SPATIAL EFFECTS ON SPECIES DISTRIBUTIONS: IMPLICATIONS FOR TROPICAL SPECIES RICHNESS, AND HABITAT CONNECTIVITY

A dissertation proposal submitted by

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OVERVIEW

Human activities are radically altering the Earth's ecosystems (Vitousek et al. 1997; Sala et al. 2000; Benton et al. 2003). These dramatic changes across the globe have given rise in increasing species extinction rates that are estimated to escalate by up to 1000 times background levels; an increase comparable to previous mass extinction events in the history of life (Pimm et al. 1995; Chapin et al. 2000). In addition to extinctions, many species have been extirpated from portions of their natural habitat coopted for anthropogenic activities, due to subsequent habitat loss and fragmentation (Tilman et al. 1994; Kerr and Currie 1995; Pimm and Raven 2000; Schnell et al. 2013).

For the long-term persistence of species in fragmented landscapes quality, quantity and optimum distribution of preferred habitat are vital (Hanski and Ovaskainen 2000; Vos et al. 2001; Turner et al. 2001; Opdam 2003). Ecology and conservation theory predicts that larger and more connected habitat patches will contain a greater number of species per area than relatively smaller, more isolated patches (MacArthur and Wilson 1967). Large, interconnected patches potentially increase species persistence through increased gene flow (Joyce and Pullin 2003) and recolonization following local extirpations, buffering against environmental stochasticity (Hanski 1998; Campbell Grant et al. 2007).

Despite the importance of spatial arrangement of habitat for species persistence (Turner et al. 2001; Turner 2005), predicting how species respond to landscape heterogeneity, and incorporating such information into large-scale conservation planning is difficult (Margules and Pressey 2000; Moilanen et al. 2005; Pressey et al. 2007). This is partially due to the fact that spatial data on species and their habitat is often incomplete on the broad scales required for conservation planning (Anderson and Martinez-Meyer 2004; Posillico et al. 2004; Gibson et al. 2011; Jenkins et al. 2013), especially when relying on field measurements (Scholes et al. 2008). However, remotely sensed data can provide such broad-scale data, and can be powerful when combined with field data depicting animal occurrences or the ranges of larger numbers of species (Turner et al. 2003; Kerr and Ostrovsky 2003). In this context, I propose to examine spatial effects on species distributions for national-scale conservation planning.

The overarching goal of my dissertation is to assess relationships between spatial heterogeneity in tropical landscapes and species distributions by integrating species richness patterns, landscape connectivity, and species occurrences. Ultimately, I hope to advance our understanding of spatial patterns and ecological processes in tropical ecosystems, and provide the information necessary for effective large-scale conservation planning.

These issues are important, but also particularly challenging, for broad-scale conservation planning in the tropics because of the rapid and extensive loss and fragmentation of tropical habitats (Laurence 1999; Achard et al. 2002; Hansen and DeFries 2004; Wright 2005; Brooks et al. 2006). Specifically, Southeast Asia has the highest relative rate of forest loss of any tropical region (Achard et al. 2002; Hansen et al 2009; FRA 2010). This is of concern because tropical forests are a major component of the terrestrial carbon cycle (Dixon et al. 1994; Malhi et al. 1999), and serve as biodiversity hotspots containing large number of species, many of them endemic (Myers et al. 2000; Brook et al. 2003; Sodhi et al. 2004; Foley et al. 2005; Wright and Muller-Landau 2006; Laurance 2007; Bradshaw et al. 2008; Laurance et al. 2012). The threat of tropical deforestation makes it particularly important to understand the patterns and the drivers of terrestrial diversity patterns, and the interplay between landscape characteristics and species distributions (DeFries et al. 2007; Soares - Filho et al. 2006). Effective conservation decisions are only possible when based on spatial distribution of biodiversity (Balmford et al. 1998; Ferrier 2002; Brooks et al. 2002; Gardner et al. 2009).

Despite an increase in research of quantified spatial patterns and ecological processes in tropical forests in the last two decades, some tropical regions have received significantly more attention than others (e.g., Skole and Tucker 1993; Brook et al. 2003; Sodhi et al. 2010; Prist et al. 2012). In addition, many research efforts have been restricted to small-scale, well-established study sites within a given tropical forest subregion (e.g., Curran et al. 2004; Gardner et al. 2009). To provide better insights into the varied responses of tropical forest biota to anthropogenic impacts (Hughes et al. 2002; Geist and Lambin 2002; Sodhi et al. 2009; Dent and Wright 2009) and develop effective large-scale conservation planning in the tropics (DeFries et al. 2005; Soares - Filho et al. 2006), quantifying the value of forest habitat for species persistence is still needed in many tropical areas at a regional or national scale (Fazey et al. 2005; Barlow et al. 2007; Gardner et al. 2010).

In my first chapter, **the goal is to evaluate relationships between the Dynamic Habitat Index and species richness in order to provide a more comprehensive understanding of the factors that drive species diversity patterns in the tropics at broad scales.** I propose to a) calculate the Dynamic Habitat Index (DHI, Mackey et al. 2004; Berry et al. 2007) derived from Terra and Aqua MODIS data, b) apply the DHI as a univariate predictor of species richness patterns for various taxa in Thailand, and c) evaluate its utility in multivariate models together with other environmental variables.

The Dynamic Habitat Index is well-grounded in ecological theory of biodiversity patterns (Gaston 2000, Rahbek and Graves 2001, Evans and Gaston 2005). It summarizes three components of vegetative productivity: (1) the overall, cumulative productivity; (2) the minimum productivity; (3) the coefficient of variation in productivity. However, the DHI has only been tested in a few studies (Coops et al. 2009a; Coops et al. 2009b), and never in the tropics. My prediction is that the DHI will reveal relationships between productivity and species richness patterns in the tropics, and thus, can help to identify priority areas for biodiversity hotspots and to develop effective strategies for biodiversity conservation at broad scales.

In the second chapter, **my goal is to assess habitat patterns, and in particular habitat connectivity for tigers.** I will develop models to identify habitat suitability for tigers, calculate the least-cost path based on habitat availability, and use graph theory to evaluate the relative importance of patches in facilitating tiger dispersal. The Indochinese tiger (*Panthera tigris*) is an umbrella species and listed as globally endangered (IUCN). Tiger populations in Thailand have decreased dramatically, and subpopulations only remain within pristine forests of wildlife sanctuaries and national parks (Rabiniwitz 1993; Walston et al. 2010; Lynam et al. 2001; Steinmetz et al. 2006; Simcharoen et al. 2007; Lynam 2010). To ensure the long-term viability of tiger populations, it is imperative to maintain connectivity between large subpopulations in order to enhance their survival and preserve smaller subpopulations through networks of patches that are sufficiently connected by dispersing individuals (Fahrig and Merriam 1985; Linkie et al. 2006).

However, assessing the connectivity of tiger habitat is difficult due to a lack of comprehensive species distribution data, habitat suitability maps (Lynam 2010; Ngoprasert et al. 2012; Steinmetz et al. 2013), measures of connectivity (Early et al.2008; Kindlmann and Burel 2008), and approaches to identify priority patches in maintaining landscape connectivity across broad spatial scales (Margules and Pressey 2000; Vos et al. 2001; Rouget et al. 2006). To resolve these spatial data issues, I will use tiger occurrence records to predict habitat suitability and then calculate tiger habitat connectivity for Thailand.

In the third chapter, **my goal is to assess species-specific responses to landscape structure.** I propose to a) assess the effects of landscape patterns on bird distributions, b) utilize landscape structure metrics in species distribution models in order to map potential habitat suitability for each of species of forest bird, c) evaluate how well existing protected areas represent suitable habitats, and d) identify priority areas for bird conservation. Forest bird populations in Thailand have sharply declined due to deforestation, habitat loss, and fragmentation (Birdlife International 2001; Round et al. 2003; Aratrakorn et al. 2006). Empirical studies of birds in the tropics show that habitat fragmentation has negative effects on bird communities (Bierregaard et al. 1992; Brooks et al. 1997; Peh et al. 2006; Ferraz et al. 2007; Ruiz-Gutiérrez et al. 2008). However, studies of birds in temperate regions show that the importance of spatial pattern on the distribution and abundance of birds varies widely (McGarigal and McComb 1995; Trzcinski et al. 1999; Villard et al. 1999; Brotons et al. 2003; Vallecillo et al. 2009).

One reason why results vary so much is that the effects of habitat loss are often difficult to disentangle from those of fragmentation, but our lack of understanding of fragmentation has important implications for how to manage remaining remnant habitats (Hughes et al. 2002; Fahrig 2003). In order to develop effective large-scale conservation planning for species persistence in the tropics, it is necessary to understand the landscape structure determinants of species distributions (Graham et al. 2001; Umetsu et al. 2008).

In summary, my research will use novel remote sensing techniques coupled with field-based datasets, and quantitative analyses of landscape patterns to address broad questions of spatial effects on species distributions including species diversity patterns, habitat connectivity, and bird distributions in a highly diverse, rapidly changing, and little-studied tropical region of the world: Thailand. To date, Thailand is experiencing rapid economic development accompanied by massive environmental degradation. Most threatened species in Thailand only persist in protected areas, which are also the last strongholds for unique ecosystems with remarkable biodiversity. In the context of a global extinction crisis, the effectiveness of broad-scale conservation planning will ultimately determine the fate of the country's biodiversity. However, Thailand still lacks the necessary information for conservation planning due to limited studies at broad scales that can inform national-level decisions. My research will provide important information which can assist Thailand's policy-makers to succeed in broad-scale conservation planning efforts.

GOALS AND OBJECTIVES

Chapter 1: Predict tropical species richness patterns using the Dynamic Habitat Index derived from MODIS

Objective 1: Produce the DHI for Thailand

Objective 2: Test the utility of the DHI in explaining species richness patterns

Objective 3: Integrate the DHI with other remotely-sensed variables in predicting spatial variation in species richness

Chapter2: Assess the structural connectivity of habitat suitability for tigers

Objective1: Map tiger habitat suitability

Objective 2: Assess tiger habitat connectivity

Objective 3: Rank potential habitat patches in terms of their importance for connectivity

Chapter 3: Effects of landscape structure on bird distributions

Objective 1: Quantify the effects of landscape structure on bird distributions

Objective 2: Integrate landscape structure metrics into species distribution models for predicting bird habitat suitability

Objective 3: Evaluate how well existing protected areas capture suitable habitats, and identify priority areas for bird conservation

STUDY AREA

Thailand, located in south-east Asia, covers an area of 513 115 km^2 between latitudes 5° 45´ and 20° 27´ N and longitudes 97° 22´ and 105° 37´ E. It is bounded by Myanmar to the north and west, by Laos to the north-east, by Cambodia and the Gulf of Thailand to the south-east, by Malaysia to the south and by the Andaman Sea and Myanmar to the south-west (Figure 1) (GISTD 2012). Altitude ranges are from 0 m to 2564 m above sea level in Chiang Mai Province in the north. Thailand's land area covers 510,890 km^2, and its agricultural area is approximately 210,600 km^2 (FAO 2011). Thailand's population is 70,243,000 (NSO 2013).

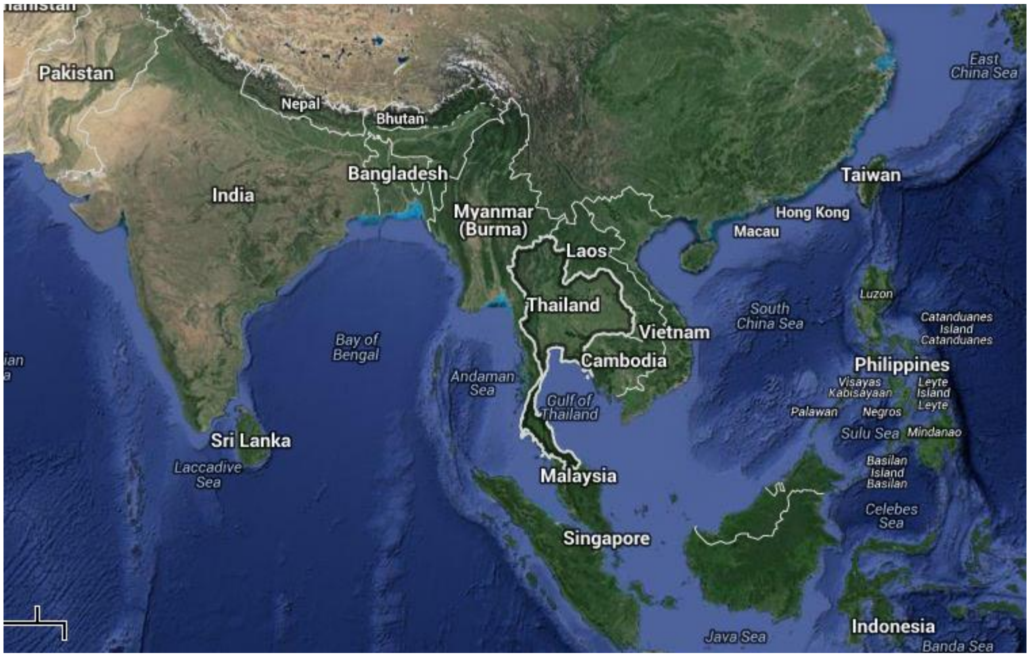

Figure 1. Location of study area, Thailand. White lines indicate boundaries of countries

The climate of Thailand is influenced by seasonal monsoons, i.e. the southwest and the northeast monsoon, plus local topography. Thailand has two seasons: rainy season, and hot-dry season. Annual precipitation decreases during the southwestern monsoon from May to October in most parts of country. Some parts receive additional rainfall from the northeast monsoon during November to January. The rainfall varies from less than 1,000 mm in the Khorat plateau, northeastern bulge to 4,000 mm in the extreme southeast and on the west coast of the peninsula. The average annual temperature is approximately 26-29 °C. The highest temperature is over 40 °C in April and the lowest under zero in the mountainous regions (TMD 2010).

Due to this monsoonal climate, the vegetation of Thailand consists of two diverse types of tropical forest: broad-leaved evergreen forest and broad-leaved deciduous forest. The tropical broad-leaved evergreen forest is subdivided into tropical rain, pine, mangrove, and beach forests. The tropical broad-leaved deciduous forest includes mixed deciduous and dry dipterocarp forests (RFD 2010).

Thailand is divided into four regions: North, Northeast, Central, and South (Figure 2). Northern Thailand covers 17 provinces and encompasses an area of 172,277 km^2 or one-third of the country. In the North, the dominant topography is mountainous, oriented north-south. Average annual temperature ranges from 20 to 34 ◦C. The average annual rainfall ranges between 600 and 1000 mm in low areas to more than 1000 mm in mountainous areas. The rainy season is from May to October. All of northern Thailand was originally covered by dense forest. Dominant vegetation includes dry dipterocarp and mixed deciduous forests in low and moderate altitudes, while pine forest, hill evergreen forest, and tropical montane cloud forest dominate in high altitudes (Santisuk 1988).

The Royal Forest Department (2010) reported that forest cover in this region declined from 69% in 1961 to 56% in 2002. Lowland forests disappeared due to extensive logging and the expansion of agricultural land. Meanwhile, swidden cultivation in mountainous areas shortened their cycles or changed to monoculture cash crops over the last 50 years (Deland 2002; Fox and Vogler 2005; Fukushima et al. 2008; Schmidt-Vogt 2001). The continuing rise of rubber prices in the last decade has stimulated a demand for rubber plantations (Department of Agriculture 2010). Approximately 50,000 ha were planted in the region in 2004–2006 (Office of Agricultural Economics, OAE 2007). In addition, forest cover inside the protected area network declined from 86% to 76% during the same period (Trisurat et al. 2010).

Northeastern Thailand also contains approximately one-third of the country's area. It covers 19 provinces. Geographically, the northerneastern region overlaps with the Khorat plateau, a wide, shallow basin underlain by Cretaceous sandstone, shale, and siltstone, though intruded in places by tertiary basalts. Layers of rock salt and other salt-bearing strata are common. Heavily leached fine sandy loams predominate the soil layer, often with poor drainage and low innate fertility. The natural vegetation consists of dry monsoon forest dominated by dwarf dipterocarp trees, plus areas of grassland, thorny shrubs, and bamboo thickets (Parnwell

1988). Vegetation phenology is largely drought-controlled (Ghassemi et al. 1995). Deforestation associated with agricultural expansion has been widespread in northeast Thailand for centuries (Feeny 1988, 1989). Prior to World War II**,** agricultural expansion accelerated due to the increased production of paddy rice. Since then, it has also been related to upland crops, particularly cassava and sugar cane (Walsh et al. 1999). During 1972-2001, forest areas declined due to expanded paddy rice in alluvial plains and lowlands, while upland field crops, mainly cassava, expanded in the middle and high terraces (Walsh et al. 2001; Walsh et al. 2008).

Central Thailand covers 26 provinces. This part is a large, low-level plain where the Ping, Wang, Yom and Nan Rivers, all originating in Northern Thailand, join together to become the Chao Phraya River in Nakhon Sawan province. The climate is dominated by tropical southwest and northeast monsoons. It is actually divided into three seasons. The hot season generally starts from the middle of February and ends in the middle of May. The rainy season, or southwest monsoon season, begins in the middle of May and lasts until the end of October. The cold season, or northeast monsoon, usually ranges from the end of October to the middle of February (Meteorology Department 2010). Land conversion in this region is mainly caused by urban sprawl, the expansion of commercial agriculture, and road development (Cropper et al. 2001)

Southern Thailand is located between 5°37´-11°42´ North latitudes and 98° 22´ - 102° 05´ East longitudes. It covers 14 provinces and encompasses an area of approximately 70,700 km^2 or 14% of the country’s land area. Southern Thailand varies in width from roughly 50 to 2 km, and a mountainous backbone runs its length from north to south. The average annual temperature is 26.6° C. Annual precipitation is over 2000 mm for most of the area and exceeds 3000 mm in some parts. Rainfall increases southward as the length of the dry season and the magnitude of pre-monsoon drought stress declines. The southern mountain ranges receive rain from both the northeast and southwest monsoons. Forest types in Southern Thailand fall into 2 categories: (1) Peninsular Wet Seasonal Evergreen Forest; (2) Malayan Mixed Dipterocarp Forest (Santisuk et al. 1991). Tropical rainforest trees in the family Dipterocarpaceae dominate forests throughout the peninsular region but species change both with elevation and latitude.

Forest cover in Southern Thailand declined from 42% in 1961 to 27% in 2008 (Royal Forest Department 2010). The main threats are plantations for rubber, oil palm, and tropical fruits, infrastructure, tourism (Panayotou and Sungsuwan 1989; Cropper et al.1999; Krukanont and Prasertsan 2004), and shrimp farms (Flaherty and Karnjanakesorn 1995).

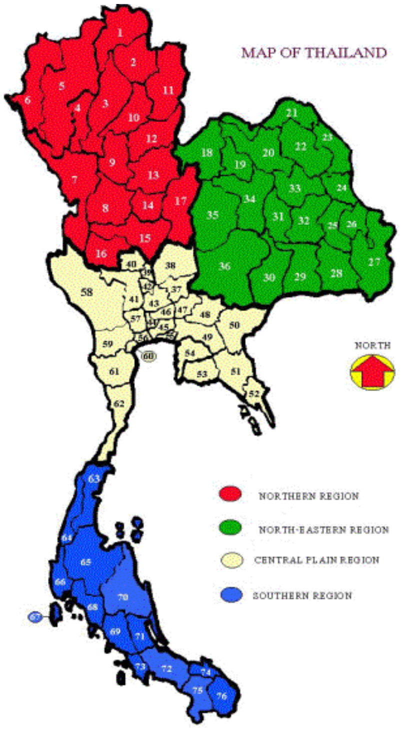

Figure 2. The four regions of Thailand.

(*Source*: http://faorap-apcas.org/thailand/thaimap.htm)

Thailand's biodiversity

Thailand overlaps with two global biodiversity hotspots: Indo-Burma and Sundaland (Myers et al. 2000). Thailand consists of fifteen terrestrial ecoregions (Olson et al. 2001), four freshwater ecoregions (Abell et al. 2008), and one marine ecoregion (Spalding et al. 2007). It is estimated that Thailand contains 87,500 species of fauna, and 18,073 species have been identified (OEPP 2000). Moreover, the number of vascular plant species in Thailand is estimated to be between 20,000 and 25,000 species (ICEM 2003). Thailand is also home to at least 982 species of birds, 302 species of mammals, 350 species of reptiles, and 137 species of amphibians; and new species are regularly being reported (IUCN 2004).

Thailand's bird species include two that are extirpated from Thailand, two that are extinct in the wild, 43 critically endangered, 66 endangered, 71 vulnerable, 89 near threatened, 9 data deficient and 2 endemic species. The extinct bird species are the giant ibis (*Pseudibis gigantea*, and the large grass warbler (*Graminicola bengalensis*). Extinct in the wild bird species are the sarus crane (*Grus antigone*) and white-shouldered ibis (*Pseudibis davisoni*). Two endemic bird species are the Deignan's Babbler (*Stachyris rodolphei*), and white-eyed river martin (*Pseudochelidon sirintarae*) (Sanguansombat 2005).

Currently, there is one extinct mammal species: the Schomburgk's Deer (*Cervus schomburgki*). There are also 4 species that are extinct in the wild, 12 critically endangered, 35 endangered, 69 vulnerable, 15 near threatened, 10 species of least concern, 13 species with deficient data, and 5 endemic species. A total of 350 species of reptiles have been reported in Thailand. The false gavial (*Tomistoma schlegelii*) is listed as extinct in the wild due to intense hunting, eleven species are classified as critically endangered, 5 species as endangered, 16 species as vulnerable, 48 as near threatened, 183 as least concern, 89 as data deficient, and 47 species as endemic. There are 137 species of amphibians that have been categorized, including 5 species that are vulnerable, 33 species that are near threatened, 64 species that are of least concern, 35 species that are deficient in data, and 7 species that are endemic (Nabhitabhata and Chan-ard 2005).

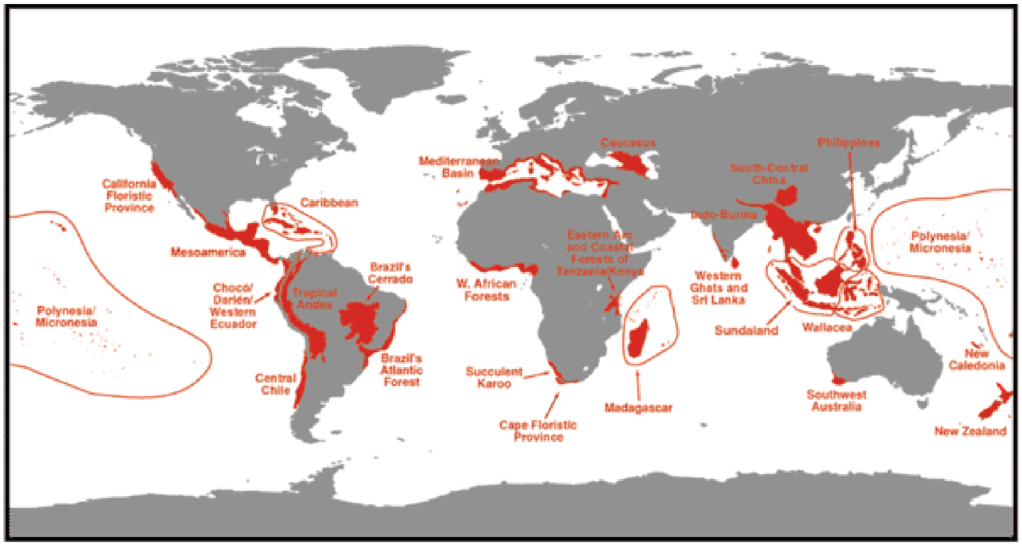

Figure 3. Thailand overlaps with Indo-Burma and Sundaland biodiversity hotspot

(*Source*: Myers *et al. 2000*, *Nature 403*)

Threats to Thailand's biodiversity

Many of Thailand's native species have been listed as extinct or threatened due to habitat loss and fragmentation resulting from broad-scale deforestation and land use change (Brockelman and Srikosamatara 1993; Pattanavibool and Dearden 2002; Lynam et al. 2006; Lynam 2010; Ngoprasert et al. 2012; Trisurat et al. 2012). Most threatened species are extirpated from non-protected forests, existing only within wildlife preserves (Pattanavibool and Dearden 2002). The major challenge of conservation and natural resource management in Thailand is primarily socioeconomic development, including deforestation, agricultural conversion, population growth, poverty, chronic shortage of conservation resources (e.g., funding), corrupt national institutes, and conflicts between authorities and indigenous people (Sodhi et al. 2004; Steinmetz et al. 2006; Emphandhu et al. 2006; Vandergeest 2003).

Population growth in Thailand has increased the rate of conversion of forest to agriculture (Feeny 1988; Panayotou and Parasuk 1990). After World War I, the population growth rate was high (Hanks and Hanks 1972) and there was a strong demand for Thai rice exports, resulting in the expansion of agricultural lands throughout Thailand until the disruption of World War II. However, after World War II, population growth rates peaked at more than 3 % per year (Piker 1976). Substantial land change during the 1950s and 1960s, which caused deforestation in the north, northeast, and central regions, was mainly due to rice cultivation and urban sprawl in central Thailand. Also, a loose regulation of land tenure allowed people to occupy available lands (Vanlandingham and Hirschman 2001).

From the 1960s to the1980s, forests were converted to shifting cultivation in Northern Thailand, and mega projects in the Northeast, such as land resettlement, dams, roads, and commercial agriculture, affected large areas as well. Total rice cultivation was roughly 1,440,000 ha in 1905 but increased to 10,509,918 ha in 1999 (NSO 2003), while the forest areas decreased by 13.6 million hectares from 1961 to 1988 (Cropper et al. 1999). The remaining forest land in Thailand was approximately 12 million ha in 1999 (NSO 2003). Population growth during 1976 and 1989 was one of the most important causes of the 28% loss of forest cover, especially in the north and northeast regions of Thailand. Most of the deforestation that occurred in Thailand during the 1980s was because policies favored clearing for agricultural expansion, logging, and conversion to ranch land (Cropper et al. 1999).

The rapid growth of Thailand's economy since the 1980s has led to an equally rapid loss in biodiversity due to unsustainable use of natural resource such as shrimp farms (Saisithi 1989; Flaherty and Vandergeest 1999), tourism (Hvenegaard and Dearden 1998; Brockelman and Dearden 1990), marine fisheries, agriculture, and forestry. Whereas, national media expressed concern about mounting environmental issues, government policies often had conflicting goals. For example, the government subsidized tapioca farmers to increase exports, which caused the loss of Thailand's eastern forests, while other government policies encouraged forest protection (McNeely and Dobias 1991; Cropper et al. 1999; Delang 2005). Since the responsibility for managing natural resources belongs to the central government in Bangkok, local people who would directly benefit from the exploitation of those resources have little power to ensure long-term and sustainable management. As a result, biodiversity loss is now at a crisis level and in urgent need of appropriate conservation policies (Trisurat et al. 2012).

In summary, forest cover in Thailand declined from 53% of the country's area in 1961 to approximately 37% in 2010 (Royal Forest Department 2010) (Figure 4 and Figure 5). In 1995, Thailand's deforestation rate was ranked the highest of all countries in the Greater Mekong Subregion (i.e., Thailand, Cambodia, China (southern provinces), Lao People's Democratic Republic, Myanmar, and Viet Nam).

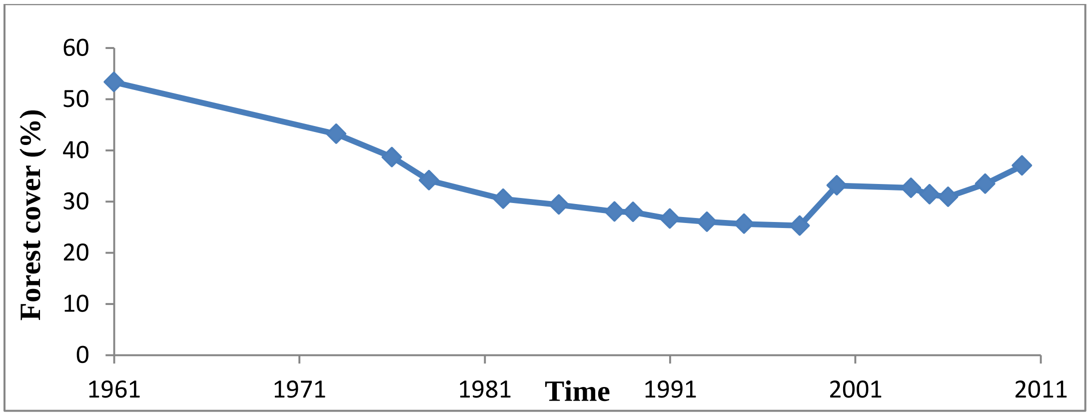

Figure 4. Trends in the proportion of forest cover from 1961 to 2010 (Royal Forest Department 2010).

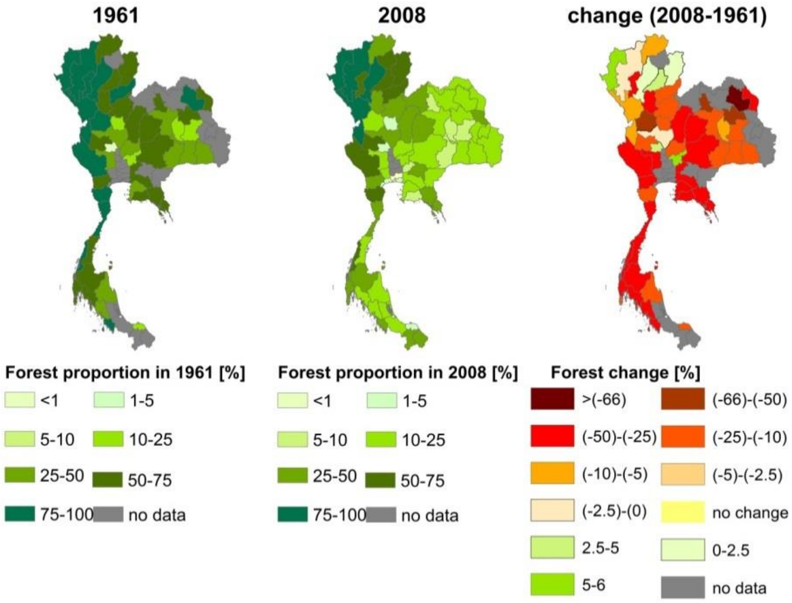

Figure 5. Proportions of forest cover at the province-level in 1961 and 2008, and deforestation rates over past 50 years (RFD 2010).

Thailand's protected area system

Deforestation and biodiversity loss have been a cause for concern for policy-makers (Figure 3). The Royal Forest Department (RFD) of Thailand established Khao Yai National Park as the first protected area in Thailand in 1962, and the first wildlife sanctuary, Salak Pra, was declared in 1965. Deforestation peaked in the mid-1970s, when the annual loss was about 776,000 ha or 6.0%. In 1989, the Royal Thai Government banned commercial logging nationwide; however, the rate of deforestation was not substantially reduced, particularly during 1991–1993, because of Thailand's rising economic activity in the early 1990s.

The protected area coverage was significantly increased after the nationwide logging ban and the completion of national forest reserve zoning (TFSMP 1992). In addition, several national policies have been instated such as the National Forest Policy and the Thai Forestry Sector Master Plan (TSFMP) approved by the Cabinet in 1985 and 1992, respectively. The aim of these legislative actions is to increase the protected area estate to 25% of the country's land area (TFSMP 1992). Recently, Thailand Policy and Prospective Plan for Enhancement and

Conservation of National Environmental Quality, 1997–2016 aimed to increase forest cover to 50% of the country. At least 30% is to be designated as conservation forest and 20% as production forest (OEPP 2000). The rapid establishment of protected areas after 1989 was opportunistic, aiming to protect the remaining forest cover in order to reduce the rate of deforestation rather than protect biodiversity per se.

In addition, national parks and wildlife sanctuaries are enforced by the National Park Act of 1961 and the Wild Animal Preservation and Protection Act of 1992, which are more effective and stronger than other forest laws. To date, the protected area system in Thailand covers 96,042 km^2 or ~ 18.5% of the country's area (Figure 6) which includes 108 national parks, 57 wildlife sanctuaries, 113 forest parks, 51 non-hunting areas, 16 botanical gardens, and 55 arboreta (Table 1) (DNP 2012).

The Royal Forest Department in Thailand estimated that more than 12 million people inhabited national reserve forests in 1990, with a significant number of them in protected areas (TFSMP 1992). Land speculation due to commercial tourism in the last decade has also contributed to forest encroachment (Trisurat 2007). Settlements within protected areas often contribute to large-scale forest loss and degradation as well as extensive hunting activities (Rabinowitz and Walker 1991). Encroachment at the perimeter reduces the effective size of protected areas. Fires affect forest configuration, and lower the carrying capacity for many mammal species (Lekagul and McNeely 1977; Rabinowitz 1990). Roads allow greater human access for illegal activities in the protected area, contributing to wildlife mortality and causing habitat fragmentation (Rabinowitz 1993).

Despite establishing extensive protected area networks and the national logging ban, Thai's Government has launched big development projects such as timber extraction, large-scale plantation and intensive commercial agriculture (Ramakrishnan et al. 2000). These conflicts between economic development and conservation polices are important issues for sustaining biodiversity in many tropical countries (Lambin et al. 2001). Due to ongoing human population growth and the rapid expansion of oil palm and rubber plantations in Thailand (Office of Agricultural Economics 2007), deforestation is expected to continue with increasing habitat loss and fragmentation, and infrastructure development (Trisurat et al. 2010).

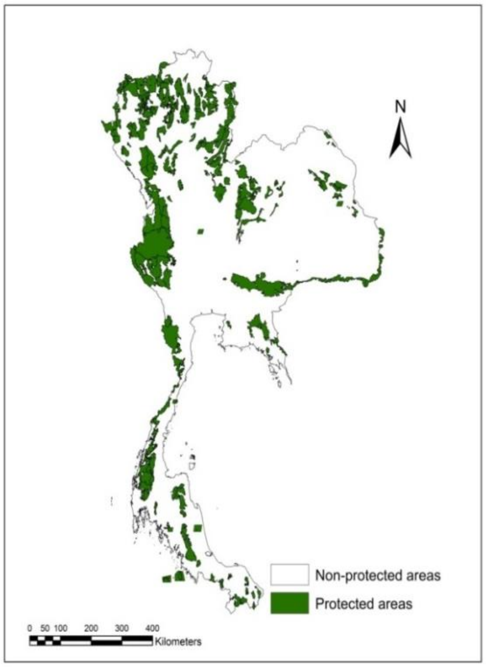

Figure 6. Protected areas of Thailand

(*Source*: IUCN and UNEP 2009)

Table 1. Protected areas in 2007 (DNP 2007)

Categories	Number	Area(km^2)	Percentage of the country	Percentage of protected areas
Wildlife Sanctuary	57	36205.4	7.1	37.7
National Park	108	54733.4	10.7	57.0
No Hunting Area	51	3776.2	0.7	3.9
Forest Park	113	1238.8	0.2	1.3
Botanical Garden	16	46.3	0.0	0.0
Arboretum	55	41.9	0.0	0.0

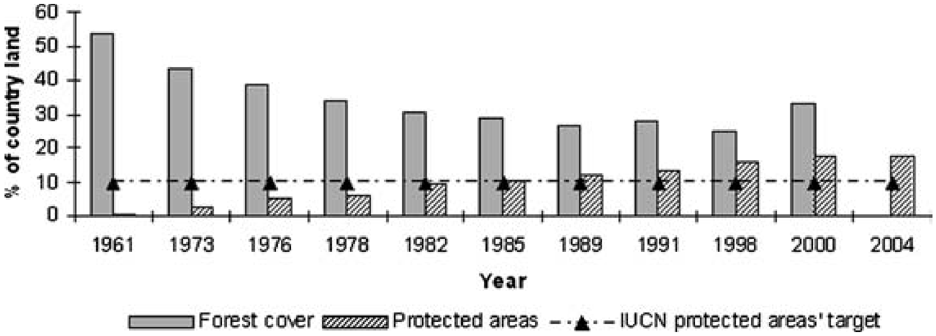

Figure 7. Establishment of protected areas in Thailand compared with loss of forest cover (according to years of forest cover monitoring)

(*Source*: Trisurat 2007, *Environmental Management, 39:235–245*)

CHAPTER 1: Dynamic Habitat Index for predicting species diversity patterns in Thailand

INTRODUCTION

Biodiversity loss is inextricably linked with anthropogenic activities (Sala et al. 2000). Dramatic changes in the environment have altered global biogeochemical cycles, transformed habitat, and changed the distribution of biota (Vitousek et al. 1997), which in turn has disrupted ecological processes and ecosystem services (Chapin et al 2000). These threats are so formidable, and the subsequent loss of biodiversity so unprecedented, especially in tropical forests, that the current extinction crisis could ultimately be at the scale of prior mass extinction events in our planet's history (Laurance 1999; Pimm et al. 2000).

The threat of extinction brings urgency to the task of protecting biodiversity. In order to support conservation efforts, a better understanding of the spatial distribution of species richness is crucial (Petraitis et al. 1989; Gaston 2000; Gotelli et al. 2009). Despite many efforts to map broad-scale patterns of biodiversity (Buckton and Ormerod 2002, Myers et al. 2000), the spatial resolution of these maps is often too coarse to be relevant for resource management and conservation planning at regional or national scales. To map species richness patterns at a finer spatial resolution, biological indices that can be used to identify the drivers of species richness patterns, both spatially and temporally, are needed (Leyquien et al. 2007; Duro et al. 2007).

However, knowledge of the spatial distribution of the factors that influence species richness, and its impact on richness patterns across landscapes is difficult to acquire due to limited spatial information (Ferrier 2002; Jetz et al. 2012).

Local and regional species richness varies by orders of magnitude across landscapes (Gaston and Blackburn 2000; Groombridge and Jenkins 2002). Understanding the factors influencing this spatial variation in species richness is a key to predicting biodiversity patterns and developing effective conservation planning (Rosenzweig 1995; Gaston 2000; Orme et al. 2005) because direct observation of species richness patterns over a large area is rarely possible (Foody and Cutler 2003).

Land area (MacArthur and Wilson 1967), environmental stability (Connell and Orias 1964), climatic factors (Klopfer 1959), habitat heterogeneity (Simpson 1949; MacArthur and MacArthur 1961), evolution (Whittaker 1972), and energy availability (Wright 1983) are primary determinants of regional, spatial variation in species richness (MacArthur 1972; Pianka 1966; Schall and Pianka 1978; Huston 1979; Rosenzweig 1995). Energy availability is often used to explain the observed variation in species richness patterns across landscapes (Rosenzweig 1995; Kerr and Packer 1997; Mittelbach et al. 2001). Species-energy theory states that, per-unit-area, available resource productivity affects species' abundance and probabilities of species occurrence (Wright 1993). Energy availability correlates positively with species richness (Connell and Orias 1964; MacArthur 1965, 1969) because higher productivity due to increased energy provides broader resource availability, resulting in greater biodiversity (Walker et al. 1992; Evans et al. 2005).

Productivity is a measure of the resource energy available to organisms (Wright 1983). Spatial heterogeneity of productivity is shaped by temporal and spatial variation in the biological, physical, and chemical components of the environment (Leyequien et al. 2007) which manifests itself through changes in vegetation productivity and biomass as a result of the interaction between vegetation, climate, and soil conditions (Townsend et al. 2008). Understanding the interaction between landscape productivity and species diversity is essential to maintain ecological function within a complex food web (Connell and Orias 1964; Paine 1966). However, patterns of productivity-to-species-diversity vary widely. Productivity-diversity patterns can be positive, negative, or parabolic, depending on the taxa, geographical scale, and ecosystem in question (Mittelbach et al. 2001).

Understanding the relationship between productivity and species richness is crucial for maintaining biodiversity, given that the resource available for habitat conservation are limited (Turner et al. 2003). The productivity-species richness can be measured with numerous metrics, such as the productive energy metric (Evans et al. 2005). However, it is difficult to obtain productivity data at an appropriate resolution that can be meaningful in exploring species–energy relationships (Evans et al. 2005). Indices derived from satellite data can provide useful spatial distribution information as a proxy for productivity and plant biomass (Oindo and Skidmore 2002; Hurlbert and Haskell 2003; Kerr and Ostrovsky 2003; Scholes et al. 2008; Pereira et al. 2013).

Remote sensing is a powerful tool for biodiversity assessments (Nagendra 2001; Kerr and Ostrovsky 2003). A main advantage of remotely sensed data over field data is the availability of high spatial and temporal resolution data over a broad extent (Innes and Koch 1998; Roy 2003), but despite advances in remotely sensed techniques, it is not clear if remotely sensed indices can be an effective tool in predicting tropical biodiversity patterns.

Remote sensing of biodiversity can be categorized into three main approaches: (1) direct measure of individual organisms, species assemblages, or ecological communities, (2) indirect mapping based on inference derived from habitat requirements (such as land cover classifications, topography, and climate) and observed species distribution (Turner et al. 2003), or (3) indirect mapping based on relationships between spectral radiance values obtained from unclassified imagery and species distribution (Nagendra 2001).

Satellite data have been used to classify vegetation types, to track resource availability through space and time, and to integrate animal location data and vegetation patterns to define habitat suitability (Liu et al. 2001; Pidgeon et al. 2007; Kuemmerle et al. 2010) and provide the necessary data to monitor landscape patterns (Radeloff et al. 2000; Hansen et al. 2001). Remote sensing indices are thus essential in conservation planning, priority-setting, future surveys, and for the monitoring of environmental changes (Turner et al. 2003; Venier et al. 2004; Nagendra et al. 2013). Consequently, a range of indices derived from remote sensing have been widely used in predicting species richness (Evans et al. 2005; Coops et al. 2009a; Michaud et al. 2012), and monitoring changes in diversity patterns at different spatial and temporal scales (Stoms and Estes 1993; Turner et al. 2003; Duro et al. 2007).

Spatial variation in primary productivity can be measured through various relationships of satellite sensors to biophysical characteristics of plants such as standing biomass, leaf area index, tree volume, or canopy light absorption (Turner et al. 2003). The relationships between species diversity and primary productivity derived from remotely sensed information have been successfully applied to broad-scale studies (e.g., Nilson et al. 2005; Culbert et al. 2012). The most commonly used remotely sensed index for quantifying productivity is the Normalized Difference Vegetation Index (NDVI) (Kerr and Ostrovsky 2003; Pettorelli et al. 2005). NDVI has been used widely to estimate seasonal variation in vegetation cover and applied to predict species diversity patterns (Jorgensen and Nohr 1996; Gould 2000; Harrison et al. 2006). However, there are limitations to the use of NDVI in the tropics, where the index is known to saturate (Boyd et al. 1996; Steininger 1996; Kerr and Ostrovsky 2003). Despite this challenge, many studies in the tropics has applied NDVI to studies of tree species richness (e.g., Gillespie 2005; Feeley et al. 2005; Nagenda et al. 2010), as well as bird and butterfly richness (e.g., Seto et al. 2004; Ding et al. 2006; Ranganathan et al. 2007; Suarez-Rubio and Thomlinson 2009).

Alternatively, the biophysical index of vegetation canopy greenness is the fraction of absorbed photosynthetically active radiation (fPAR). fPAR is a measure of the proportion of available solar radiation in photosynthetically active wavelengths that is absorbed by vegetation, thus quantifying vegetative productivity (Veroustraete et al. 1996; Sellers et al. 1997; Herfindal et al. 2005). In theory, the higher the average fPAR level observed over the growing cycle, the denser the green leaf cover, the higher the productivity, and the less disturbed the vegetation cover. fPAR values vary from zero on barren land to one in dense vegetation cover (Knyazikhin et al. 1998).

While fPAR is less commonly applied to biodiversity studies, it is required to calculate the rate at which carbon dioxide and energy from sunlight are assimilated into carbohydrates during photosynthesis of plant tissues. fPAR accumulates carbon assimilated by the vegetation canopy over time, thus it yields the landscape gross primary productivity (Monteith and Unsworth 1990). Several studies demonstrated that fPAR observed by daily satellite observations could successfully be used to monitor large-area ecosystem behavior (Potter et al. 2003). Moreover, fPAR can be used as a potential tool in predicting area-specific home-range sizes of carnivores (Nilsen et al. 2005). Despite ecological applications of fPAR in studies of biodiversity patterns in temperate regions, it is not clear if fPAR can be an effective tool in predicting tropical biodiversity patterns.

The Dynamic Habitat Index (DHI, Mackey et al. 2004; Berry et al. 2007) is a measure of vegetation productivity. The index, based on fPAR, is derived solely from satellite data. The DHI integrates time series of satellite observations of greenness which represent vegetation dynamics. The DHI summarizes three components of vegetative productivity: The first component is the annual productivity, providing an indication of overall light absorbed by vegetation. Annual productivity represents the productive capacity of a landscape across a year and has long been recognized as a strong predictor of species richness (Connell and Orias 1964). If areas have high productivity, they have more energy to support diversity of species. The second component is the annual minimum productivity, providing an indication of the minimal level of vegetative cover to support organisms throughout the year (Schwartz et al. 2006). If the productivity of an area has a high minimum, it should support more biological diversity. The third component is the seasonal variation in productivity, measuring the coefficient of variation in productivity over the course of a year. If any areas have less intra-annual variability, they are more biologically diverse.

The three components of the DHI have been developed to predict species richness as a component of the habitat suitability index because it measures landscape productivity which represents available food at the foundation of ecological food webs and habitat resources for fauna (Mackey et al. 2004; Berry et al. 2007). Recently, the DHI has been successfully used to predict bird species richness in the U.S. (Coops et al. 2009a) and Ontario, Canada (Coops et al 2009b). The DHI has great potential for studies of biodiversity because it corresponds with ecological theory of biodiversity patterns. However, the DHI has been applied in a few studies. It is necessary to explore the relationship between the DHI and species richness across a range of taxa in order to understand broad-scale interactions of ecological processes that drive tropical biodiversity patterns.

The overall goal of this chapter is **to assess relationships between species richness and the Dynamic Habitat Index, and determine the relative importance of the DHI and other environmental variables in explaining nationwide patterns of terrestrial species richness in Thailand**. To achieve this goal, I will address three specific objectives:

Objective 1: Calculate the Dynamic Habitat Index (DHI) derived from the fraction of photosynthetically active radiation (fPAR) across Thailand from 2002 to 2012.

Objective 2: Test the utility of the DHI in predicting species richness patterns for terrestrial taxa.

Objective 3: Investigate potential synergies between the DHI and other human-related and environmental factors in explaining species richness patterns.

METHODS

DATA

Distribution range maps

To quantify species richness, I will use species distribution maps for terrestrial species in Thailand derived from the global species distribution maps for 2013 (IUCN 2013). The range maps include birds, mammals, reptiles, and amphibians. Polygon range maps will be converted to rasters with 1-km resolution on a Universal Transverse Mercator (UTM) projection. For this analysis, a species will be counted as present if any part of the cell is covered by the species' range polygon. Then, I will add up all species presences for each grid cell to quantify species richness following the similar approach of Sandom et al. (2013). All data handling will be performed in ArcGIS version 10.1.

Fraction of photosynthetically active radiation (fPAR) intercepted by vegetation

NASA's MODIS sensors Terra and Aqua, launched in 2000 and 2002 respectively, provide near-daily coverage of the globe at a 1-km spatial resolution in 36 spectral bands (Heinsch et al. 2006). Also, the MODIS data are available as standardized data products, processed with advanced algorithms for geo-referencing, atmospheric corrections, and cloud-screening (Justice et al. 2002). Therefore, MODIS data are well-suited to study vegetation dynamics at different spatial and temporal scales which provide insights on changes in biodiversity patterns and climate systems (Duro et al. 2007).

fPAR is one of a range of MODIS products that describe vegetation. fPAR is calculated from daily surface reflectances, and based on a physical model that describes the propagation of light in plant canopies (Tian et al. 2000). To minimize the effect of cloud cover, atmospheric variation and other confounding environmental conditions, the maximum daily fPAR is selected for each 8-day period, and these 8-day composites are combined into monthly maximum fPAR products. fPAR monthly images with 1-km resolution for Thailand, from 2001 to 2011 will be obtained from the Boston University website (climate and vegetation research group: http://cliveg.bu.edu).

Topography

Topography strongly correlates with species richness patterns. In the tropics, the highest species diversity often occurs at mid-elevations (Rosenzweig and Sandlin 1997; Patterson et al. 1998; Colwell and Lees 2000). NASA and the United States National Imagery and Mapping Agency (NIMA) launched the Shuttle Radar Topography Mission (SRTM) on the space shuttle in 2000. The SRTM mission obtained data for 80% of the land surface between ±60º latitude which provides elevation data across globe at 90 m spatial resolution (Farr and Kobrick 2000). Elevation data for Thailand will be obtained from the SRTM version 4.1 (http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1). I will calculate the topographic coefficient of variation as the mean of the elevation within a 1 km grid cell divided by its standard deviation. Slope data will be calculated from the elevation data.

Land cover

Spatial heterogeneity of landscapes strongly relates to species richness (reviews in Lawton 1983; McCoy and Bell 1991; Turner 2005). Land cover types are crucial to species diversity assessments because it provides first order information of species’ occurrence (Turner et al. 2003).

The Land Development Department of Thailand generated a land cover map for the whole country in 2008. The land cover map was derived using supervised classification algorithms based on Landsat TM and ETM+ imagery, aerial photos, and ground truth data. Land use/cover data is available as a vector format at the ratio of 1:25,000. The land cover map identifies 16 land cover classes: (1) intact forest, (2) disturbed forest, (3) aquaculture, (4) aquatic plant, (5) field crop, (6) horticulture, (7) agroforestry, (8) wetland, (9) miscellaneous land, (10) orchard, (11) paddy field, (12) pasture and farm, (13) perennial, (14) swidden cultivation, (15) urban, and (16) water.

For this analysis, I will consider effects of proportions of land cover, land cover richness, land cover diversity, protected areas, and forest fragmentation at a 1 km grain size. For the proportion of land cover, I will include: (1) forest (forest, disturbed forest), (2) wetland, (3) agriculture (field crop, horticulture, agroforestry, orchard, paddy field, perennial, swidden cultivation), and (4) urban (miscellaneous land, pasture and farm, urban). Proportions of land cover dominance will be computed as the proportion of the area covered by those dominant land cover classes in each pixel. The richness of land cover classes will be calculated by the total number of land cover classes within a 1 km resolution (Hill and Smith 2005). Land cover diversity will be computed by the Shannon index (Peet 1974). Protected area data will be obtained from the World Database of Protected Areas IUCN I-IV (WDPA, IUCN and UNEP 2009; http://maps.geog.umd.edu/WDPA/WDPA_info/English/index.html). I will calculate the proportion of protected areas in each 1 km grid cell.

Forest fragmentation has strong effects on species richness in the tropics (reviews in Laurance 1997; Turner 1996). To assess forest fragmentation, I will use a land cover map with 30 m resolution and a morphological image segmentation approach (Vogt et al. 2007). Each forest pixel will be categorized to core forest, Islet forest (patches too small to contain core forest), edge forest, and perforated forest (edges inside core forest) (Soille and Vogt 2009; Saura et al. 2011). To assess different edge effects with respect to various taxa, I will use seven forest fragmentation maps from 30 m to 210 m edge widths, detailed in chapter 3 (Laurance 1991; Restrapo and Gómez 1998; Urbina-Cardona et al. 2006). I will also calculate the Euclidian distance of each pixel to the closest core forest pixel (Kuemmerle et al. 2010).

Anthropogenic factors

Human activities have high negative ecological impacts on biodiversity (Chapin et al. 2000; Foley et al. 2005). I will integrate human influence variables, including roads and railroads, human settlement, and population density. Roads and railroads are available in vector format which will be extracted from the Digital Chart of the World using ArcGIS 10.1. Human settlements will be derived from the circa 2013 DMSP-OLS Nighttime Lights Time Series produced by the NOAA National Geophysical Data Center (NOAA 2013). Population density for the year 2000 is available at a 1 km resolution, which will be obtained from Center for International Earth Science Information Network (CIESIN). I will calculate the distance of each pixel to roads and railroads. I will similarly calculate distances to the closest human settlements.

Climate data

Climate has been widely recognized as a factor driving species diversity patterns at broad-scales (Pianka 1966; Willig et al. 2003; Thomas et al. 2004). Information on current climate conditions (1950-2000) is available at 1 km resolution from WorldClim. I consider climate variables that are important in determining vegetation and species distribution patterns in Thailand which include annual precipitation, precipitation in wettest quarter, precipitation in the driest quarter; and minimum, maximum, and mean temperature (Trisurat et al. 2011, 2012).

Table 2. Description of predictor variables used in this study

Variable	Comments	Source
Productivity	Dynamic Habitat Index.	MODIS FPAR; 1km raster
Land cover		
Land cover dominance	Proportion of forest, wetland, agriculture, and urban in 1km resolution.	Landsat TM/ETM images Land Development Department; vector 1:25,000
Land cover diversity	Diversity of land cover classes (Shannon index).	
Land cover richness	Total numbers of land cover within 1 km grid cell.	
Forest fragmentation	Image morphological processing (Vogt et al. 2007); edge width 1-7 pixels (30 m resolution)	
Distance to core forest	Calculated from fragmentation maps	
Proportion of protected area	Total area of all protected areas within 1 km resolution	The World Database on Protected Areas (WDPA)
Distance to river	The distance of each pixel to rivers	Digital Chart of the World; vector
Topography		
Elevation Slope	Topographic coefficient of variation; Calculated from SRTM	SRTM Digital Elevation Model (DEM)
Climate		
Precipitation	Annual precipitation, precipitation in wettest, and driest quarters	WorldClim; 1 km raster
Temperature	Range and mean annual temperature	
Human disturbance		
Population density	Number of inhabitants per 1 km^2	CIESIN; 1 km raster
Distance to road and railway	The distance of each pixel to roads and railways	Digital Chart of the World; vector
Distance to settlement	The distance of each pixel to the closest settlement	NOAA

APPROACH

Calculation of the Dynamic Habitat Index

I will calculate the three DHI components for each of ten years from 2001 to 2011. Then, I will average each component of the DHI across the ten years. The three components are (a) annual average productivity, (b) annual minimum productivity, and (c) seasonal variation in productivity.

Annual average productivity is the integrated productive capacity of a landscape over an entire year. I will calculate the annual productivity by summing monthly fPAR observations for each year, and then averaging these estimates over the ten years.

Annual minimum productivity relates to the potential of a given landscape to support resident species throughout the year (Schwartz et al. 2006). The annual minimum value of fPAR will be extracted by calculating the annual minimum monthly fPAR observation for each year, and averaging over the ten years.

Seasonal variation in productivity is an integrated measure of climate, topography, and land use. To assess variation in fPAR throughout the year, I will compute the standard deviation of monthly values for each 1 km grid cell. Then, I will divide that value by the mean annual fPAR to acquire the coefficient of variation (CV). High CV values refer to areas with large variation in productivity over the annual cycle compared to mean values, such as agricultural areas. On the contrary, low CV values represent areas with consistent vegetation production throughout the year, such as evergreen forests and barren land (Coops et al. 2008).

The DHI as a predictor variable for species richness

I will use multiple linear regression analysis to assess the relationships between species richness and the three components of the DHI (Coops et al. 2009a) with *leaps* and *hier.part* packages in R. First, I will randomly sample 5000 1 km grid cells across Thailand with a minimum distance of 5 km between pixels to minimize the effects of spatial autocorrelation. Second, I will use best-subsets regression using adjusted R^2 (Furnival and Wilson 1974; Miller 2002) to obtain a subset of models that best explain the response variables. Fitting several models instead of one best model highlights which variables are repeatedly chosen in the best models, and whether they have a consistent effect on the response variables (Furnival and Wilson 1974; Miller 2002). Third, I will use the best model as selected by best subset regression to perform a hierarchical partitioning analysis (Chevan and Sutherland 1991; MacNally 2002), which will identify the relative importance of variables in the best model. In hierarchical partitioning regression, all possible combinations of predictor variables are fitted in the models, and for each model the variable of interest is dropped and the model fitted again. The importance of such predictor variable is calculated as the average change in R^2 when the predictor variable is dropped from all of the fitted models (Chevan and Sutherland 1991; MacNally 2002).

The best subsets method measures how often a variable is entered in a set of models, while hierarchical partitioning computes the amount of variance explained when a predictor variable is introduced into a model (Gavier-Pizarro et al. 2010; Lesak et al 2011; Baumann et al. 2011).

Integration of satellite-derived predictor variables

The DHI alone may not be sufficient in explaining species richness patterns, which is why I will integrate the DHI components with other environmental variables. Predictor variables will include the DHI components, elevation, land cover, forest fragmentation, the proportion of protected area, climate, distance to river, road, railroad, and settlement, and population density (Table 2). All variables will be re-sampled to a 1x1 km cell to match the fPAR resolution.

To assess the relative importance of the predictor variables included in the models for explaining species richness patterns, I will also use best subsets (Furnival and Wilson 1974; Miller 2002) and hierarchical partitioning analysis (Chevan and Sutherland 1991; MacNally 2002) in three steps. First, I will use the same sampling dataset from the previous analysis. Second, I will use best subset regression to attain a subset of models that best explain the response variable based on adjusted R^2 (Furnival and Wilson 1974; Miller 2002). Third, I will use hierarchical partitioning analysis to calculate the amount of variance explained by the predictor variable of interest when all other variables are included in the model (Chevan and Sutherland 1991; MacNally 2002).

EXPECTED RESULTS: CHAPTER 1

Calculation of the Dynamic Habitat Index

This analysis will quantify the dynamic range of three DHI components derived from fPAR across Thailand. These results will highlight where the DHI may be most effective to identify variability that is relevant for species richness patterns.

The DHI as a predictor variable of species richness

I will assess the capacity of the DHI to predict species richness. I expect that the combination of the DHI components can be used to explain species richness patterns for a variety of terrestrial taxa in Thailand.

Integration with other environmental variables

I expect that models that include other environmental and anthropogenic variables will highlight the unique predictive power of the DHI in explaining species richness patterns. In addition, I expect to determine the relative importance of factors influencing species richness patterns in Thailand.

SIGNIFICANCE: CHAPTER 1

As biodiversity loss proceeds at alarming rates, there is an urgent need to identify and monitor species diversity patterns at broad scales. The proposed research will highlight the utility of advanced remote sensing technology to increase our understanding of factors driving species richness patterns in the tropics. The evaluation of relationships between species richness patterns and the Dynamic Habitat Index derived from remotely sensed data will provide an effective tool for predicting and monitoring tropical biodiversity. In addition, this research will provide insightful information for resource managers and policy-makers to understand what drives biodiversity patterns in Thailand and to predict how biodiversity patterns may be affected by increased human activities and environmental change.

CHAPTER 2: The structural connectivity of habitat suitability for the Indochinese tiger in Thailand

INTRODUCTION

Global biodiversity loss is occurring at an unprecedented rate as humans are now utilizing the majority of the World's resources (Chapin et al 2000). As a consequence of increased anthropogenic activities, natural habitats have been lost or become more fragmented (Turner and Ruscher 1988; Saunders et al. 1993). Habitat loss and fragmentation directly impacts the viability of species (Fahrig 2003) and is a major reason for rapid species extinctions (Pimm and Raven 2000) because of edge effects, increased distance between suitable habitats, and alteration of composition and structure of landscape mosaics (Turner et al. 2001).

For many species, local extinctions of fragmented populations are common (Fahrig and Merriam 1994). Survival of the species thus depends on the dispersal availability of organisms between patches and maintaining a threshold of landscape connectivity (Fahrig and Merriam 1985; Adler and Nuernberger 1994; Bowne and Bowers 2004). Connectivity of a landscape can facilitate access to resources for individuals, gene flow between subpopulations (Cushman et al. 2006), recolonization after local extinction, and community stability (Fahrig and Merriam 1994; Debinski and Holt 2000; Bennett et al. 2006; Campbell Grant et al. 2007: Kindlmann and Burel 2008). Establishing connectivity among species-suitable habitat patches is a challenge. Conservation planners need to preserve landscape connectivity in order to sustain viability of populations and allow for species' range shifts in response to climate change (Beier et al. 2008).

Landscape connectivity is defined as the degree to which the landscape facilitates or impedes individual dispersal between resource patches (Taylor et al. 1993; Kindlmann and Burel 2008). Numerous connectivity measures have been proposed, and they are based either on structural or functional concepts (Bélisle 2005). Structural connectivity is related to the physical structure of a landscape, independent of any attributes of the organism of interest. Functional connectivity refers to the behavioral response of individuals as they move through landscape elements. In other words, functional connectivity results from ecological characteristics of the organism (e.g. species dispersal ability through the intervening matrix) as it interacts with the structure of a landscape (Tischendorf and Fahrig 2000; Moilanen and Hanski 2001; Goodwin and Fahrig 2002; Uezu et al. 2005).

Commonly used modeling approaches to identifying and quantifying landscape connectivity are: least-cost path analysis (e.g., Tischendorf and Fahrig 2000; Adriaensen et al. 2003; Rabinowitz and Zeller 2010), graph theory (see reviews Dale and Fortin 2010; Galpern et al. 2011; Moilanen 2011), circuit theory (McRae et al. 2008), and resistant kernels (e.g., Compton et al. 2007). However, each method has drawbacks, and no single approach can provide complete guidance as to where conservation efforts can be successful to maintain or improve connectivity. It is often necessary to integrate multiple approaches (Tischendorf and Fahrig 2000; Kindlmann and Burel 2008). Specifically, integrating least-cost path analysis and graph theory can be an effective way to assess the connectivity of suitable habitats by using least-cost paths as edges in graph analysis (Galpern et al 2011; Ziołkowska et al. 2012), which can then be tied to species-level conservation (Bunn et al 2000).

Graph theoretic connectivity (Urban and Keitt 2001; Pascual-Hortal and Saura 2006; Urban et al. 2009) is commonly used in ecology and conservation applications (e.g. Bunn et al. 2000; Minor and Urban 2008; Ziołkowska et al. 2012). Graph theory can be applied to quantify either structural or functional habitat connectivity at patch and landscape scales (Urban and Keitt 2001; Jordán et al. 2003; Saura and Pascual-Hortal 2007). In addition, graph theory is preferable for many large-scale conservation problems because of its ability to provide a detailed picture of connectivity using current data (Calabrese and Fagan 2004). It does not require knowledge of behavior, fecundity, or mortality, but can be integrated with these variables to create an ecologically-rich graph model, and a dispersal model (Rhodes et al. 2006; Ovaskainen 2004).

Least-cost path analysis integrates the matrix between patches using an individual's movement routes within a landscape (Knaapen et al. 1992; Verbeylen et al. 2003). Least-cost paths can be identified by accumulating cost surfaces for two or more source patches. A cost surface is derived by quantifying resistance of different land cover classes and summing the travel cost over the route of least resistance when an individual moves between two patches (Adriaensen et al. 2003). The limitation of this analysis for landscape connectivity is that only a single path is identified, even though alternative paths with comparable costs may exist (Driezen et al. 2007). Therefore, connectivity measures focusing on optimum routes fail to incorporate variation in an organisms' behavior (Bélisle 2005).

Integrating least-cost path analysis and graph theoretic approach (i.e., defining the edges of a graph using least-cost routes) allows incorporation of spatial information on habitat and matrix into connectivity analyses and measures of graph theory (Galpern et al. 2011). This combined approach is increasingly applied for species-level conservation management, such as habitat connectivity restoration (e.g., Bunn et al. 2000; Saura and Pascual-Hortal 2007; Kuemmerle et al. 2010). Nevertheless, matrix cost values reflect ecological costs related to individuals dispersing through a landscape. The relative cost values assigned are often sensitive to location of least-cost paths and spatial configurations of habitats (Rayfield et al. 2009). Therefore, conducting a least-cost path analysis using habitat suitability to yield cost surface values of species movement can provide meaningful information (Kusak et al. 2009). Habitat connectivity analysis integrating such a modeling framework can be applied to species conservationby identifying priority areas for reintroduction or restoration (Gardner and Gustafson 2004; Kuemmerle et al. 2010; Ziołkowska et al. 2012).

Large carnivores and herbivores are often represented as conservation targets because they provide crucial roles in ecosystem functioning (Woodroffe 2000; Gordon 2009) and they can serve as umbrella species for conservation (Terborgh et al. 2001; Pringle et al. 2007). Importantly, these large mammals are often particularly sensitive to human disturbance and land use change (Noss et al. 1996). Therefore, it is critical to identify habitat suitability, promote connectivity, and target priority areas for large mammals (Beazley et al. 2005).

Tigers (*Panthera tigris*) of the Indochinese peninsula and southern China are a typical example of a focal species for conservation. Indochinese Tigers are listed as a globally endangered species (IUCN 2004). Tigers now occupy only 7% of their historical range (Dinerstein et al. 2007), and have declined precipitously over the last century due to human threats, including habitat loss, degradation and fragmentation, poaching (Milner-Gulland and Bennett 2003; Walston et al. 2010), and decreased prey availability (Lekagul and McNeely 1977; Lynam et al. 2007; Karanth and Chellam 2009; Lynam 2010). Long-term persistence of tigers will depend on large, well-connected habitat patches. Thus, it is urgent to assess connectivity of suitable habitat for tigers with an aim to provide information for conservation planning such as habitat restoration projects (e.g., Trisurat et al. 2010, 2012), translocations, and reintroductions (e.g., Fernández et al. 2006, Klar et al. 2008, Cook et al. 2010).

Tiger populations in Thailand are at risk of extinction, even though Thailand occupies the historical center of the tiger’s range (Mouhot 1864; Bock 1884). To date, no more than 350 tigers exist in Thailand, with subpopulations potentially present in up to 15 protected forest complexes

(Smith et al. 1999). These subpopulations are vulnerable to extinction due to deforestation, illegal trade, and insufficient prey due to poaching (Steinmetz et al. 2006; Simcharoen et al. 2007; Ngoprasert et al. 2012; Trisurat et al. 2012). In addition, tigers are absent from many places where habitat suitability models would predict their presence (Lynam et al. 2006; Steinmetz et al. 2013). A numbers of studies and efforts seeking to understand tiger status, threats and distribution have led to the development of National Tiger Action Plans (NTAPs) with support from the Thai Government, National Fish and Wildlife Foundation (NFWF), and Wildlife Conservation Society (WCS Thailand) (Tunhikorn et al. 2004; Lynam 2010). However, quantitative information on connectivity and habitat suitability for tigers at a national scale is still lacking. Addressing this information gap is recognized as a priority of broad-scale conservation planning (Lynam et al. 2006).

The goal of my study is **to assess structural connectivity of tiger habitat across Thailand using a combination of three approaches: species distribution modeling, least-cost path analysis, and graph theory in order to target priority areas for maintaining viability of tiger populations and promoting overall connectivity among subpopulations.** My specific objectives are to:

Objective 1: Map habitat suitability for the tiger across Thailand

Objective 2: Assess tiger habitat connectivity

Objective 3: Identify relative importance of potential patches for tiger habitat connectivity

METHODS

Tiger status in Thailand

Tigers serve as an umbrella species in conservation planning because they are a pinnacle predator, are found across a wide range of habitat types, occupy large home ranges, overlap with other species of concern, and are sensitive to forest degradation (Beazley et al. 2005; Sergio et al. 2006; Morrison et al. 2007; Dinerstein et al. 2007; Branton and Richardson 2011). In this study, I will use the tiger as a focal species for connectivity analyses based on the above criteria (Lekakul and McNeely 1977; Robinowitz 1993; Smith et al. 1999; Prommakul 2003; Lynam et al. 2006; Lynam 2010; Ngoprasert et al. 2012; Steinmetz et al. 2013).

Wild tigers in Thailand exist only within protected areas. Probably 250-350 tigers remain in Thailand (Robinowitz 1993; Walston et al. 2010). The tiger's threatened status in Thailand is exacerbated by the fragmentation of the larger population into up to 15 small disjunct subpopulations, each of which has a greater risk of local extinction because of their smaller population sizes (Robinowitz 1993; Smith et al. 1999; Steinmetz et al. 2013). Two of these subpopulations are in Khao Yai National park. The subpopulations are effectively isolated by a major highway that runs between them from north to south. Tigers are absent from many protected areas where suitable habitat predicts their presence (Lynam et al. 2006; Lynam 2010). For example, the available habitat in Khao Yai should be able to support up to 32 tigers (Smith et al. 1999) but surveys during 1999-2002 detected only two individuals (Lynam et al. 2003).

Countrywide surveys using camera-traps from 1997-2010 confirmed the presences of tigers in 8 to 13 protected areas, but occurrence data suggests that most protected areas have very low densities (Ngoprasert et al. 2012). Some protected areas are suggested as potentially important habitats for supporting subpopulations of tigers, such as Halabala wildlife sanctuary and Bang Lang national park in southern Thailand (Lynam et al. 2001), Hui Kha Keng wildlife sanctuary and Western forest complex in central Thailand (Simcharoen et al. 2007), and Kaeng Krachan national park (Ngopresert and Lynam 2002; Walston et al. 2010). While, tigers exist at very low density at Kuiburi (Steinmetz et al. 2009), Phu Khieo wildlife sanctuary (Lynam et al. 2001), the Dong Phayayen-Khao Yai complex (Lynam et al. 2006).

Tigers are found in a wide variety of forest types, from foothill evergreen forest, semi-evergreen forest, mixed dipterocarp and deciduous forests to alluvial grasslands which provide sufficient prey, water, and cover (Schaller 1966; Karanth et al. 2004; Schaller 2009; Ngoprasert et al. 2012). Home range and movements vary depending on sex, location of protected areas, and seasonality. For example, in the Eastern Thung Yai Naresaun wildlife sanctuary, male tigers home ranges are 114-200 km^2, while female tigers home ranges are 54-101 km^2 (Prommakul 2003). At Huai Kha Kheang wildlife sanctuary, tigers home ranges are 78 km^2 (Lynam et al 2001).

Tiger occurrence data

Tiger occurrence data was obtained from collaborators at Kasetsart University, Thailand. Surveys were conducted between 1997 and 2009 using field survey and camera trap approaches. Field surveys for information on the presence of tigers were conducted by direct surveys of tracks, claw marks, feces, and other signs. However, the reliability of field surveys for detecting tigers depends on the detectability of signs, the substrates in the study areas, and the skill of the observer (Wemmer et al. 1996). Tiger signs may not be detectable during dry seasons or after heavy rainfall, and in places where leaf litter is dense, or on rock or other hard substrates.

Camera trap surveys were set at 17 protected areas across Thailand because repeated surveys have shown that tiger populations in Thailand only exist inside protected areas (Robinowitz 1993; Ngoprasert et al. 2012). The locations of camera traps were selected based on information from field surveys. Cameras (Camtrakker™ Camtrak South Inc., Georgia USA) were placed in areas with a high probability of being used by tigers with two study designs: (1) plot-based survey design and (2) trail-based survey design. First, in some areas, field surveys were concentrated in 10 x 4 km plots. Camera-traps were randomly placed at predetermined random UTM locations and spaced 1-2 km apart in alternate 1 km^2 grid cells within the plot. Second, in other places, camera-traps were placed at least 2 km apart along wildlife trails, water bodies, and ridges where wildlife signs were detected or where there was a high probability of tiger use for dispersal through patches. The dataset consists of 504 occurrence points (Figure 7).

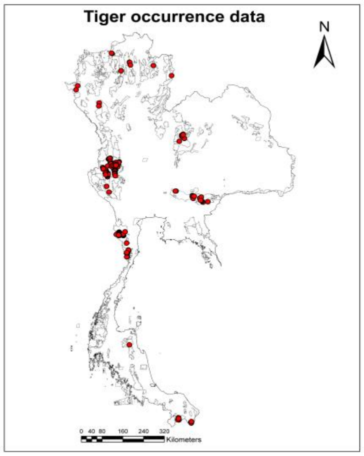

Figure 8. Occurrence data for tigers from 1997-2009

(*Source*: Sukmasuang and Pongpattananurak, *unpublish data*)

Predictor variables

I will include environmental variables that affect tiger abundance and distribution as predictor variables in the habitat suitability analysis. Environmental variables include: land cover types, the Dynamic Habitat Index (DHI) (as a surrogate for productivity), elevation, climate, distance to rivers, protected areas, forest fragmentation, and anthropogenic influence variables. For anthropogenic influence variables, I will include: population density, distance to roads and railways, and distance to human settlement. Descriptions for all predictor variables used in habitat suitability analysis are included in the methods section of chapter 1 and in Table 2.

APPROACH

Habitat suitability modeling

I will use logistic regression models (McCullagh and Nelder 1989) to compute the habitat suitability map for tigers in Thailand based on presence/pseudoabsence data (Guisan et al. 2002; Guisan ans Thuiller 2005; Austin 2002, 2007) with four steps. In a first step, I will define presence/pseudoabsence datasets. For the presence dataset, I will use 504 tiger occurrence records. For the absence dataset, I will randomly sample 1000 pixels at 1-km resolution across Thailand, excluding non-forest areas. Second, I will compute logistic regression models for the whole presence/pseudoabsence dataset using function *glm* as implemented in R (R Development Core Team 2009). The predictor variables are those listed in Table 2. Third, I will apply best-subsets regression to select the top five best models based on the AIC criterion (Akaike 1973) using the *bestglm* package in R. Best subset regression performs an exhaustive search of all possible models, given a maximum number of predictor variables allowed, to specify the best model explained response variable (Furnival and Wilson 1974; Miller 2002). Finally, I will use the five best performing models as selected by best subset regression to predict tiger habitat suitability for Thailand.

Model validation

Before the predicted models can be used to map tiger habitat suitability, I will evaluate the predictive performance and significance of the models using the area under the curve (AUC) of receiver operating characteristic (ROC) plots (Fielding and Bell 1997). First, I will randomly sample 20% of both presence and pseudoabsence datasets to use for model evaluation, then use the remaining 80% of both datasets for model calibration based on a data-splitting approach. Second, I will calculate AUCs for each of the top five models chosen by best subset selection. Third, I will choose the best model for predicting tiger habitat suitability based on the highest value of AUC. Once the best performing model is selected, I will use it to project a map of tiger habitat suitability. Finally, I will summarize the amount of suitable habitat and the number of habitat patches that are larger than 50, 100, and 200 km^2 (tigers' home range 54 - 200 km^2) for three habitat suitability index (HSI) thresholds.

Least-cost modeling

I will define suitable habitat patches using the bottom value of the HSI distribution. Next, I will calculate the Euclidean distance between suitable habitat patches, i.e., structure connections. Least-cost paths will be constructed between a given habitat patch and its nearest neighbors.

I will also calculate an effective distance as the sum of its grid cell dimensions (vertical/horizontal or diagonal) multiplied by their cost values for each least-cost path. Total effective distances of paths are comparable to Euclidean distances in areas with no matrix resistance, following the similar approach of Ziołkowska et al. (2012).

Connectivity assessment

To evaluate the relative important of each least-cost path for the overall connectivity of tiger habitat network, I will first use effective distances to calculate inter-patch-cost-dispersal probabilities p_{ij} (Saura and Pascual-Hortal 2007), according to equation (1):

$$p_{ij} = e^{-kd}ij \tag{1}$$

Where k is a cost distance-decay coefficient and d_{ij} is an effective distance between patch i and j.

Second, I will assess the importance of habitat patches for landscape connectivity and identify priority areas for tiger conservation based on graph theory method. Habitat patches refer to nodes and least-cost paths linking habitat patches are edges in graph theory technique (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007) (Figure 9).

I will use Conefor Sensinode 2.6 software (Saura and Torné 2009; Saura and Pascual-Hortal 2007), which performs node removal operations to assess the importance of each individual node (Urban and Keitt 2001). This allows me to evaluate the importance of each habitat patch for maintaining connectivity of a landscape (Saura and Torné 2009).

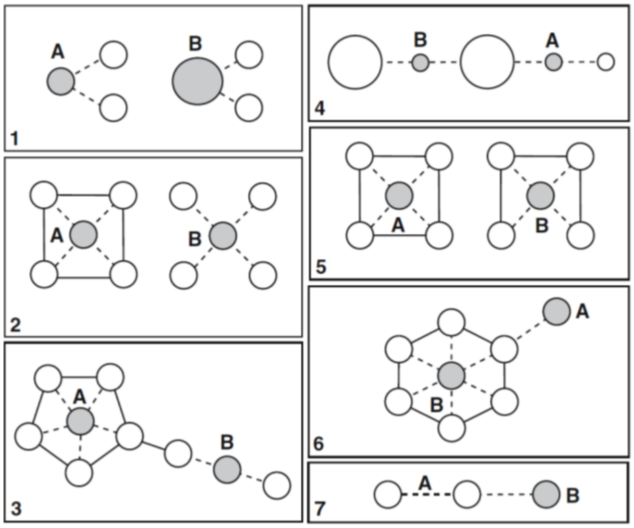

Figure 9. The graph shows the structural network. Different types of change corresponding to the loss of habitat patches. Circles represent node, and lines represent edges. Patches that are lost are indicated by grey color, and links that are lost are indicated in dashed lines.

(*Source*: Pascual-Hortal and Saura 2006, *Landscape Ecology, 21*)

In the Conefor Sensinode software, I will use the equivalent connected area (ECA) index as the connectivity metric to compute habitat patch importance (Saura et al. 2011). ECA is a modification of the probability of connectivity index (PC, Saura and Pascual-Hortal 2007; Saura and Rubio 2010), defined as:

$$\mathrm{PC} = \frac{\sum_{i-1}^{n}\sum_{j-1}^{n} a_i\ a_j\, p_{ij}^{max}}{A_L^2} \qquad (2)$$

Where a_i and a_j are the areas of habitat patches i and j, p_{ij}^{max} is the maximum product probability of all the possible paths between habitat patches i and j (including direct route between the two patches), and A_L is the study area (Saura and Pascual-Hortal 2007; Saura and Torné 2009).

PC values affect the relative importance $d(PC)_k$ of each habitat patch *k*. The $d(PC)_k$ is a change in probability of connectivity which can be used to quantify how individual landscape elements contribute to habitat connectivity and availability in the landscape. It can be calculated as the percentage of change in connectivity metric when a given node or edge is removed from the graph (Saura and Torné 2009), as defined:

$$d(PC)_k = 100 \times \frac{PC - PC_k}{PC} \quad (3)$$

The $d(PC)_k$ for a landscape can be partitioned into three fractions which quantify how landscape element k (i.e. node or edge) can contribute to habitat connectivity (Saura and Rubio 2010):

$$dPC_k = dPC\mathit{intra}_k + dPC\mathit{flux}_k + dPC\mathit{connector}_k \quad (4)$$

The intra fraction ($PC\mathit{intra}_k$) refers to the amount of connected area within the patch, (2) flux fraction ($PC\mathit{flux}_k$) measures the dispersal flux through the connections of an individual habitat patch *k* to or from all other habitat patches in the landscape, and (3) connector fraction ($dPC\mathit{connector}_k$) corresponds to the contribution of a habitat patch or edge *k* to the connectivity between other habitat patches, as a connectivity provider within the landscape (Saura and Rubio 2010).

ECA is the size that a single habitat patch (maximum connection) needs to provide the same value of PC as the actual habitat pattern in the landscape. ECA is calculated by the square root of the value of PC. Moreover, ECA is preferable to PC as a summary of overall connectivity since it has area units and is thus easier to interpret and has more range of variation (Saura et al. 2011), defined as:

$$ECA = \sqrt{\frac{\sum_{i-1}^{n} \sum_{j-1}^{n} a_i \, a_j \, p_{ij}^{max}}{A_L^2}} \quad (5)$$

The importance of each node or edge for maintaining structure connectivity can be measured as the relative decrease (%) in the overall connectivity metric (dECA) caused by the removal of the element *k* (i.e. node or edge) from the graph (Saura et al. 2011a; Saura et al. 2011b). Thus, the importance of each landscape element *k* is influenced by patch size, and the inter-patch cost-dispersal probabilities of connection between patches (Ziołkowska et al. 2012).

Finally, after all the dECA values are calculated, I will compare the number of graph components and their distribution within each habitat network in order to indicate the relative important habitat patches (nodes) and links between patches (edges) based on their network connectedness.

EXPECTED RESULTS: CHAPTER 2

Expected outcomes of this chapter are: a tiger habitat suitability map for Thailand, an evaluation of structural habitat connectivity, and the identification of essential suitable habitat patches for the overall connectivity of tiger habitat, which jointly will help to support tiger conservation efforts and promote connectivity between subpopulations.

SIGNIFICANCE: CHAPTER 2

Large-scale conservation requires the identification of priority areas where species have a high likelihood of long-term persistence in the face of rapid land use and climate change. My study will generate a suitable habitat map and I will couple this with methods to identify least-cost paths, and graph theory to prioritize patches and corridors. As such, my connectivity analysis of tiger habitat will provide insights for tiger conservation, and will benefit other species with similar habitat needs and dispersal abilities. The tiger connectivity map can serve as a preliminary linkage design to facilitate movements between subpopulations, species' range shifts in response to climate change, and potential core habitats to buffer against the continued loss and degradation of habitats from landscape change.

CHAPTER 3: The effects of landscape structure on bird distributions

INTRODUCTION

Avian biodiversity is facing severe threats from anthropogenic habitat loss and fragmentation worldwide, (Gaston et al. 2003; Pimm et al. 2006) and the rapid and extensive loss and fragmentation of tropical habitats has become an especially serious threat to avian diversity (Turner 1996; Brooks et al. 1997; Laurance et al. 1999; Sodhi et al. 2004). If the degradation of tropical habitats continues at current rates, the tropics will be the epicenter of mass extinction of avian taxa (Brooks et al. 1999; Brook et al. 2003; Bradshaw et al. 2009). This impending crisis requires immediate conservation action (Gardner et al. 2009; Hoffmann et al. 2010; Laurance et al. 2012).

The identification of high quality habitat is a crucial step for mitigating avian biodiversity loss, given that the availability of tropical forest for habitat conservation is limited (Brooks et al. 1999; Sodhi et al. 2004). Current global changes in landscapes and climate have prompted considerable efforts to identify priority areas for conservation of a variety taxa including birds (Myers et al. 2000; Margules and Pressey 2000; Wilson et al. 2006; Brooks et al. 2006; Knight et al. 2008; Iwamura et al. 2013). However, identifying conservation priority areas for birds in tropical regions is challenging, owing to a paucity of studies on the current state of avian habitats and the effects of human-modified landscapes on their distributions in many tropical regions (Sodhi et al. 2005; Peh et al. 2006).

In order to protect avifaunal diversity in the tropics, it is important to understand how landscape structure affects avian populations at the landscape scale. Habitat heterogeneity and landscape structure (i.e., the spatial composition and configuration of a landscape) has a strong influence on the abundance, distribution, and population dynamics of species (Simpson 1949; MacArthur and Wilson 1967; Lack 1969; Wiens 1976). Landscape structure greatly influences ecological processes (Urban et al. 1987; Turner 1989; Turner 2005). Habitat loss and fragmentation alter the spatial composition and configuration of habitats by reducing habitat areas, increasing numbers of habitat patches, decreasing sizes of habitat patches, and increasing the isolation of patches (Fahrig 2003). These processes lead to a metapopulation structure, which affects population persistence and stability. For such species, fragmented populations are at risk of local extinction (Fahrig and Merriam 1994). Spatial heterogeneity of a species' habitat affects populations by influencing movement patterns of individuals, intra- and interspecific interactions among organisms, and exposure to physical structure of habitats such as edge effects (see reviews in Lawton 1983; McCoy and Bell 1991; Tews et al. 2004).

The impact of anthropogenic habitat loss and fragmentation on individual species and communities is one of major concerns in ecological research and conservation of biodiversity (Turner et al. 2001). Yet, relationships between landscape structure and fundamental processes determining species distributions are often unclear (Moilanen and Hanski 2001; Graham 2001; Hernandez et al. 2006). One reasons for this is that the impacts of habitat loss within the landscape are difficult to disentangle from the effects of habitat fragmentation (Fahrig 2003). Habitat loss has large, consistently negative effects on biodiversity, while habitat fragmentation has varying effects on organisms; the effect of fragmentation can be both positive and negative (Fahrig 2003). To correctly interpret the influence of habitat fragmentation on species and population dynamics, the effects of habitat fragmentation and habitat loss must be measured independently (Fahrig 2003).

Support for the importance of landscape structure on wildlife populations is based mainly on empirical studies. However, studies of habitat loss and fragmentation have varied in their results depending on the organism of interest, the habitat needs of a given species, geographical location, and scale (Terborgh 1989; Saunders et al. 1991; McGarigal and McComb 1995; Wiens 1989, 1995; Pearson et al. 1996,). Specifically, the effects of habitat loss and fragmentation on birds in temperate regions have yielded contradictory outcomes. Even within a given species, the effect of landscape loss and fragmentation has been showed to vary across spatial and temporal scales (e.g., Fahrig 2002; McGarigal and McComb 1995; Meyer et al. 1998; Rosenberg et al. 1999; Radeloff et al. 2000; Donovan and Flather 2002; Brotons et al. 2003; Westphal et al. 2003).Similarly, habitat loss of tropical forests has largely negative effects on bird communities (e.g., Koh et al. 2002; Brooks et al. 1999; Brook et al. 2003; Laurance et al. 2011), while habitat fragmentation has varying effects (e.g., Newmark 1991; Beier et al. 2002; Şekercioḡlu et al. 2002; Barlow et al. 2007; Ruiz-Gutierre et al. 2008; Peters and Okalo 2009). Fahrig (2003) suggested that the effects of fragmentation may be greater in tropical systems than in temperate systems, but this prediction still needs to be verified by more empirical studies of the independent effects of habitat loss and fragmentation in different tropical regions (see review Turner 1996; Laurance et al. 2002).

The ability to investigate species-specific responses to landscape structure, and predict habitat suitability of tropical birds requires the integration of appropriate species distribution models that elucidate the effects of the spatial patterns of habitats and their landscape matrix (Loiselle et al. 2003). Quantifying landscape patterns is a prerequisite to understanding species distributions (Fahrig 2003; Opdam et al. 2003; Turner 2005), thus emphasis has been placed on developing methods to measure landscape structure for better understanding ecological processes driving species dynamics (e.g., O'Neill et al. 1988; Turner and Gardner 1991; Li and Reynolds 1995; Vogt et al. 2007). Similarly, models predicting the spatial distribution of species have been widely applied to understand species niche requirement and predict habitat suitability (Guisan and Thuiller 2005; Hirzel et al. 2006; Peterson et al. 2011).

Recent studies have developed landscape-wide habitat suitability models to identify priority conservation areas for species threatened by habitat loss and fragmentation (Fouquet et al. 2010; Torres et al. 2008). The use of species distribution models is increasingly applied to wildlife management and conservation, emphasizing the need for reliable approaches to identify conservation targets (Araujo et al. 2004; Heikkinen et al. 2007; Elith and Leathwick 2009). There is a need to apply those approaches to better understand how habitat loss and fragmentation affect bird distributions, to predict habitat suitability, and to identify priority areas for tropical bird conservation (Buermann et al. 2008; Freile et al. 2010).

Forest birds in Thailand have sharply declined in numbers in the past decades due to ongoing forest loss and fragmentation from anthropogenic activities (Round 1988; Pattanavibool and Dearden 2002; Round et al. 2003; Aratrakorn et al. 2006). Thailand has developed an extensive protected area system, covering 18% of the land area (RFD 2012). Despite these efforts, many bird species in Thailand have already been extirpated and others reduced to such low abundance that they are ecologically extinct (Hughes et al. 2003; Round and Gardner 2008). Thailand's extirpated bird species include giant ibis (*Pseudibis gigantean*), and large grass warbler (*Graminicola bengalensis*). Species that are extinct in the wild are sarus crane (*Grus antigone*), and white-shouldered ibis (*Pseudibis davisoni*). Two endemic bird species are

Deignan's Babbler (*Stachyris rodolphei*) and white–eyed river–martin (*Pseudochelidon sirintarae*) (Tresssucon and Round 1990; Sanguansombat 2005).

Despite these conservation problems, it remains unclear how habitat loss and fragmentation of tropical forests in Thailand influence bird distributions and their suitable habitats. Thus, more empirical studies from tropical regions such as Thailand can provide more insights of landscape effects on bird persistence (Opdam et al. 2003; Tscharntke et al. 2005), and this important quantitative information can help identify conservation priorities in light of tropical habitat loss and fragmentation (Brooks et al. 1999, Tscharntke et al. 2008).

The overarching goal of my study is **to assess species-specific responses to habitat composition and configuration with the aim to predict habitat suitability and identify priority areas for tropical bird conservation**. To achieve this goal, my specific objectives are:

Objective 1: Identify the relative importance of landscape structure variables in explaining bird distributions in Thailand.

Objective 2: Map bird habitat suitability using landscape structure metrics and other environmental variables.

Objective 3: Identify priority conservation areas for birds of Thailand, and examine whether existing protected areas protect predicted suitable habitat for birds species.

METHODS

DATA

Bird distribution data

My study focuses on forest bird species in Thailand because they are mainly resident in forest habitats and sensitive to changes in forest composition and configuration. In addition, most forest bird species show significant decline in abundance and richness due to forest loss and fragmentation (Round et al. 2003; Aratrakorn et al. 2006). I will use two types of bird occurrence data: (1) the Global Biodiversity Information Facility (GBIF), and (2) bird survey records from MASS version 3.0 (MacKinnon 1990). The GBIF data includes 926 bird species, and 31,444 observations from 1972-2011 with spatial coordinates (Figure 10). To assess effects of landscape structure and map habitat suitability, I will consider only forest bird species with at least 50 occurrence records based on the GBIF data. This gives a total of 9 species (Table 3). The MASS dataset is the most detailed set of bird records based on field observations over the period 1979–2011 (Round 1988; Round et al. 2003). These records formed the basis of the species range maps in the standard field guide to the birds of Thailand (Lekagul and Round 1991; Robson 2002). This dataset includes 936 species across 153 protected areas in Thailand.

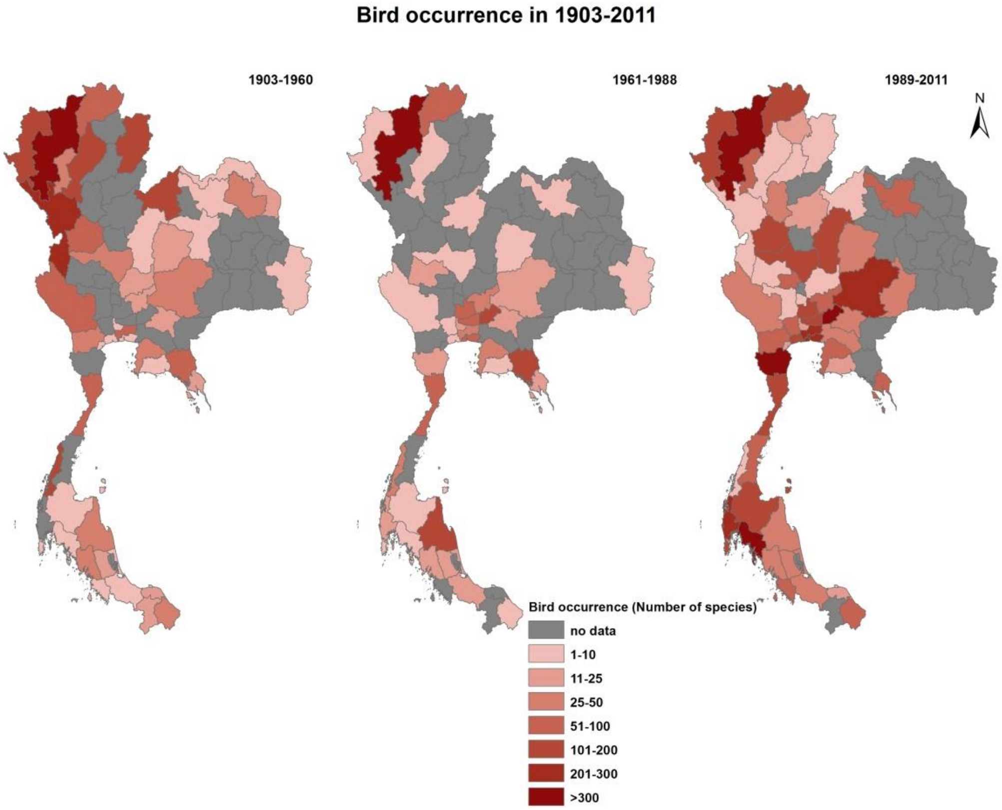

Figure 10. Birds’ occurrence records for Thailand from GBIF.

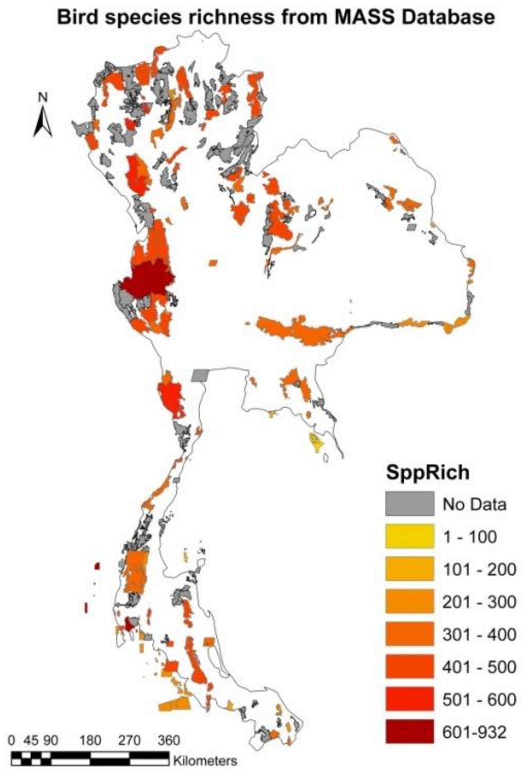

Figure 11. Birds' occurrence records from MASS database.

Table 3. Forest bird species in Thailand with presence > 50 occurrence records of GBIF.

Species	GBIF	MASS	
Yellow-bellied Warbler (*Abroscopus superciliaris*)	140	122	
Crested Goshawk (*Accipiter trivirgatus*)	208	132	
Greater Coucal (*Centropus sinensis*)	97	145	
White-throated Kingfisher (*Halcyon smyrnensis*)	78	147	
Brahminy Kite (*Haliastur indus*)	66	113	
Scaly-breasted Munia (*Lonchura punctulata*)	68	126	
Little Cormorant (*Phalacrocorax niger*)	87	39	
Plain Prinia (*Prinia inornata*)	68	88	
Yellow-vented Bulbul (*Pycnonotus goiavier*)	55	85	

Environmental variables

To quantify spatial patterns of forest, I will use morphological image segmentation (Vogt et al. 2007; Soille and Vogt 2009). This approach will classify spatial patterns of a landscape at pixel level on binary land cover maps. I will aggregate the land cover map of 2008 at a 30 m resolution into two main classes: (1) forest class or habitat, and (2) a non-forest class or non-habitat. Forest class includes intact forest and disturbed forest classes, while non-forest class will include the remaining land cover classes. For other environmental variables in the habitat suitability modeling, I will use the same environmental variable dataset as described in chapter 1 (Table 2).

APPROACH

1. Effects of landscape structure on bird distributions

1.1 Morphological analysis of forest spatial patterns

I will quantify spatial patterns of forest using the Morphological Spatial Pattern Analysis (MSPA) from GUIDOS analytical tool based on morphological image segmentation. The MSPA allows an automated per pixel classification and description of the geometry, pattern, fragmentation, and connectivity of a landscape. The MSPA will segment a raster forest binary map (i.e. forest vs. non-forest) into seven different, and mutually exclusive, landscape pattern categories: core, edge, islet, proliferation, bridge, loop, and branch (Vogt et al. 2007; Soille and Vogt 2009).

(1) Core: core pixels are defined as those forest pixels whose distance to the non-forested areas is greater than the given edge width. Cores will be considered as the focal habitat area for birds, (2) Islet: islet pixels are isolated forest patches that are too small to contain core pixels, (3) Edge: edge is defined as a set of forest pixels whose distance to the patch edge is lower than or equal to the given edge width and corresponds to the outer boundary of a forest core area, (4) Perforation: perforation is similar to edge, but it corresponds to the inner boundary of a core area, (5) Bridge: a bridge is a set of contiguous non-core forest pixels connecting at least two disjoint core areas at their ends, (6) Loop: a loop is a groups of pixels that connect their ends to different parts of the same core area, (7) Branch: a branch consists of pixels that do not correspond to any

of the previous categories (Figure 8) (Soille and Vogt 2009; Saura et al. 2011). A key criterion for classifying forest pixels into the seven MSPA classes is the edge width. The MSPA classification can be conducted with a 4- or 8-neighbourhood rule (Vogt et al. 2007; Soille and Vogt 2009).

For this study, I will consider the forest and non-forest classes as mapped in the raster format with a 30-m grain size. To assess different effects of landscape structure, I will use seven different edge widths from 30m to 210m based on studies of forest edge effects on tropical birds (Laurance 1991; Restrepo and Gómez 1998; Laurance et al. 2002). This will provide seven different spatial pattern maps. Also, the MSPA classification will be conducted with an 8-neighbourhood rule, corresponding to bird movement (Temple and Cary 1988; Zipperer 1993).

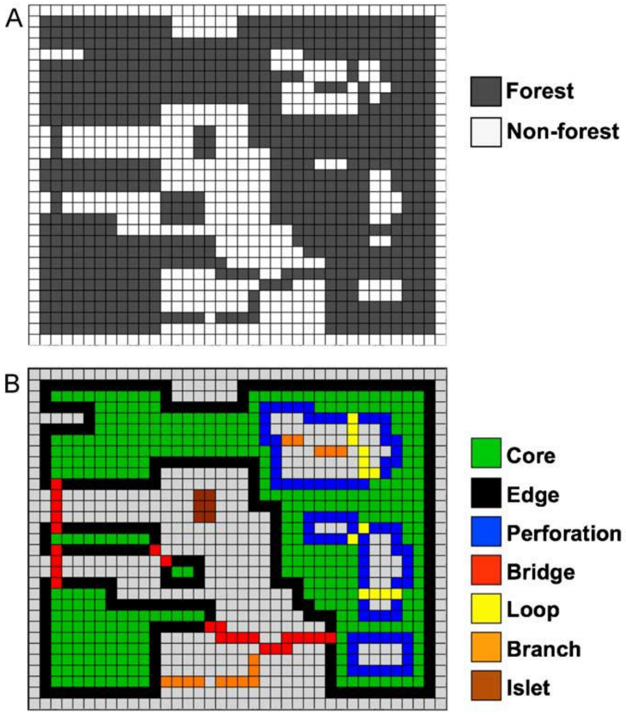

Figure 8. (A) a land cover binary map with forest and non-forest classes, (B) the seven forest spatial pattern classes provided by MSPA with an edge width of one pixel. (*Source*: Soille and Vogt 2009, *Pattern Recognition Letters, 30*)

1.2 Statistical analysis

To investigate relationships between landscape structure metrics and bird distributions, I will use logistic regression analysis (McCullagh and Nelder 1989) and best subset selection

(Furnival and Wilson 1974; Miller 2002) using the GBIF occurrence data as my presence points, and a set of randomly selected points as pseudo-absences. First, I will evaluate all possible combinations of the seven landscape metrics in the logistic regression models, computing seven edge widths separately. Second, I will use best subset regression (Furnival and Wilson 1974; Miller 2002) to analyze the relative importance of landscape metrics that best explain bird distributions. For each bird species, best-subsets regression will result in an exhaustive search for a set of best models by ranking all possible models based on the AIC criterion (Akaike 1973). As a result of best subset selection, I will choose the 10 best models for each of the seven edge widths.

2. Habitat suitability maps

2.1 Habitat suitability modeling

To predict habitat suitability for each bird species, I will also use logistic regression models (McCullagh and Nelder 1989) based on presence/pseudoabsence dataset (Guisan et al. 2002; Guisan ans Thuiller 2005; Austin 2002, 2007). First, I will use birds' occurrence data from GBIF as presence dataset. I will randomly sample 1-km grid cells across Thailand excluding the non-forested area as pseudoabsence dataset by weighting a presence/pseudoabsencen-ratio of 1:2 (Tsoar et al. 2007; Peterson et al. 2011). Second, I will fit logistic regression models with presence/pseudoabsence datasets and environmental variables (Table 2), including landscape metrics from previous analysis. Third, I will select the top five models that well explain bird distributions using best subset model selection based on AIC (Furnival and Wilson 1974; Miller 2002).

2.2 Model validation

To obtain the best model for predicting habitat suitability, I will compute the area under the curve (AUC) of receiver operating characteristic (ROC) plots (Fielding and Bell 1997) using a k-fold cross-validation process (with k=5) (Hirzel et al. 2006) for top five models of each bird species selected by the best subset regression. Finally, I will apply the best model to predict bird habitat suitability for Thailand.

In addition, I will use the independent MASS dataset for model validation. This independent dataset is an observed field survey which assembled species richness and abundance of birds for each protected area across Thailand (Round et al. 2003). To validate predicted habitat suitability models, I will calculate the area predicted as suitable habitat for each bird species and in each protected areas. Then, I will compare those predicted habitat suitability maps of protected areas to observed field data in order to test how well the models explain bird distributions.

3. ***Determining priority conservation areas***

To examine whether existing protected area networks do protect the key habitat for each bird species, I will use the predicted habitat suitability maps from the previous step overlaid with 232 protected area boundaries from the World Database on Protected Areas (WDPA, IUCN and UNEP 2009). Next, I will assemble the predicted distribution maps of all species to identify priority areas for forest bird conservation. The output map will include total extent of predicted distributions and the sum of habitat suitability index values for all species which can be used to identify priority areas for bird conservation in Thailand.

EXPECTED RESULTS: CHAPTER 3

Effects of landscape structure on bird distributions

I expect that the results of the logistic regression analyses for 9 species will demonstrate how bird distributions respond to the different composition and configuration of forest landscapes. In addition, I expect that best subsets regression models will identify which landscape metrics are relatively important in explaining bird distributions.

Habitat suitability models

I expect that predicted habitat suitability of 9 bird species will be largely concentrated across forest landscapes and separate from anthropogenic disturbance.

Priority areas for conservation

Predicted habitat suitability maps will provide spatial information that can be used to identify priority areas for bird conservation which can assist policy-makers to develop effective broad-scale conservation planning.

SIGNIFICANCE: CHAPTER 3

The proposed research in my third chapter contributes to scientific knowledge in two ways. First, this empirical study will provide more insights on how tropical bird species respond to habitat loss and fragmentation. Second, the integration of spatial heterogeneity of landscapes into species distribution models can improve predicted habitat suitability maps.

In addition, results from the research will contribute to conservation. The establishment of priority areas for species conservation in tropical regions is a challenging task, given that those high species diversity regions are facing intensive habitat loss and fragmentation. Predicting habitat suitability at a broad-scale can help natural resource managers to identify important areas for maintaining species viability. Furthermore, if protected area managers aim to maintain integrity of bird species in Thailand, additional strategies, such as decreasing habitat fragmentation and increasing connectivity of suitable habitats around small and fragmented protected areas, are required.

OVERALL SIGNIFICANCE OF MY PROPOSED DISSERTATION

The current biodiversity crisis is the impetus for ecologist and biological conservationists to provide better understanding of how biodiversity responds to environmental change in order to deliver effective conservation planning. A fundamental requirement for species protection is how to decide where to target priority areas to ensure long term persistence of species against ongoing anthropogenic activities. However, spatial distribution information of species and their habitats are still limited in many parts of the world. A lack of such baseline information makes conservation planning difficult to achieve, and my dissertation will help to fill this gap.

The proposed research will contribute to the fields of landscape ecology, remote sensing science, and conservation biology in three ways.

First, the proposed study will make advances in **ecological knowledge**. Tropical ecosystems are experiencing species losses at unprecedented rates. Understanding the factors driving the geographical variation in species diversity and predicting their patterns across regions and biomes is thus crucial for species conservation. However, many tropical regions still need quantitative information on species responses to human-dominated landscapes at broader scales. My dissertation will help to fill these knowledge gaps**,** because it takes place in a tropical region where biodiversity information is limited. As such, assessing quantitative, baseline information on tropical ecosystems is a necessary initial step on which to base future ecological research in Thailand and other tropical regions.

The utility of the dynamic habitat index, derived from remotely sensing data, can provide more insights into understanding the factors controlling spatial variation in species richness. In addition, the dynamic habitat index can improve predictions of how biodiversity patterns respond to the alteration of environment across broad spatial and temporal scales. Furthermore, the dynamic habitat index can be used as a surrogate for habitat suitability which is important in order to assess habitat connectivity.

Landscape connectivity is vital to the survival of fragmented populations that occupy patches too small to sustain isolated populations. My proposed research on structural connectivity of habitat suitability for tigers will provide more ecological knowledge about habitat requirements, factors influencing abundance and distribution, the relative importance of habitat patches that can sustain viable subpopulations, and landscape connectivity among suitable habitat patches.

Habitat loss and fragmentation have strong effects on species diversity. However, understanding the impacts of these processes on species distribution requires more empirical data from tropical regions. My research on the effects of landscape structure on bird distributions will provide better understanding of how landscape composition and configuration influences species distribution and predictions of habitat suitability.

Second, my research will advance **technical approaches**. Because of the complexity of tropical ecosystems and the intensity of human alteration to tropical landscapes, conservation biologists need better indices to explain species diversity patterns and monitoring their changes over broad areas and long periods of time. Satellite imagery and advances in remote sensing analyses provide effective tools in quantifying landscape patterns and understanding their influence on ecosystem processes at spatial and temporal scales that were previously unavailable. However, ecological applications of such advanced remote sensing approaches are still needed in tropical biodiversity studies.

My proposed research will close this gap by testing a new remotely sensed index, the Dynamic Habitat Index, for the first time in a tropical ecosystem. This index is specifically designed to analyze primary productivity that positively correlates to species richness. I will make effective use of productivity components of the DHI derived from MODIS sensors to predict species richness patterns. The DHI can serve as a biological indicator in assessing and monitoring spatial variation of tropical species richness at broad spatial and temporal scales. In addition, the integrated approaches of other remotely sensed environmental data can provide a variety of ecological applications in biodiversity assessments.

Finally, my research is highly relevant for **conservation** in Thailand, and around the world. The proposed dissertation examines the effects of spatial heterogeneity on species distributions. The proposed research includes relationships between the remotely sensed index and spatial variation of species richness, the structural connectivity of habitat suitability for tigers, and the effects of landscape structure on bird distributions. This spatial distribution information is essential for broad scale conservation and management because most decisions regarding priority targets for species protection are made at regional or national scales.

The Dynamic Habitat Index derived from Terra and Aqua MODIS sensors will be tested as indicators for assessing and monitoring species richness patterns. In addition, I will make more rigorous use of the Dynamic Habitat Index in conservation planning by incorporating knowledge of spatial heterogeneity of energy availability in landscapes into the identification of high quality habitats. This comprehensive information will help policy-makers in compiling data on the species richness patterns of planning areas to maintain biodiversity.

Importantly, broad-scale conservation planning for tigers cannot be successful without understanding the relationship between tiger viability and landscape heterogeneity, high-quality habitat patches for tiger in the structural connectivity chapter will provide more insights on factors affecting spatial variation of tiger distributions. Additionally, my chapter will provide guidelines on priority areas for habitat connectivity and potential corridors for tiger. This will assist the survival of tiger fragmented populations in Thailand by promoting connectivity among subpopulations.

Characterizing the effects of landscape structure and ecological processes on bird distributions will provide information for broad-scale conservation planning. Such information will enhance understanding of threats posed to habitat suitability and avian biodiversity in Thailand. This will enhance the development of efficient conservation planning by identifying likely targets of future conservation efforts, including existing protected areas that may be improved.

This research contributes to a better understanding of landscape patterns and ecological processes influencing species distributions and biodiversity in Thailand. Thailand is experiencing dramatic ecological and socioeconomic changes against the backdrop of a rapidly changing, human-dominated landscape. Likewise, other tropical countries still need more comprehensive spatial distribution information to improve national-scale conservation planning in order to sustain the integrity of ecological processes and ecosystem services. The achievement of conservation goals and natural management can determine the fate of tropical biodiversity.

Given this, improved knowledge of tropical ecosystems will reduce current rates of extinction and facilitate long-term persistence of species across the globe.

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