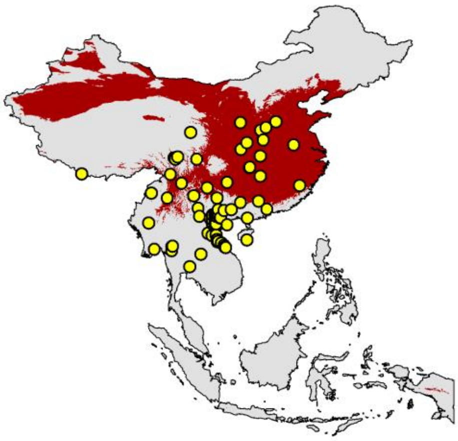
(a)



(b)



(c)



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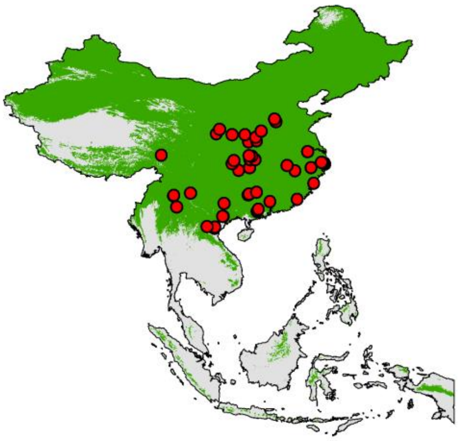
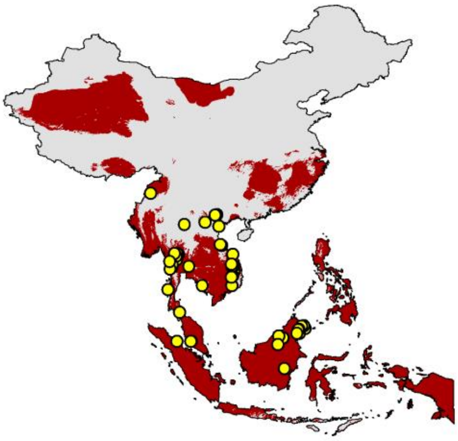


Macaca nemestrina

(a)

(b)



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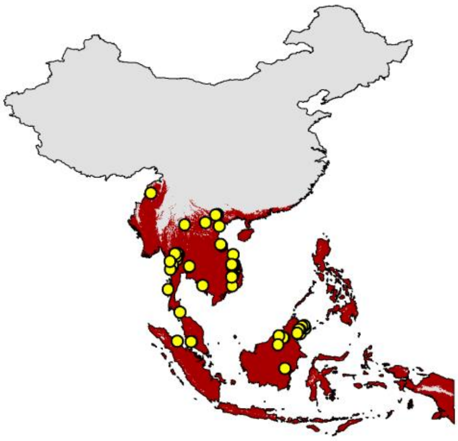

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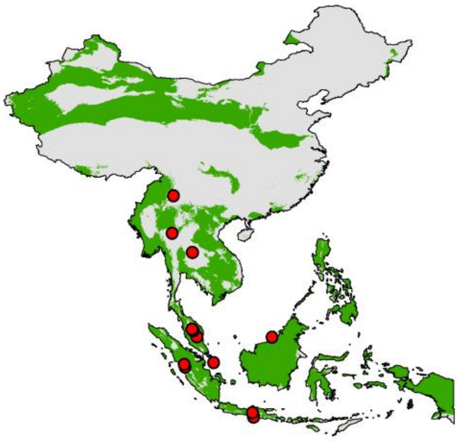
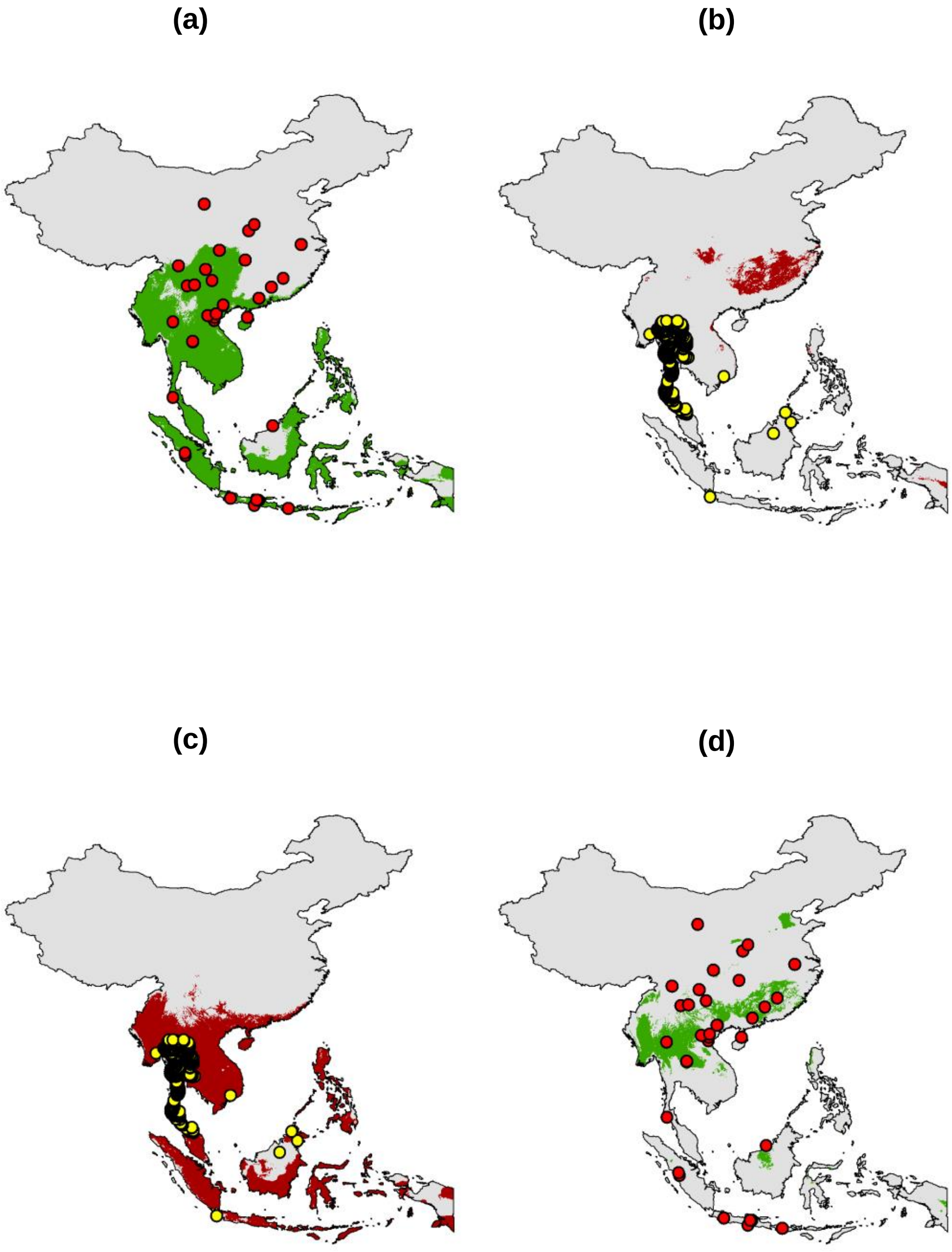
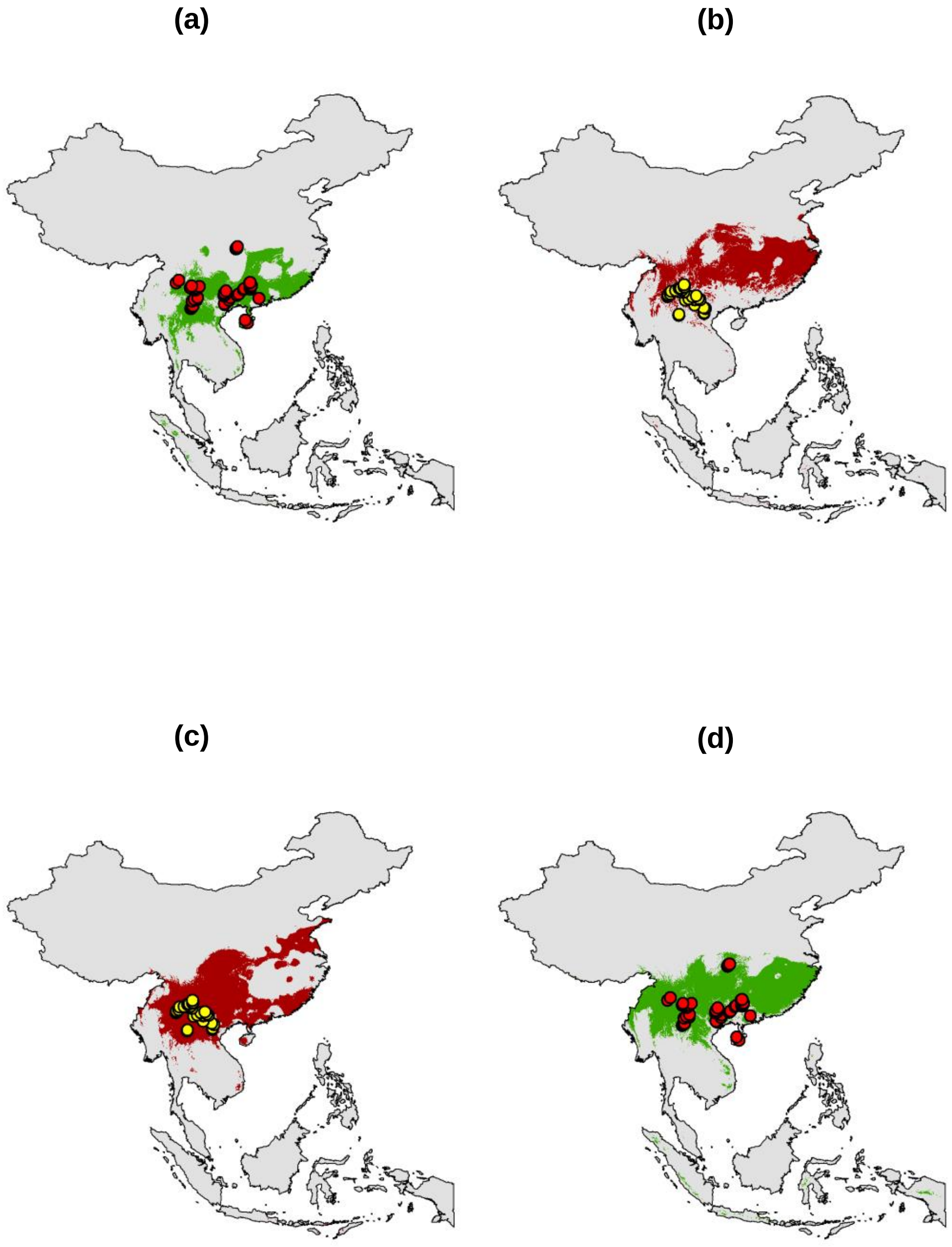


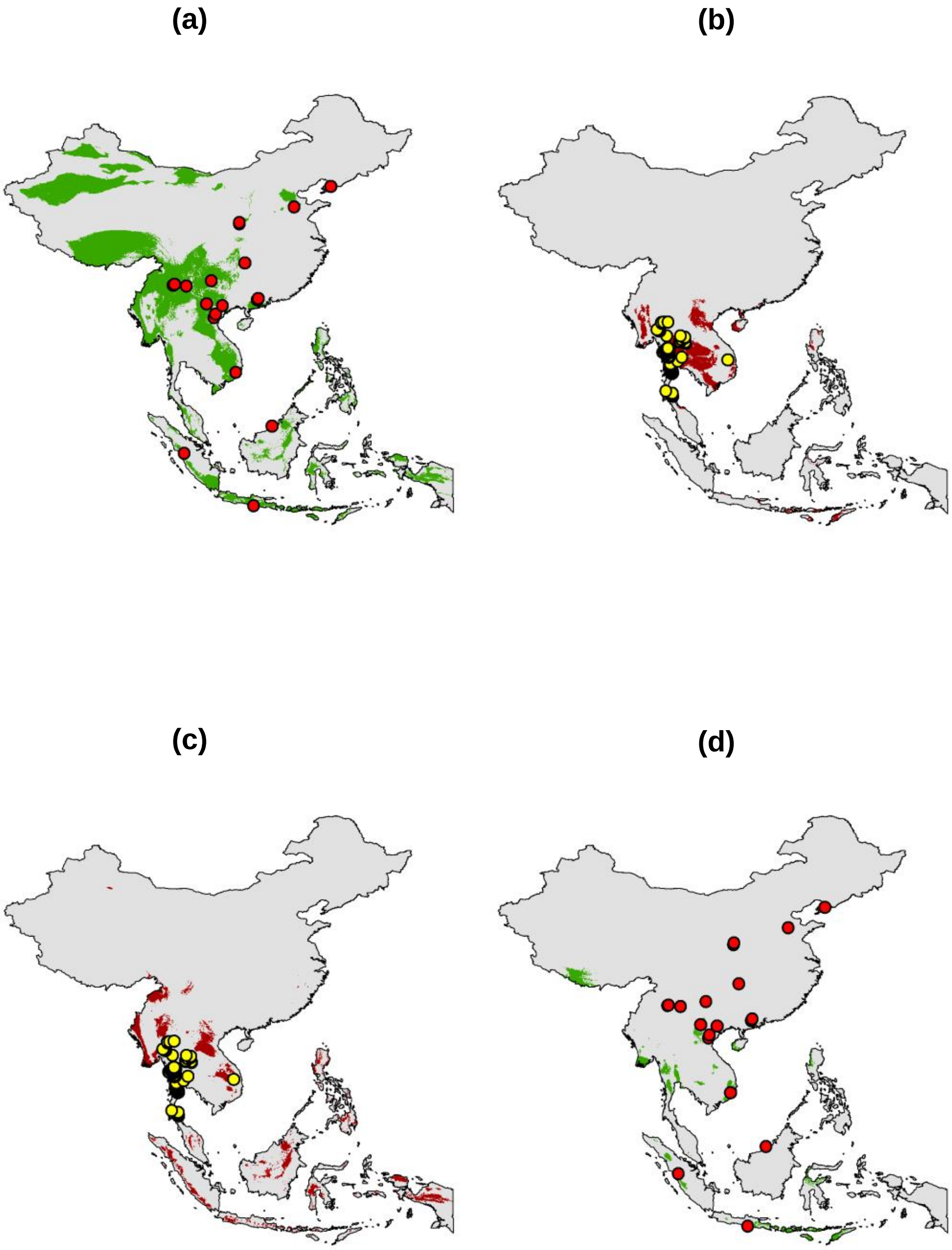
Muntiacus muntjak



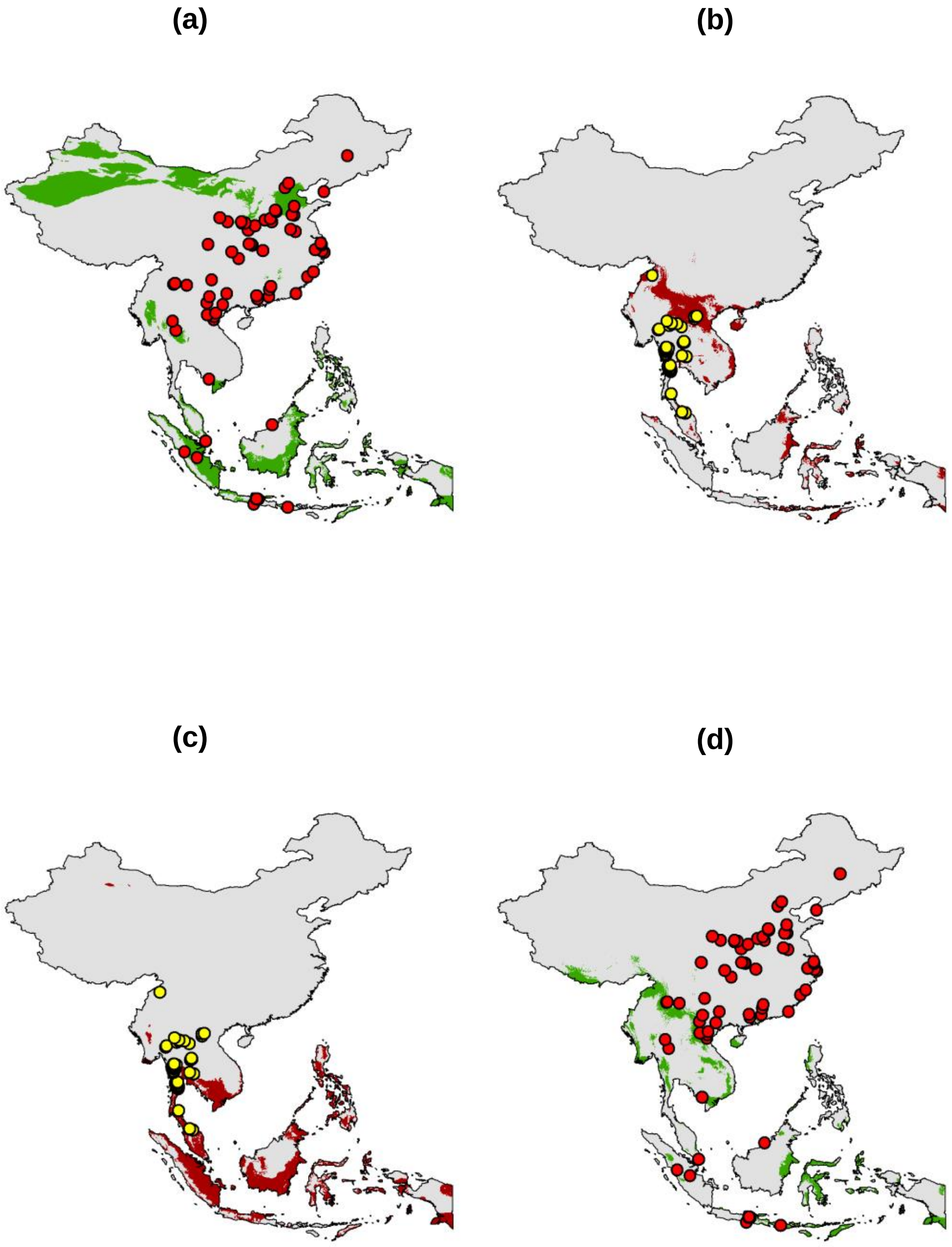
Nomascus concolor



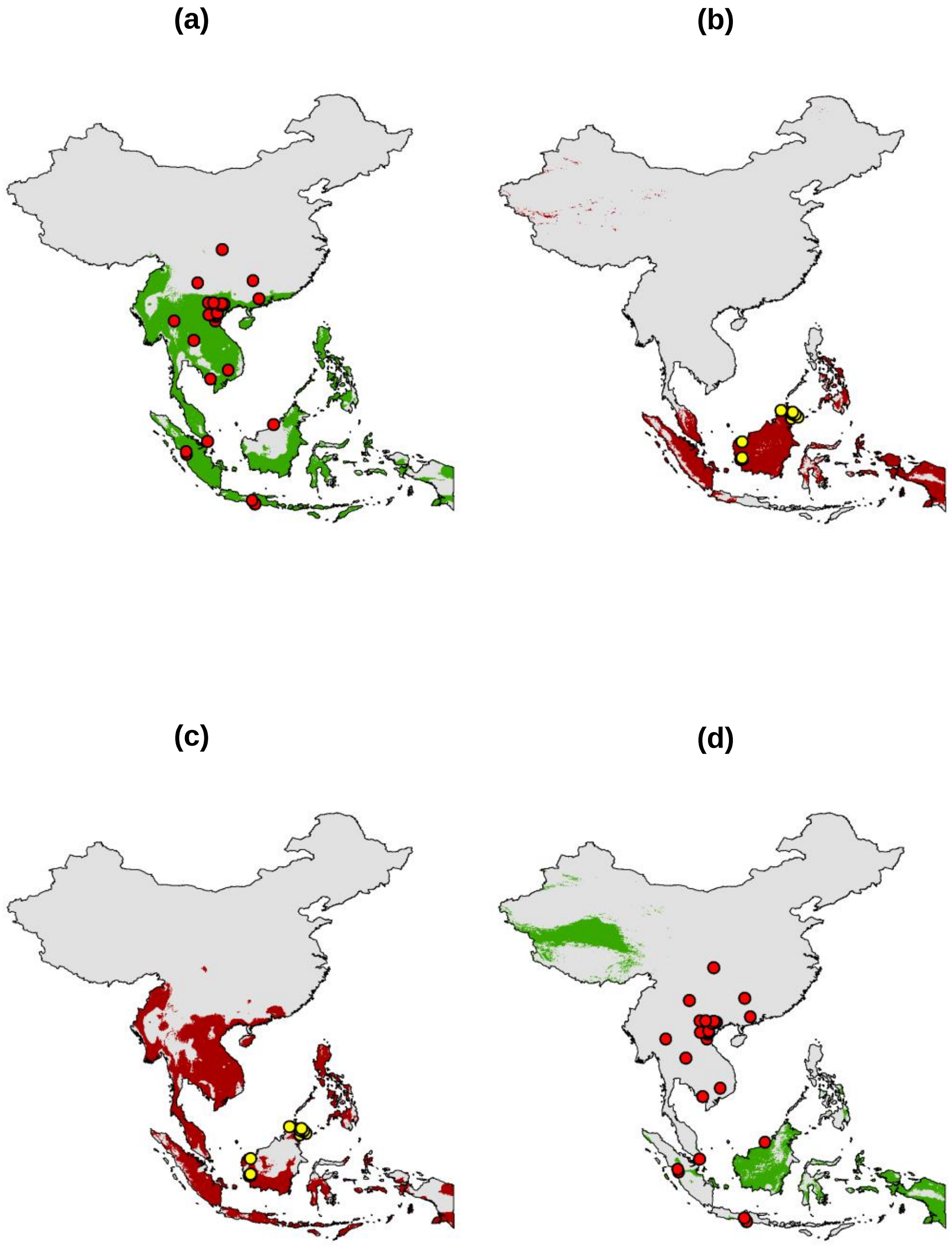
Panthera pardus



Panthera tigris



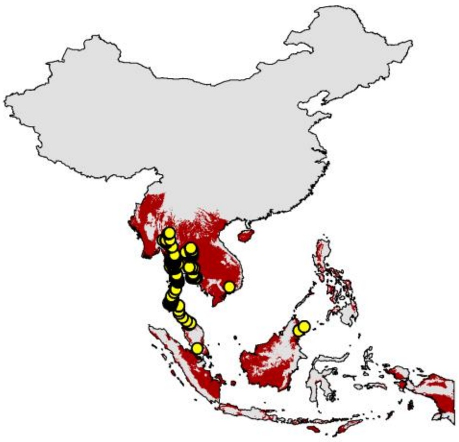
Pongo pygmaeus



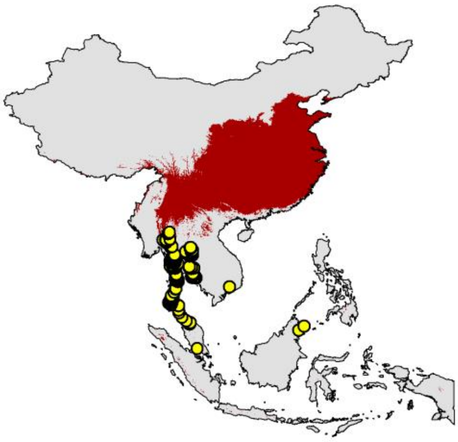
Rusa unicolor

(a)

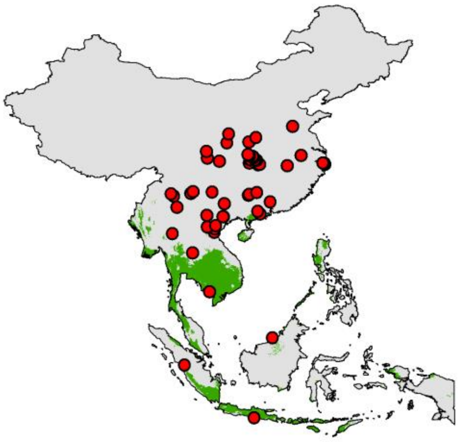
(b)



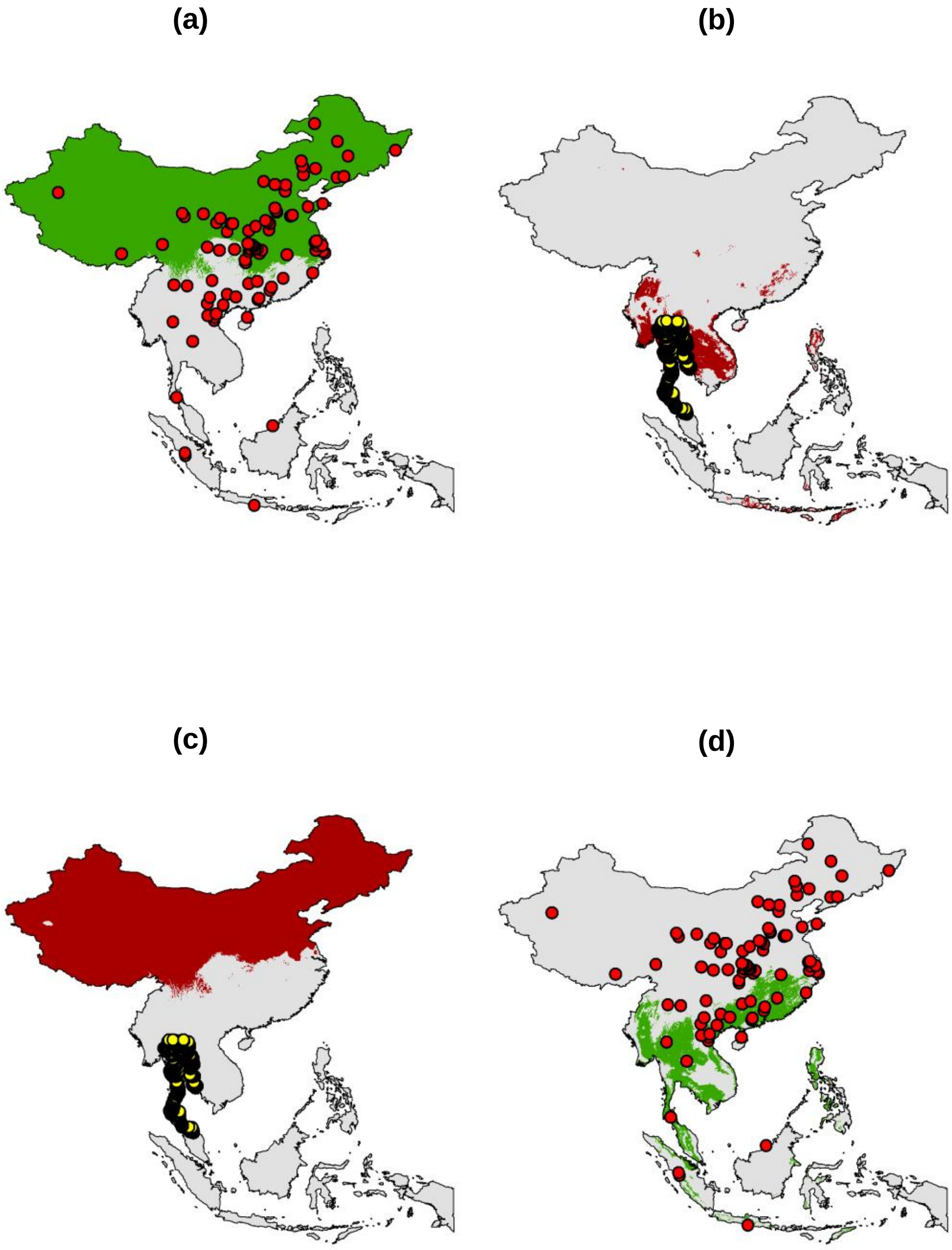
(c)



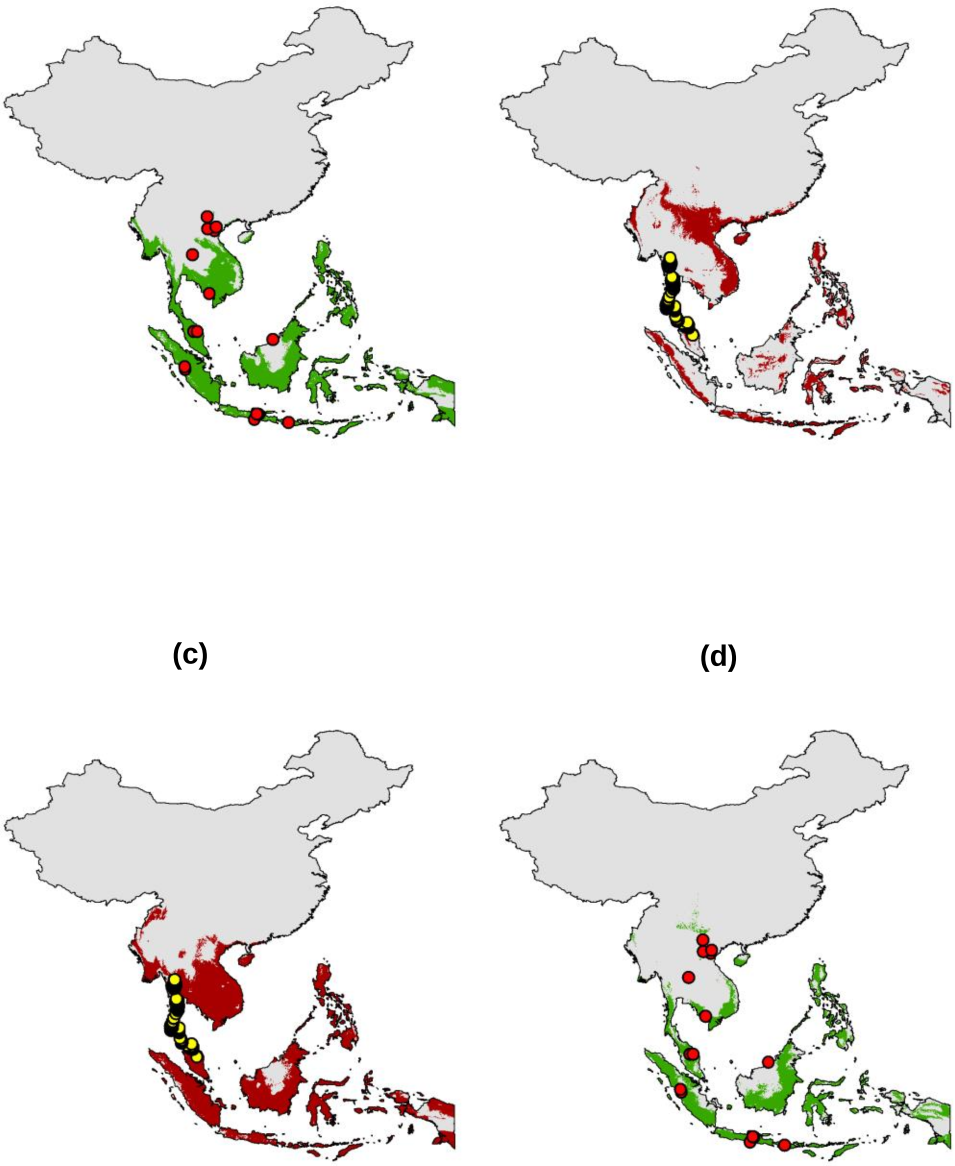
(d)



Sus scrofa



Tapirus indicus



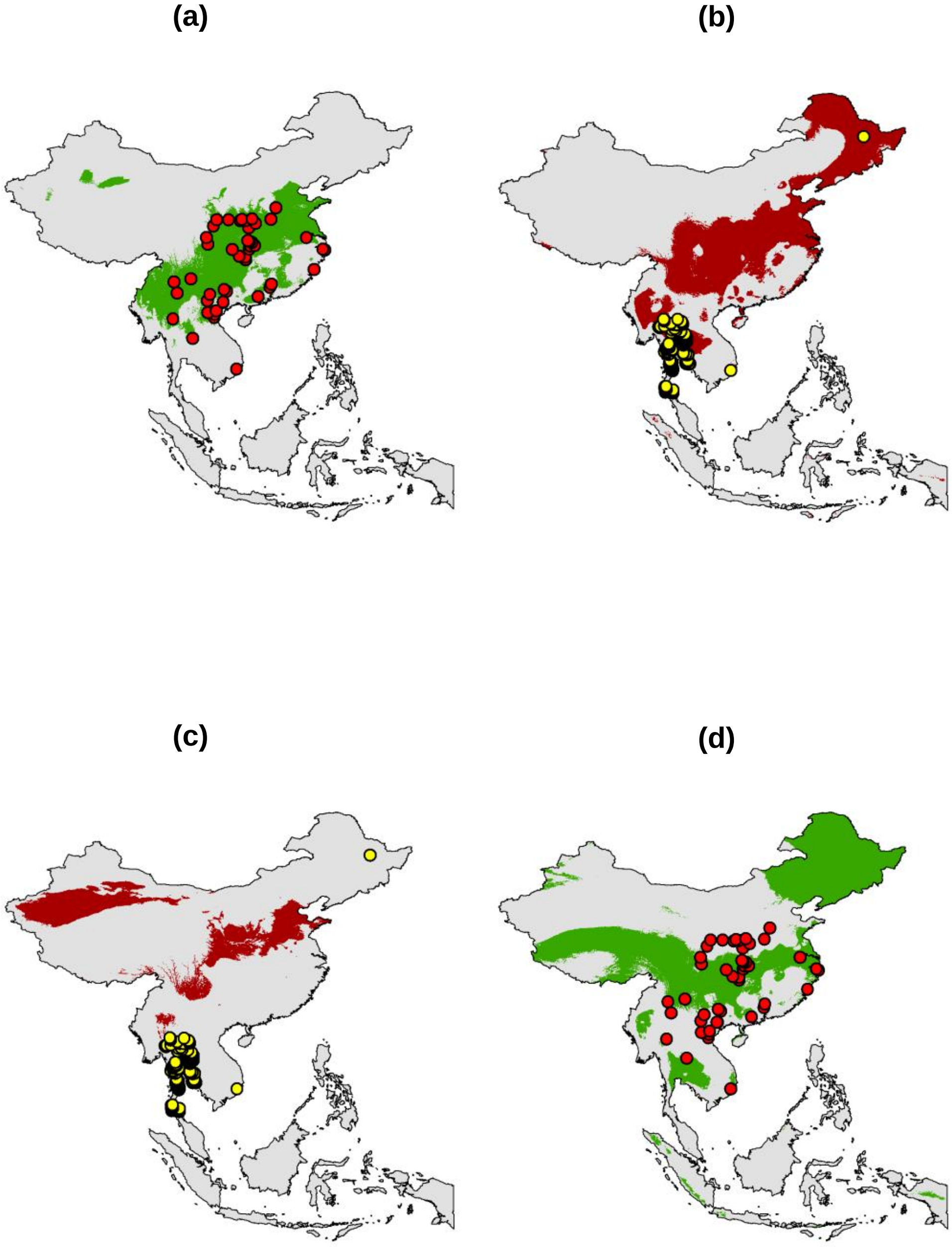
(a)

(b)

(c)

(d)

Ursus thibetanus



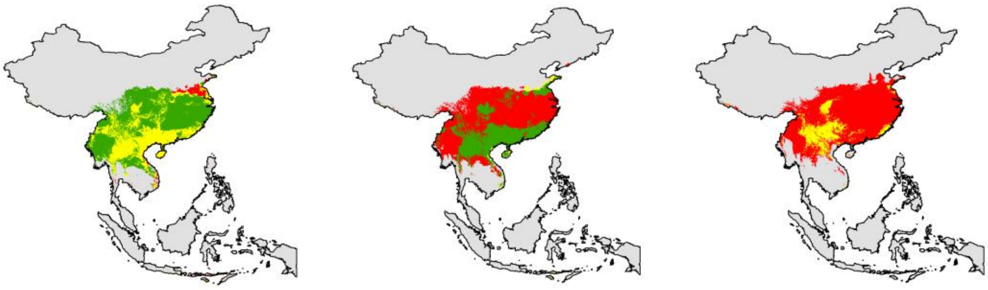
Appendix 4

Data from species distribution modelling in Chapter 4

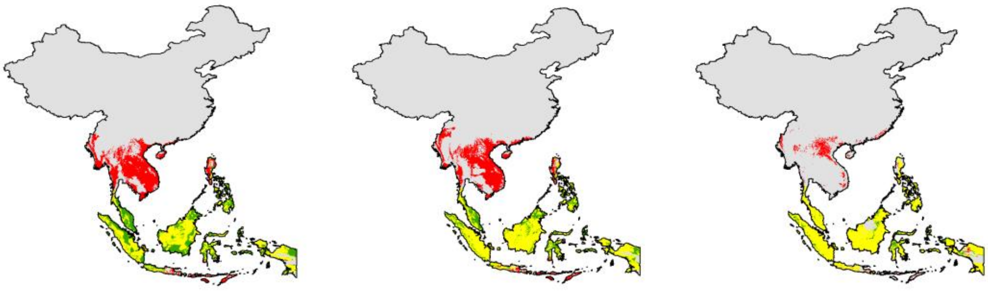
Maps of suitable habitats for 8 primate species predicted by the IUCN range maps and species point localities under current (left), RCP2.6 (middle) and RCP8.5 (right) conditions.

Current **RCP2.6** **RCP8.5**

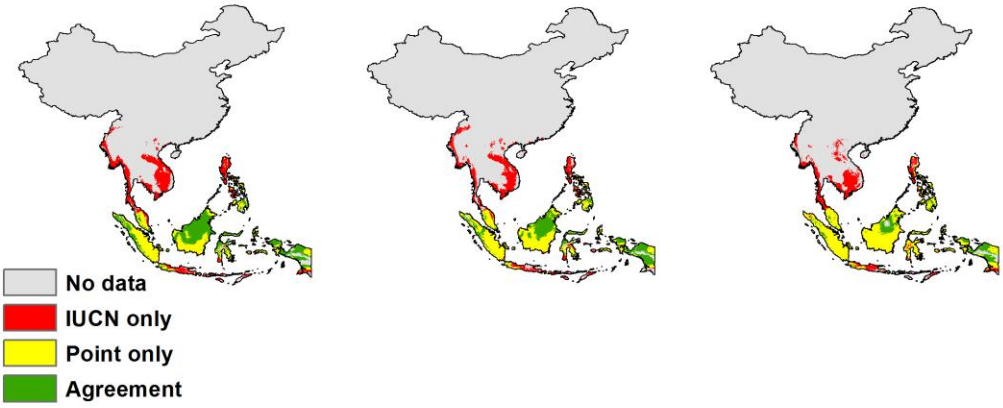
(a) *Macaca mulatta*



(b) *Macaca nemestrina*

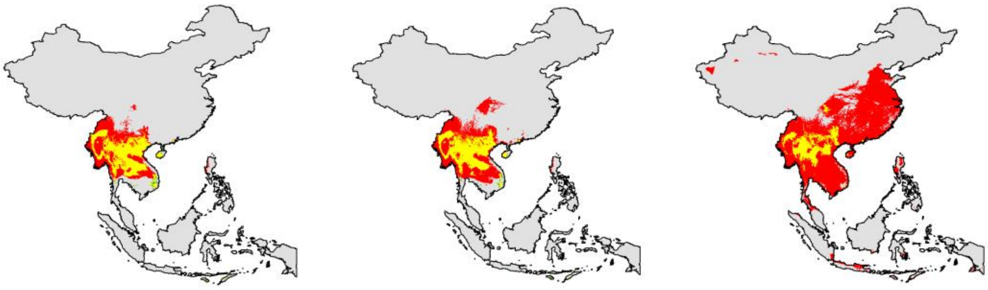


(c) *Trachypithecus cristatus*

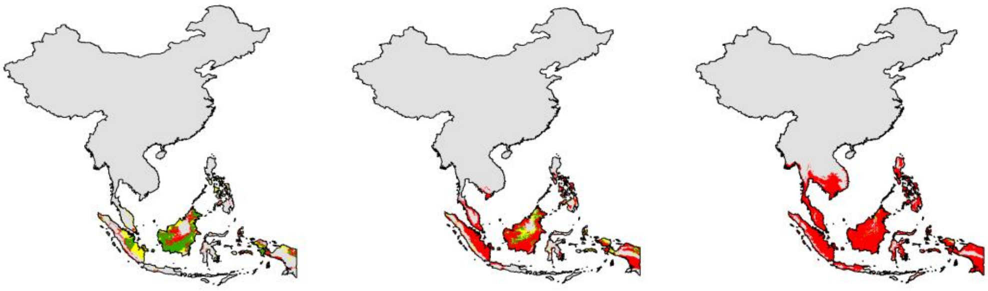


Current **RCP2.6** **RCP8.5**

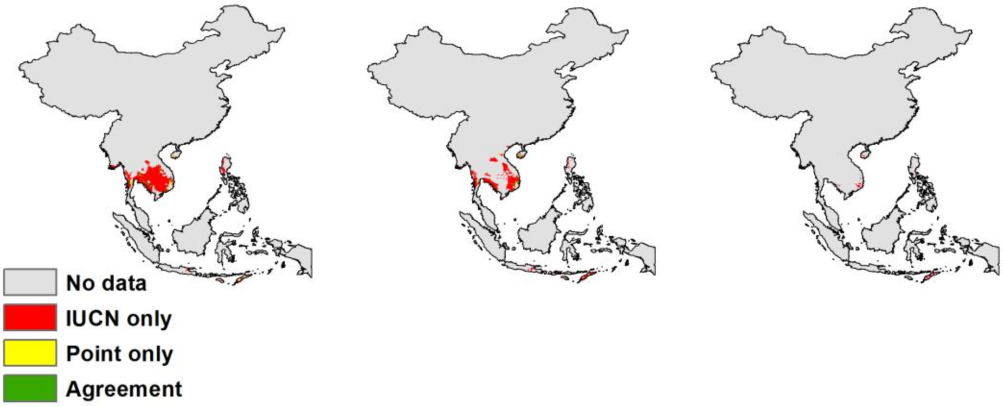
(d) *Trachypithecus phayrei*



(e) *Pongo pygmaeus*



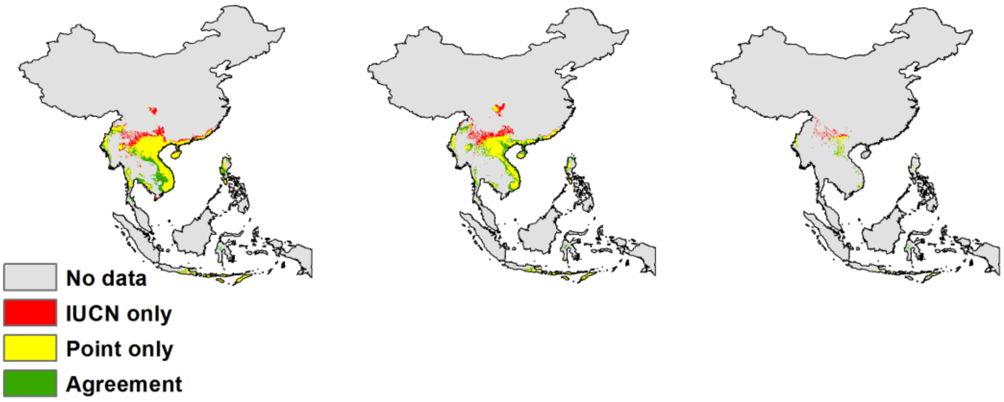
(f) *Hylobates pileatus*



Current **RCP2.6** **RCP8.5**

(g) *Nomascus concolor*

(h) *Nycticebus pygmaeus*



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