

**Spatial patterns of primary productivity derived from the Dynamic Habitat Indices predict  
patterns of species richness and distributions in the tropics**

By

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A dissertation submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

(Wildlife Ecology)

at the

UNIVERSITY OF WISCONSIN – MADISON

2016

Date of final oral examination: 12/16/2015

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## Acknowledgements

I am thankful to numerous people and organizations that have helped and supported me during my time as a graduate student. I will always be grateful to my advisor, Volker Radeloff, for being a great mentor. Dr. Radeloff has always been so generous with his advice, time, and support on research, comments on manuscripts, and career advice. I am thankful to Volker for giving me all the opportunities I have had as part of the SILVIS family. I am grateful to my committee members for their expert and enthusiastic guidance: I especially appreciate Anna Pidgeon for her suggestions and feedback throughout all stages of my research, and for her insights in furthering my understanding of avian ecology. I am grateful to Ian Baird for setting me off on my scientific path in Thailand, and his insights on Thai's ecology and human science aspects. Benjamin Zuckerberg has given me his extremely helpful suggestions and comments on my research. Mutlu Özdoğan has helped make my dissertation possible through helpful advice.

I am indebted to all of my collaborators who have contributed to make this dissertation accomplished, special thanks to Philip Round, Warren Brockelman, Ronglarp Sukmasuang, Antony Lynam, Robert Steinmetz, Kate Jenks, Dusit Ngoprasert, Wanlop Chutipong, Megan Baker, Shumpei Kitamura, Brooke Bateman, Elżbieta Ziółkowska, Nicholas Coops, Dave Helmers, and Nick Keuler have been helpful with my dissertation by sharing data, ideas, suggestions, GIS, and statistical support. I am grateful for financial support from the Royal Thai Government and NASA's Biodiversity and Ecological Forecasting Program. I also thank Lev Ginzburg, Reşit Akçakaya, Adisorn Aderektawan, and Augustine Waitayanon, for all their support. I would like to dedicate to this work to Thongchai Chalearmchaikit and Pitiwong Tantichodok, mentors of mine that have passed away.

Many members of the SILVIS lab have assisted me over the years and collaborated on my research. I thank Jodi Brandt for helping me early on in my research, classes, and her friendship. I am grateful to all of the members of the SILVIS lab and visiting scientists in the past and present for their friendship and insights on research. I thank my friends, Supranart Sisala, Pannapat Prompen, Siranan Prammanee, Jaruwat Chatwichian, Nattakarn Sukomon, Monsikarn Jansrang, Jennifer Rollins, Huan Gu, and many others.

Finally, I could not make it without my parents, Somjit and Chumnong Suttidate who always love me unconditionally and have provided support throughout my life, my siblings, Wanitcha Jitthamma and Pattiya Suttidate for being my best friends, and my grandmother. My husband, Matthew Morrill deserves special thanks, especially for helping me with everything and giving me a family in the U.S. His love and all his hard work over the last six years have been crucial to my success.

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## **Introduction**

Human activities are changing the Earth's ecosystems, which has profound consequences for biodiversity. The alarming trend of biodiversity loss is most pronounced in the tropics (Laurance et al. 2012; Pimm et al. 1995). Accuracy and efficient assessments of broad-scale patterns of biodiversity is necessary to understand the factors determining biodiversity patterns, and the responses of species to environmental change (Sutherland et al. 2009). Although knowledge of the causes of spatial heterogeneity in biodiversity has increased considerably, incomplete assessments of biodiversity patterns in many tropical regions continue to hamper the understanding of the underlying mechanisms that shape such patterns, hindering conservation efforts (Jetz et al. 2012). Biodiversity science requires better assessments of current patterns of species diversity and distributions in order to greatly improve conservation planning and protect biodiversity (Pereira et al. 2013; Scholes et al. 2008). Remote sensing is essential to develop such assessments (Kerr and Ostrovsky 2003; Turner 2014; Turner et al. 2003).

Remotely sensed measures of key habitat factors, such as productivity, can reveal the mechanisms and constraints that shape patterns of biodiversity at broad spatial and temporal scales. Measures of productivity and seasonality are strong predictors of biodiversity, even though the positive species-productivity relationship is still debated (Evans et al. 2005; Hawkins et al. 2003; Mittelbach et al. 2001). While satellite data provide a suite of productivity measures to assess broad-scale habitat and biodiversity patterns, the challenge is how to quantify patterns of species diversity and distribution using remotely sensed productivity measures that are ecologically relevant to species. Furthermore, the utility of remotely sensed productivity measures for biodiversity assessments have largely been conducted in temperate ecosystems (Nagendra et al. 2013), and not yet been assessed in many tropical regions. This is why it still

remains unclear if the remotely sensed productivity measures can effectively assess patterns of species richness and distribution in the tropics.

MODIS satellite data provides a great opportunity to develop relevant measures for biodiversity assessments (Duro et al. 2007). The Dynamic Habitat Indices (DHIs) integrate three measures of dynamic patterns of annual primary productivity: (a) cumulative annual productivity, (b) minimum annual productivity, and (c) seasonal variation in productivity (Berry et al. 2007; Coops et al. 2008; Mackey et al. 2004). The cumulative annual productivity captures the availability of primary productivity throughout a year (Coops et al. 2009a; Coops et al. 2008; Coops et al. 2009b), and species richness is generally high where energy availability is high (Connell and Orias 1964). The minimum annual productivity relates to the potential of a landscape in maintaining productivity level throughout the year, and species richness is generally high where energy availability never reaches a low minimum. The seasonal variation in productivity reflects the variation in phenology of primary productivity in a landscape throughout a year, and areas with less intra-annual variability may support more species (Hurlbert and Haskell 2003; Rahbek et al. 2007). The DHIs are promising for biodiversity and conservation, and unique from other MODIS productivity products, in that they are well grounded in biodiversity theory (Coops et al. 2009a; Coops et al. 2009b).

The strength of the DHIs are that the three measures are rooted in a number of hypotheses regarding the relationship between patterns of species richness and distribution and productivity (Hawkins et al. 2003; Mittelbach et al. 2001; Storch et al. 2006). For example, species-energy theory hypothesizes a strong correlation between species richness and productivity (Wright 1983), even though the strength of the species richness–productivity relationship is still debated (Bonn et al. 2004; Currie et al. 2004; Storch et al. 2005). Additionally, the DHIs are designed

specifically to be derived from satellite data that are available at high temporal resolution and over broad scales (Kerr and Ostrovsky 2003). The DHIs thus provides a unique opportunity to utilize satellite data for biodiversity assessments.

The DHIs have successfully predicted biodiversity patterns for fauna in the temperate regions. The DHIs explain up to 88% of the variation in breeding bird species richness across the United States, with seasonal variation in productivity being the most important measure of the DHIs while cumulative productivity is the least important factor (Coops et al. 2009a). Similarly, the DHIs explain a high proportion of the variation in breeding bird species richness in Ontario, Canada, but here minimum productivity is the most important factor (Coops et al. 2009b). Diversity of Canadian butterfly communities positively associate with cumulative annual and annual minimum productivity (Andrew et al. 2012). The DHIs significantly predict the probability of occurrence and abundance for moose (*Alces alces*) in Ontario (Michaud et al. 2014). However, the DHIs have not yet been evaluated in the tropics, and it is not clear if the patterns of primary productivity derived from the DHIs can predict patterns of species richness and distributions in the tropical ecosystems.

**The overarching goal of my dissertation was to evaluate the importance of dynamic patterns of primary productivity measured via the Dynamic Habitat Indices (DHIs) for assessing patterns of species richness and distributions in the tropics.** Specifically, my research questions were:

**Question 1: How well does productivity as measured by the Dynamic Habitat Indices (DHIs) based on MODIS fPAR data explain tropical bird species richness patterns?**

Species richness is a fundamental aspect of biodiversity and related to both ecological processes and ecosystem services (Currie 1991; MacArthur 1957; Whittaker et al. 2001). However, current bird extinction rates are at least 30 times higher than expected rates (Pimm et al. 2006). Bird species are a focal taxonomic group for investigations of the relationship between richness and dynamics of productivity because productivity is closely related to various aspects of bird life history such as habitat preferences for nesting, feeding, mating, and migratory behavior. The dynamic patterns of primary productivity strongly influences species richness patterns (Evans and Gaston 2005; Hawkins et al. 2003; Storch et al. 2005). Assessing the ability of the three DHIs to explain bird diversity patterns in tropical ecosystems, such as Thailand, is important to understand the underlying mechanisms shaping such pattern and could help mitigate potential avian diversity losses.

I assessed the relationships between the DHIs and tropical bird species richness for different functional guilds. I also evaluated the complementarity of the DHIs measures with topography, climate, latitudinal gradients, habitat heterogeneity, and habitat area in explaining tropical bird species richness. I hypothesized that the bird species richness is highest where the cumulative productivity and minimum productivity is highest, and seasonal variability of productivity is lowest. I also hypothesized that among three DHIs, cumulative productivity would be the most important factor in explaining the patterns of species richness, and that the DHIs would outperform other environmental variables.

**Question 2: How well do texture measures derived from the cumulative productivity index of the DHIs predict tropical bird distribution patterns in forest ecosystems?**

Habitat heterogeneity is one of the most important landscape attributes shaping species distribution patterns (Hutchinson and MacArthur 1959; MacArthur and MacArthur 1961; Stein et al. 2014). Understanding the relationship between species and habitat heterogeneity is crucial for maintaining biodiversity, and identifying high quality habitat is key for conservation management (Kreft and Jetz 2007). However, the pattern of species-heterogeneity relationship still remains a debate (Kerr and Packer 1997; Stein et al. 2014; Tews et al. 2004) and requires more empirical evidence, especially from tropical ecosystems. This work has been accomplished in my dissertation.

Texture measures, a proxy for habitat heterogeneity, strongly associate with bird diversity and distribution patterns (Culbert et al. 2012; St-Louis et al. 2006; Bellis et al. 2008). I developed texture measures derive from the DHI cumulative annual productivity, and evaluated if texture measures compare favorably with habitat composition and fragmentation in improving the predictions of distribution patterns for tropical forest birds. I hypothesized that the incorporation of texture measures into habitat composition and fragmentation models would improve model performance for predicting tropical bird distributions because texture measures capture both within and between habitat heterogeneity which are complementary to the effects of habitat composition and fragmentation in predicting area- and edge-sensitive tropical forest bird species.

**Question 3: How important are trophic interactions in identifying the spatial patterns of habitat connectivity for the Indochinese tiger?**

Many endangered carnivores such as the Indochinese tiger (*Panthera tigris*) persists only in small, fragmented, and isolated populations within human-dominated landscapes (Karanth et

al. 2004b; Lynam 2010; Wikramanayake et al. 2004). Habitat connectivity is crucial to long-term persistence of tigers (Kanagaraj et al. 2013; Sanderson et al. 2010; Wikramanayake et al. 2011). Yet, limited understanding of the distribution patterns of suitable habitats and dispersal corridors of tigers still constrains conservation efforts (Dinerstein et al. 2007; Seidensticker et al. 2010b; Smith et al. 2010).

I employed species distribution models to predict habitat suitability of ungulate prey species based on productivity and other environmental variables, and then habitat suitability of the endangered Indochinese tigers based on its prey distributions plus other factors. I subsequently assessed habitat connectivity for tigers. I hypothesized that the probability of occurrence of tigers would be high in areas where habitat suitability for prey is high because primary productivity, the base of food webs of herbivores and their predators, is high. These direct effects of consumption and productivity through trophic interactions influence the distributions of prey and predator species in a community (Power 1992). Suitable habitat for tigers in Thailand may be fragmented because of highly heterogeneous prey density (Steinmetz et al. 2010; Steinmetz et al. 2013), habitat loss and fragmentation (Lynam 2010; Lynam et al. 2001).

### **Study area**

My research was in Thailand, an ideal tropical region in which to conduct my dissertation research for several reasons. First, Thailand is a global biodiversity hotspot (Myers et al. 2000), and home to more than 1,000 bird and 302 mammal species (IUCN 2014; Bird Conservation Society of Thailand Records Committee 2012). However, these species are facing rapid habitat loss and degradation due to economic development and land use change (Trisurat et al. 2010; Woodruff 2013), rates of which will likely rise due to international free market policies in 2015

(i.e., ASEAN Economic Community, (Fox and Vogler 2005). Second, broad-scale biodiversity assessments are needed for conservation planning (Laurance et al. 2012). Forest bird species of Thailand are declining in richness and density (Round and Gale 2008). Thailand's native mammal community is collapsing, with up to 12 species threatened by extirpation (Gibson et al. 2013) and the endangered Indochinese tigers only persisting in isolated, fragmented populations (Lynam 2010; Rabinowitz 1999; Smith et al. 1999). Although Thailand's situation is not unique, assessments of Thailand's biodiversity with the DHIs are novel for better understanding underlying mechanisms shaping such patterns, and can assist conservation efforts which will be important for biodiversity conservation across the tropics as well.

In the following pages I provide a summary of three chapters, which examine specific research questions in detail.



## Chapter 1 Summary

### **Question 1: How well does productivity as measured by the Dynamic Habitat Indices (DHIs) based on MODIS fPAR data explain tropical bird species richness patterns?**

Avian biodiversity is facing severe threats from anthropogenic activities, it is important to assess current patterns of bird species richness in order to mitigate potential losses.

My goal was to investigate the relationship of the dynamic patterns of primary productivity derived from the DHIs in explaining tropical bird species richness in Thailand. My objectives were to (1) examine the relationship between the three DHI measures and the patterns of species richness for tropical birds and for different functional guilds, and (2) evaluate the effects of the combination of the DHIs and other environmental factors in explaining patterns of species richness.

I performed best-subsets regression to assess the patterns of species richness. I analyzed species richness of all bird species and for several functional guilds based on habitat preferences including (a) forest birds; (b) early-successional birds (c) grassland birds; (d) wetland birds; (e) farmland birds, and migratory status: (f) resident birds; and (g) migratory birds derived from range map as well as species distribution models. I also conducted a regression analysis to examine the relationships between species richness of all bird species, and that of each functional guild, versus the DHIs and other environmental variables (i.e., latitudinal gradients, elevation, topographic relief, annual precipitation, annual temperature, temperature range, land cover richness, and habitat area). I then used a hierarchical partitioning regression to assess the relative importance of the DHIs and environmental variables in each model.

My results showed that the highest cumulative annual productivity, highest annual minimum productivity, and lowest seasonal variation in productivity occurred where bird species

richness was highest. Among the three DHIs, I found that cumulative annual productivity was the most important factor in explaining the patterns of bird richness. Forest birds and resident birds strongly associated with the DHIs. In comparison to other environmental factors, the DHIs were the most important factor in explaining bird species richness in Thailand, outcompeting latitudinal gradients, topography, climate, habitat heterogeneity, and area, but these other factors were complementary to the DHIs.

In summary, my results indicated that the dynamic patterns of primary productivity as captured by the DHIs are important in shaping the patterns of tropical bird richness in Thailand at nationwide scale. The relationship between the DHIs and tropical bird species richness provides a more complete understanding of tropical species richness and spatial patterns of energy availability in a tropical landscape, as well as an effective tool for tropical biodiversity assessments and bird conservation.

**Resulting paper:** Naparat Suttidate, Philip D. Round, Anna M. Pidgeon, Nicholas C. Coops, Nicholas S. Keuler, David Helmers, Warren Y. Brockelman, and Volker C. Radeloff. *Journal of Biogeography*, not submitted yet.

## Chapter 2 Summary

### **Question 2: How well do texture measures derived from the cumulative productivity index of the DHIs predict tropical bird distribution patterns in forest ecosystems?**

The identification of high quality habitat is critical for prioritizing limited conservation resources and hence maintaining the integrity of biodiversity and ecosystem functions. Texture measures derived from satellite data are a proxy measure for habitat heterogeneity, and have been effectively used to predict species richness and distributions. However, texture measures have been tested mainly in temperate ecosystems which limit understanding of the tropical diversity-habitat heterogeneity relationship.

My goal was to evaluate the ability of texture measures derived from 1-km MODIS fPAR to predict patterns of bird distribution in tropical forest ecosystems. I was specifically interested in (1) whether image texture measures can predict forest bird species distributions, and (2) whether combining texture measures with habitat composition and fragmentation can improve the prediction performance.

I developed texture measures from the cumulative annual productivity of the DHIs using 1-km MODIS fPAR data averaged from 2003-2014 over forested areas across Thailand. I selected occurrence data of 86 forest bird species, including to 5 taxonomic orders: (a) Bucerotiformes, (b) Cuculiformes, (c) Galliformes, (d) Passeriformes, and (e) Piciformes. I modeled forest bird distributions using generalized logistic regression models. I subsequently compared the predictive power of texture models with models fitted using habitat composition and fragmentation derived from categorical land cover classification, as well as models fitted using the combination measures of texture, habitat composition, and fragmentation.

Measures of texture, particularly second-order homogeneity was effective in modeling tropical forest bird distributions. Specifically, Bucerotiformes forest bird species, such as hornbill species had the highest model performance when fitted with texture measures. The combination of texture measures with habitat composition and fragmentation significantly improved model performance compared with habitat composition measures.

In conclusion, my results for this chapter highlight the ability of texture measures in predicting forest bird distributions in tropical ecosystems, especially when combined with habitat composition and fragmentation measures. Texture measures capture habitat heterogeneity making them complementary to the effects of habitat composition and fragmentation in tropical forest ecosystems where the patterns of habitat strongly affect patterns of species distributions. Combining texture measures for mapping and assessing status of biodiversity patterns can greatly assist conservation planning and habitat management.

**Resulting paper:** Naparat Suttidate, Anna M. Pidgeon, Volker C. Radeloff, The effects of habitat heterogeneity on tropical forest bird distributions. *Remote Sensing of Environment*, not submitted yet.

## Chapter 3 Summary

### Question 3: How important are trophic interactions in identifying the spatial patterns of habitat connectivity for the Indochinese tiger?

Many endangered carnivores such as the Indochinese tiger (*Panthera tigris*) persists only in small, fragmented, and isolated populations within human-dominated landscapes. Restoring habitat connectivity is crucial for the long-term persistence of tigers, and to minimize their extinction risk because their need for large home ranges require well-connected habitat patches. Yet limited understanding of current distributions of tigers and their ungulate prey species constrains connectivity assessments.

My goal was to assess habitat connectivity for Indochinese tigers in Thailand. My objectives were to (1) assess the effect of trophic interactions between primary productivity, prey availability, and predator on the prediction of habitat suitability for apex predator and patterns of prey-predator system, (2) identify the spatial patterns of suitable habitat and dispersal corridors for tigers, and (3) assess the relative importance of suitable habitat patches and dispersal corridors in maintaining an overall connectivity network across Thailand.

I obtained large mammal occurrence data from camera-trap surveys of 15 protected areas in Thailand, which provided *in situ* occurrence data for Indochinese tigers, Eurasian wild boar (*Sus scrofa*), Gaur (*Bos gaurus*), Red muntjac (*Muntiacus muntjac*), and Sambar deer (*Rusa unicolor*). To assess the effect of trophic interactions in predicting large mammal distributions, I compared predictions of habitat suitability models with abiotic variables, ungulate prey variables, and their trophic interaction (i.e., the combination of primary productivity, ungulate prey, and abiotic variables). To evaluate habitat connectivity for tigers, I used the habitat suitability map derived from the trophic interaction model to identify suitable habitat patches for

tigers with a patch size greater than 70 km<sup>2</sup>, and to estimate a dispersal resistance surface in order to identify potential dispersal corridors using least-cost paths and circuit analysis. I then employed graph theory to evaluate the relative importance of each potential habitat patch and dispersal corridor in maintaining an overall habitat connectivity network, and thus prioritize areas for potential corridors and reintroduction.

My analyses showed that including trophic interactions significantly improved model prediction of habitat suitability for tigers. Currently occupied and potential suitable habitats for tigers in Thailand were fragmented and isolated. However, I identified potential habitat patches and dispersal corridors connecting existing populations in Thailand's Western Forest Complex that could support the viability of tiger populations.

In conclusion, my results demonstrated the importance of trophic interactions in shaping spatial distribution patterns of predator and prey species in mammal communities, and hence improved the assessment of habitat quality and connectivity for apex predators in a fragmented landscape of Thailand. Protecting prey species and decreasing human activities in both currently-occupied and potential habitat patches and corridors that are integral for maintaining an overall connectivity among populations can help to restore the connectivity among tigers' small and isolated populations, and offer an applicable and robust approach for conservation planning for Indochinese tigers and other endangered carnivores.

**Resulting paper:** Naparat Suttidate, Antony J. Lynam, Ronglarp Sukmasuang, Robert Steinmetz, Dusit Ngoprasert, Wanlop Chutipong, Kate E. Jenks, Megan Baker, Shumpei Kitamura, Elżbieta Ziółkowska, Brooke L. Bateman, Volker C. Radeloff. Habitat connectivity for endangered Indochinese tigers. *Biological Conservation*, not submitted yet.

## **Significance**

Human activities are changing the Earth's ecosystems, which has profound consequences for biodiversity. To predict how species will respond to these changes, biodiversity science requires indicators of biodiversity patterns at relevant temporal and spatial scales. However, biodiversity assessments are still limited, especially in tropical regions, due to a lack of applicable and relevant indices. New approaches using satellite data may play a key role in filling this gap. The Dynamic Habitat Indices (DHIs), derived from satellite data, are designed for biodiversity studies, and have been evaluated for the first time in the tropical ecosystems by this dissertation research. My dissertation research thus contributes to the fields of landscape ecology, remote sensing science, and conservation biology in three aspects: science, methodology, and conservation.

## **Scientific contribution**

Assessments of the factors driving the variability in species diversity and predicting their patterns across regions and biomes is crucial for understanding underlying mechanisms shaping those patterns and how species responses to human-dominated landscapes at broader scales. Tropical ecosystems are experiencing species losses at unprecedented rates (Laurance et al. 2012), making it crucial to better assess current patterns of species diversity and distributions. However, many aspects of tropical diversity patterns are complex and not well understood due to lack of broad-scale ecological measures that can reveal such patterns. My dissertation fills this knowledge gap by evaluating the use of satellite productivity measures, which capture the dynamics of energy availability and habitat heterogeneity, to understand patterns of species richness, distribution, as well as species interactions within communities. Additionally, my research provides insights into which environmental factors species respond most to in tropical

ecosystems where broad-scale biodiversity assessments are 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.

In *chapter 1*, the relationship between the DHIs and tropical bird species richness provides a more complete understanding of tropical species richness and dynamics of energy availability. This dissertation chapter also indicates how well the DHIs can explain patterns of tropical bird richness as well as different functional guilds, and thus highlights the DHIs as effective measures for better understanding patterns of tropical biodiversity.

In *chapter 2*, the relationship between species distributions and texture measures, a proxy for habitat heterogeneity, are mostly non-linear. Different tropical forest bird species and taxonomic orders respond to dynamics of habitat heterogeneity vary depending on how species or group of species perceive the landscape, their body size, habitat requirements, and scales of texture measures (i.e., 1-km texture measures in this study). Importantly, chapter 2 highlights the complementary effects of texture measures with habitat composition and fragmentation in predicting distribution patterns.

In *chapter 3*, I provide more ecological knowledge about distribution patterns and habitat suitability for tigers through trophic interactions among tigers and their ungulate prey in food webs connecting vegetation productivity directly - via consumption - with herbivores, and indirectly - via the consumption of herbivores - to carnivores. Additionally, fragmented habitat patches and long, ill-suited dispersal corridors emphasize the effect of humans-altered landscape on the viability of endangered species. The relative importance of habitat patches and dispersal



corridors can sustain viable subpopulations, and landscape connectivity among suitable habitat patches.

### **Methodological contribution**

The current global biodiversity crisis requires accurate and efficient mapping and monitoring broad-scale patterns of biodiversity. Developing methods for effective assessments of biodiversity is necessary, in particular in the tropics where ecosystems are complex, and experience the intensity of human alteration to tropical landscapes. Advances in remotely sensed data provide effective tools in quantifying the influence of environmental changes on biodiversity and ecosystem processes at spatial and temporal scales (Turner 2014). However, ecological applications of such advanced remotely sensed approaches are still needed to evaluate in tropical biodiversity studies.

My dissertation research makes methodological advances by developing and testing the Dynamic Habitat Indices for models of species richness and species distribution patterns for the first time in tropical ecosystems. Specifically, my dissertation research contributes to remote sensing and biodiversity science by seizing the opportunity presented by global, consistent well-calibrated satellite MODIS data. The DHIs are specifically designed to capture the dynamics of primary productivity that strongly correlates to patterns of species richness and distribution.

In *chapter 1*, the DHIs explained the patterns of species richness for all species and different functional guilds well because the DHIs capture the energy availability within birds' habitat through the cumulative annual productivity and phenology of productivity. The DHIs thus can serve as ecological measures when assessing and monitoring broad-scale patterns of

tropical bird richness in Thailand. In addition, the integration with other environmental data can provide a variety of ecological applications in biodiversity assessments.

In *chapter 2*, texture measures derived from the cumulative annual productivity of the DHIs provide between and within habitat heterogeneity of forest ecosystems, which commonly used habitat variables (i.e., habitat composition and fragmentation) ignore. The combined measures of texture and habitat composition and fragmentation improved species distribution models. This highlights the ability of texture measures as a valuable tool to capture habitat heterogeneity, and should be considered in conjunction with habitat composition and fragmentation in species distribution modeling. Because of the strong relationship between forest bird distributions and habitat heterogeneity, and hence texture measures can be used as a tool to assess biodiversity and monitor habitat quality over broad scales.

In *chapter 3*, the integration of trophic interactions (primary productivity, seasonality in productivity, and ungulate prey species) improved the prediction of habitat suitability for tigers in Thailand. This indicates that primary productivity and ungulate prey can be used as proxies for food availability and add ecologically realism to habitat suitability models for apex predators. In addition to trophic interactions, integrating connectivity methods with ecology of species such as home range size, dispersal distance, and dispersal barrier data can greatly improve connectivity assessments. I used ensemble species distribution models, which use multiple species distribution model algorithms, and their outcomes yield the best possible habitat suitability model for tigers. For connectivity methods, we integrated least-cost path modeling and circuit analysis to identify dispersal corridors and quantify possible routes for tigers' movements within the corridors. I also ranked the relative importance of suitable habitat patches and dispersal corridors to an overall habitat connectivity network using the graph theory method which

performs removal operations of habitat patches and corridors, and thus prioritize sites for potential corridors and reintroduction.

### **Conservation contribution**

Thailand is a global biodiversity hotspot experiencing dramatic ecological and socioeconomic changes. As is the case for most tropical countries, Thailand still needs better biodiversity assessments and 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. The dissertation research contributes greatly to conservation of Thailand, and around the world by improving assessments of the patterns of species richness and distributions as well as ecological processes influencing broad-scale patterns of biodiversity.

In *chapter 1*, incorporating knowledge of the relationship between patterns of bird species richness of different functional guilds and the dynamics of primary productivity (i.e., energy availability) into the identification of important factors shaping richness patterns highlights the effectiveness of the DHIs as an ecological tool to prioritize areas for bird conservation. In the process of this chapter, I also developed new bird richness and functional guild maps, which by themselves will be valuable for conservation and biodiversity science. Comprehensive information from chapter 1 can help policy-makers in compiling data on the species richness patterns of planning areas to maintain biodiversity.

In *chapter 2*, I tested and improved methods of characterizing complex forest habitat in Thailand, which will serve as a model for other tropical studies. Synergistic remotely sensed data can enhance the ability to quantify habitat quality and habitat biodiversity values. The most important contribution of my work on the ground is its direct application to conservation and management in Thailand. Characterizing the effects of landscape structure and ecological processes on bird distributions will provide information for broad-scale conservation planning. Such information enhances the understanding of threats posed to habitat suitability and avian biodiversity in Thailand. This fosters the development of efficient conservation planning by identifying likely targets of future conservation efforts, including existing protected areas that may be improved.

In *chapter 3*, broad-scale conservation planning for tigers cannot be successful without identifying suitable habitat patches, dispersal corridors, and an effective assessment of connectivity network that can maintain viability of tiger populations and facilitating gene flow among populations. My third dissertation chapter provides maps of spatial distribution patterns on (a) currently occupied and potential suitable habitat patches of tigers, (b) potential dispersal corridors connecting among those suitable patches, (c) a ranking of the importance of suitable habitat patches and corridors to maintain overall connectivity network for the Indochinese tigers in Thailand, and (d) habitat suitability maps for five large mammal species in Thailand, including tigers, gaur, muntjac, sambar deer, and wild boar. These spatial data are crucial information for prioritizing areas for tiger conservation planning, and identifying potential reintroduction sites for tigers as well as their prey species, which can greatly improve conservation efforts for tigers in Thailand as well as their current distribution ranges in other regions.

## Summary

My evaluation of dynamic patterns of primary productivity as measured by the Dynamic Habitat Indices (DHIs) for biodiversity assessments in the tropics is highly novel. In addition to assessing the relationship between species diversity and the DHIs as effective measures to understand underlying mechanisms and identifying important factors shaping broad-scale patterns of species richness and distribution in tropical ecosystems, it provides insights into conservation planning and resource management in Thailand. Assessing current patterns and predicting future changes in biodiversity in tropical regions is urgently needed for science, conservation, and land management, given high rates of global biodiversity loss and the impacts of rapid environmental change. My dissertation research helps to close this gap by successfully evaluating the DHIs from MODIS as a valuable measure to detect and predict patterns of tropical biodiversity, in order to advance the development of essential biodiversity variables (EBVs) (Pereira et al., 2013). Additionally, my dissertation research addresses the need for accurate assessment of biodiversity data at relevant spatial and temporal scales as stated in conventions such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), and The Convention on Biological Diversity (CBD) (Pimm et al. 2014). As such, my dissertation research contributes substantially to biodiversity science, and has broad societal relevance, striving globally to protect biodiversity and the ecosystem services that sustain human well-being within the context of rapid environmental changes.

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## **Chapter 1: The relationship of tropical bird species richness and primary productivity as measured by the Dynamic Habitat Indices based on MODIS satellite data**

### **Abstract**

Avian biodiversity is facing severe threats from anthropogenic activities. It is important to assess current patterns of bird species richness in order to mitigate potential losses. Our goal was to investigate the relationships between tropical bird species richness patterns in Thailand and primary productivity as measured by the Dynamic Habitat Indices (DHIs). We calculated the Dynamic Habitat Indices (DHIs) based on the fraction of absorbed photosynthetically active radiation (fPAR) derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS). The DHIs summarize three measures of productivity: cumulative annual productivity, annual minimum productivity, and seasonal variation in productivity. We estimated species richness for all birds and different functional guilds by combining (a) 888 individual bird species range maps and (b) 336 species distribution model (SDM) prediction maps. We modeled species richness for all bird species, and for different functional guilds, based on habitat preferences and migratory status, as a function of the DHIs. We also evaluated these relationships in multivariate models adding climate, topography, latitudinal gradients, habitat heterogeneity, and area, with best-subsets and hierarchical partitioning regressions. Our results showed that the highest cumulative annual productivity, highest annual minimum productivity, and lowest seasonal variation in productivity occurred where bird species richness was highest. Among the three DHIs, cumulative annual productivity was the most important factor in explaining the species richness patterns of birds in Thailand. Cumulative annual productivity explained the highest proportion of the variation in species richness patterns for all birds, forest birds, and resident birds from both range and SDM prediction maps (up to 63%). When estimating richness with all

three DHIs, resident bird species richness showed the strongest correlation among the range map based richness estimates ( $R^2 = 0.65$ ,  $P < 0.001$ ), while forest bird species showed the strongest correlation based on SDM prediction maps ( $R^2 = 0.61$ ,  $P < 0.001$ ). The DHIs and other environmental factors were complementary in explaining the species richness patterns of all bird species richness and functional guilds (up to 87%). In comparison to other environmental factors, the DHIs were the most important factors outcompeting latitudinal gradients, topography, climate, habitat heterogeneity, and area. The strong relationships between the DHIs and tropical bird species richness patterns in Thailand suggested that the DHIs provide an efficient quantification of energy availability shaping tropical bird species richness at broad scales, and can assist biodiversity assessments and hence bird conservation.

## **Introduction**

Biodiversity loss is a global crisis and tropical regions are experiencing the greatest declines (Brook et al. 2008; Laurance et al. 2012; Sala et al. 2000). Accurate and efficient assessments of broad-scale patterns of biodiversity are necessary to understand the factors determining biodiversity patterns, and the responses of species to changing environments (Sutherland et al. 2009). Although knowledge of the spatial variation in biodiversity patterns has increased considerably, incomplete assessment of biodiversity patterns in many tropical regions continues to hamper the understanding of the underlying mechanisms that shape such patterns, hindering conservation efforts (Gaston 2000; Jetz et al. 2012). Biodiversity science requires better assessments of current patterns of species diversity and distributions in order to protect biodiversity and advance conservation planning (Pereira et al. 2013; Scholes et al. 2008). Remote sensing is essential to develop such assessments (Kerr and Ostrovsky 2003; Turner 2014; Turner et al. 2003).

Species richness is a fundamental aspect of biodiversity, and is strongly associated with primary productivity (MacArthur 1957; Wright 1983; Evans et al. 2005). The underlying mechanisms shaping broad scale richness patterns are still subject to debate due to the confounding effects of observation scales (Rahbek and Graves 2001; Whittaker et al. 2001), and the complexity of relationships between species and their environments (Jetz et al. 2004; Orme et al. 2005). Empirically, species richness patterns show strong relationships to energy availability though (Bonn et al. 2004; Currie et al. 1991; Storch et al. 2005). The energy within a landscape is usually indirectly estimated from other variables, and often used interchangeably with primary productivity (Gaston 2000). In addition to cumulative energy, seasonal variation in productivity

influences how prevalent migration is among the members of a given bird community (Coops et al. 2009a; Hurlbert and Haskell 2003).

Remotely sensed measures of dynamic patterns of productivity and phenological variation in productivity can reveal underlying mechanisms and ecosystem functions of species richness patterns (Evans and Gaston 2005; Hawkins et al. 2003; Mittelbach et al. 2001), and be used to test the species-energy hypothesis (Hutchinson and Macarthur 1959; Wright 1983; Wright et al. 1993). The relationship of species richness as a function of productivity in fauna can be positive, negative, or non-linear (Gaston 2000; Mittelbach et al. 2001; Storch et al. 2006). Although the species richness-energy relationship is still debated (Currie et al. 2004; Evans et al. 2005; Storch et al. 2005), the dynamic patterns of primary productivity are among the most important factors shaping species richness at broad scales (Field et al. 2009; Hawkins et al. 2003). Given the complexity in the species-productivity relationship and the important role productivity plays in species richness patterns, the challenge is how to derive productivity indices that can capture the dynamic patterns of primary productivity and effectively assess broad-scale patterns of species richness.

Satellite observations provide a suite of productivity data and are increasingly used to model and understand species richness patterns at broad scales in space and time (Nagendra 2001; Nagendra et al. 2013). The main advantage of remotely sensed data over field data is the availability of consistent data with high spatial and temporal resolution for large areas (Innes and Koch 1998; Roy and Tomar 2000). Typically, remote sensing data are used to measure environmental variables that predict species richness rather than by identifying species in the satellite imagery directly (Kerr and Ostrovsky 2003; Turner et al. 2003). For example, the Normalized Difference Vegetation Index (NDVI), a measure of photosynthetic activity (Tucker

et al. 2005), can predict the species richness patterns of fauna and flora (Hurlbert and Haskell 2003). NDVI is, however, an indirect measure of productivity, with limitations to its use in tropical ecosystems where NDVI saturates at low to medium productivity levels as vegetation canopy increases (Foody et al. 2001; Nagendra and Rocchini 2008; Steininger 1996).

Productivity can be directly measured through biophysical parameters, such as standing biomass, tree volume, foliage vigor as measured by Leaf Area Index (LAI), and photosynthesis as measured by the fraction of light absorbed by the vegetation (fPAR) (Turner et al. 2003; Duro et al. 2007).

The fraction of absorbed photosynthetically active radiation (fPAR) is a measure of the proportion of available solar radiation in photosynthetically active wavelengths that is absorbed by vegetation for photosynthesis, and thus can quantify the dynamic patterns of primary productivity (Myneni et al. 2002; Sellers et al. 1996). In theory, the higher average fPAR level during the growing cycle, the denser the green leaf cover, and hence the higher the productivity. fPAR values vary from zero for barren land to one for dense vegetation cover (Knyazikhin et al. 1998). While fPAR is not commonly applied to biodiversity studies, it holds promise because it captures landscape gross primary productivity (Duro et al. 2007). Previous studies have successfully used fPAR measures to predict broad-scale species patterns of diversity, distribution, and ecosystem processes, yet those studies have been conducted in temperate regions (Coops et al. 2009a; Coops et al. 2009b; Michaud et al. 2014). The relationship between species richness in the tropics and dynamic patterns of primary productivity derived from fPAR still remains unclear and it is not known if it could be an effective tool in predicting tropical biodiversity patterns.

The Dynamic Habitat Indices (DHIs) summarize three aspects of the dynamic patterns of primary productivity: (a) cumulative annual productivity, (b) annual minimum productivity, and (c) seasonal variation in productivity (Berry et al. 2007; Mackey et al. 2004, Coops et al. 2008). The cumulative annual productivity captures the availability of primary productivity throughout a year (Coops et al. 2009a; Coops et al. 2008; Coops et al. 2009b), and species richness is generally high where energy availability is high (Connell and Orias 1964). The annual minimum productivity relates to the potential of a landscape in maintaining productivity levels throughout the year, and species richness is generally high where energy availability never falls to a low minimum (Schwartz et al. 2006). The seasonal variation in productivity reflects the variation in phenology of primary productivity in a landscape throughout a year, and areas with less intra-annual variability may support more species (Hurlbert and Haskell 2003; Rahbek et al. 2007). The DHIs are promising for biodiversity assessments, and unique from other MODIS productivity products, in that they are well grounded in biodiversity theory (Duro et al. 2007; Coops et al. 2009a; Coops et al. 2009b).

The DHIs have been successfully used for assessments of faunal biodiversity patterns in temperate regions. For example, in the U.S., the DHIs explain up to 88% of the variation in breeding bird species richness among ecoregions, with seasonal variation in productivity being the most important measure and cumulative annual productivity the least important factor (Coops et al. 2009a). Similarly, the DHIs explain a high proportion of the variation in breeding bird species richness in Ontario, Canada, but here minimum productivity is the most important factor (Coops et al. 2009b). Diversity of Canadian butterfly communities associated positively with cumulative and minimum productivity (Andrew et al. 2012), and the DHIs significantly predicted the probability of occurrence and abundance for moose in Ontario (Michaud et al.

2014). However, the DHIs have not yet been evaluated in the tropics, and it is not clear if the patterns of primary productivity derived from the DHIs can predict patterns of species richness in tropical ecosystems.

Our overall goal was to investigate the relationship of tropical bird species richness and the dynamic patterns of primary productivity captured by the DHIs. To achieve the goal, our first objective was to assess the relationships between tropical bird species richness for all birds and different functional guilds and the DHIs. Our second objective was to determine the relative importance of the complementarity of the DHIs, topography, latitudinal gradients, climate, habitat heterogeneity, and area in explaining species richness patterns for tropical birds. We hypothesized that the bird species richness is highest where the cumulative annual productivity and annual minimum productivity are highest, and seasonal variation in productivity is lowest. We also hypothesized that among three DHIs, cumulative annual productivity would be the most important factor in explaining the patterns of species richness, and that the DHIs would outperform other environmental variables.

## **Methods**

### *Study area*

Thailand (Figure 1) is located in Southeast Asia and covers an area of 513,115 km<sup>2</sup> between latitudes 5° 45' and 20° 27' N and longitudes 97° 22' and 105° 37' E with elevation ranges from 0 to 2,564 m. The climate is dominated by seasonal monsoons with a pronounced rainy season and dry season. Annual precipitation ranges between 1000 and 4000 mm and most precipitation falls in the rainy season from May to October. The average annual temperature is approximately 26-29 °C, and the highest temperature is approximately 40 °C in April (TMD 2010). Thailand has two major diverse types of tropical forest: broad-leaved evergreen forest and

broad-leaved deciduous forest. The tropical broad-leaved evergreen forest contains multiple forest habitat types including montane evergreen forest, dry evergreen forest, rain forest, pine forest, swamp forest, mangrove forest, and beach forest. The tropical broad-leaved deciduous forest includes mixed deciduous forest and dry dipterocarp forest (RFD 2013). Thailand is a global biodiversity hotspot (Myers et al. 2000), and is home to more than 1,000 bird species (Bird Conservation Society of Thailand Records Committee 2012). However, Thailand's birds are facing extensive habitat loss, fragmentation, and climate change, which has led to declines in bird diversity (Pattanaivibool and Dearden 2002; Round and Gale 2008; Round et al. 2006).

### *Study species*

Birds of Thailand are ideal study taxa for our study goal because they differ widely in migratory behavior, nesting requirements, feeding and mating habitats, and other life history traits (Newbold et al. 2013; Petchey and Gaston 2006; Sekercioglu et al. 2004) In order to capture these differences, we defined functional guilds of birds based on habitat preference (i.e., foraging site, nesting placement), and migratory status. We grouped bird functional guilds into: (a) forest birds that use any type of forests including mangrove forest and limestone outcrops because they often remain forested, (b) early-successional birds that occur in areas after disturbance, mostly by fire, including bamboo forest, secondary growth, and scrub, (c) farmland birds, which are ecologically tolerant deciduous forest or grassland birds that can survive in intensely cultivated areas which provide a scattering of trees rough scrub, and grassland, (d) fresh-water wetland birds that use marshes, lakes, rivers, rice paddy fields, and water reservoirs, and (e) seacoast birds that occur in coastal area. For migratory status, we distinguished between (f) resident and (g) migratory guilds (Appendix 1) (Lekagul and Round 1991; Robson 2000; Round 1988). We calculated each bird species richness twice based on two different data



sources: (1) range maps, and (2) species distribution model prediction (SDM) maps (see details below). The reason for this was that range maps are available for a much larger number of species, but have been questioned in their ability to capture diversity patterns, which is why we included the SDM prediction maps as a robustness check.

### *Range maps*

Range maps for all birds have recently been developed by IUCN and BirdLife International (IUCN 2014). Similarly, albeit cruder, range maps for subsets of species have been used to identify biodiversity hotspots (Mittermeier et al. 2003; Myers et al. 2000), examine human population density in hotspots (Cincotta et al. 2000; Jha and Bawa 2006), and model determinants of species (Roy et al. 2009). We downloaded the IUCN distribution range maps of 888 bird species, excluding extinct species and small range species. To obtain species richness, we converted the polygon range maps to grid cells and created maps of species presence (Sandom et al. 2013) in a 8-km grid to match the resolution of the DHI data (Figure 1).

### *Species distribution model (SDM) prediction maps*

We obtained 338 bird species occurrence data from the Global Biodiversity Information Facility (GBIF) from year 2000 to 2013 with a minimum 20 unique occurrences. We used MAXENT version 3.3.1 (Phillips et al. 2006) to model distributions of 338 bird species. We retained 11 environmental variables for species distribution models (Lekagul and Round 1991; Trisurat et al. 2013): (1) annual mean temperature; (2) temperature seasonality, (3) maximum temperature of the warmest month, (4) minimum temperature of the coldest month, (5) annual precipitation, (6) precipitation during the driest quarter, (7) precipitation seasonality, (8) average elevation, (9) slope, (10) five habitat types, and (11) the percent tree cover (MODIS Vegetation Continuous Fields, VCF, Hansen et al. 2003). We parameterized MAXENT with default settings

(Phillips and Dudik 2008). To reduce the effects of biased sampling, we selected pseudo-absences from occurrence locations of other bird species (Phillips et al. 2009). To evaluate model performance, we applied 10-fold cross-validation and calculated the AUC each time (Elith et al. 2011). To validate our predicted maps, we developed a bias corrected null-model to test whether our species distribution model prediction maps significantly differed from the null model of a random distribution of species (Raes and ter Steege 2007). The SDM prediction maps for Thick-billed warbler (*Acrocephalus aedon*) and Plaintive cuckoo (*Cacomantis merulinus*) were not better than random distributions, so we excluded them from further analyses (Appendix 2). We then transformed the results of 336 species distribution models to species distribution maps using the maximum sensitivity and specificity threshold (Liu et al. 2005). We compiled 336 species distribution maps into 8-km resolution species richness maps (Figure 2).

#### *Dynamic habitat indices*

We obtained the monthly fPAR MODIS from 2000-2009 from Boston University (climate and vegetation research group: <http://cliveg.bu.edu>). We calculated the DHIs as the integration of multiple years (ten years in our study), and extracted the three DHI measures as follows. To estimate *cumulative annual productivity*, we summed monthly fPAR observations for each year to produce a cumulative annual productivity, and then averaged them to produce a long-term cumulative annual productivity measure. The cumulative annual productivity relates to net primary productivity and is an indicator of vegetation production over a variety of land cover types (Figure 3a). For *annual minimum productivity*, we selected the lowest fPAR monthly value of each year, and averaged them to produce a long-term annual minimum productivity measure. Change in vegetation cover is detectable from satellite observations by estimating the minimum amount of primary productivity over the year. Areas which maintain varying degrees of

vegetated cover throughout the year with no snow cover will have positive values of annual minimum productivity. In contrast, in areas with snow cover for significant portions of the year, the annual minimum productivity of fPAR DHIs will be zero (Figure 3b). To assess seasonal variation in fPAR throughout the year, we divided the standard deviation of monthly values for each cell by the mean annual fPAR to obtain the coefficient of variation (CV). High CV values represent seasonal extremes in climatic conditions or limited growing seasons (Figure 3c). Low coefficient of variation typically represents irrigated pasture, barren land, or evergreen forests (Coops et al. 2009a; Coops et al. 2008; Coops et al. 2009b). We calculated the DHIs at 8-km resolution (Figure 3d), because that is the native resolution of the fPAR data time series, which incorporates both AVHRR (1980-2005) and MODIS (2000-2009) data (Zhu et al. 2013).

#### *Environmental variables*

To evaluate the relative importance of the DHIs and other environmental variables, we used five other major variables that influence species richness patterns of tropical birds: (a) latitudinal gradient, (b) average elevation, (c) habitat area, (d) habitat heterogeneity, and (e) climate (Rahbek 1997; Rahbek and Graves 2001; Rahbek et al. 2007). To obtain average elevation, we used the 90-m elevation data from Shuttle Radar Topography Mission (SRTM). To obtain habitat area, we calculated the proportion of bird habitat types in each 8-km grid cell: old-growth forest, secondary-growth forest, agriculture and build-up, wetland, and coastal areas from the 2000 Thailand land cover map. To obtain habitat heterogeneity, we calculated the number of habitat types in each 8-km cell (Hill and Smith 2005), and topographic relief as the difference between maximum and minimum elevation in a given grid cell (Rahbek 1997). We considered climate variables that are important in determining species richness patterns of tropical birds,

including annual mean precipitation, annual mean temperature, and mean annual temperature range (Currie et al. 2004; Jetz et al. 2012; Rahbek et al. 2007).

### *Statistical analyses*

To assess the relationships between bird species richness patterns and the DHIs, as well as the complementarity of DHIs and potential environmental variables for both bird data sets, we (1) parameterized simple ordinary least squares regressions to examine the potential of individual factors in explaining species richness patterns of all birds and different functional guilds, (2) examined the normality and homoscedasticity of variables to ensure that the assumption of linear regressions were met (Osborne & Waters, 2002), (3) limited multicollinearity by removing variables with Pearson's correlation coefficient  $|r| > 0.8$ , (4) performed best-subsets regression, i.e., a multiple linear regression approach, that measures how often a variable is entered in a set of models (Miller 2002), (5) performed hierarchical partitioning to assess the relative importance of different explanatory variables in the best models derived from best-subsets regressions (Mac Nally 2002), and (6) examined semivariograms to check for spatial autocorrelation in model residuals (Appendix 3) (Lennon et al. 2000).

We analyzed the species richness of each species guild (all birds, forest birds, early-successional birds, farmland birds, wetland birds, seacoast birds, resident birds, and migratory birds) against each of the potential explanatory variables using simple ordinary least squares regressions. We reported adjusted  $R^2$  and  $P$ -values. We included 14 explanatory variables of the DHIs (cumulative annual productivity, annual minimum productivity, seasonal variation in productivity), topography (average elevation), habitat area (proportions of old-growth forest, secondary-growth forest, agriculture and build-up, wetland, and coastal areas), habitat

heterogeneity (habitat richness, and topographic relief), and climate (annual mean temperature, mean annual temperature range, and mean annual precipitation) (Appendix 5 and Appendix 6).

To minimize the effects of spatial autocorrelation, we randomly sampled 1,000 grid cells from 8,046 cells across Thailand with a minimum distance of 10 km. In addition, we checked the normality and homoscedasticity in the relationships of bird species richness and each environmental variable (Osborne & Waters, 2002). The species richness and variables were normally distributed and their variances were homogeneous (results not shown). Only variables that yielded an  $R^2$  value  $> 0.05$  for at least one bird guild were retained for further analysis.

We used multiple linear regression models with best-subsets regressions (Miller 2002) to assess the relationships between bird species richness and the DHIs, as well as the complementarity of the DHIs, together with topography, area, latitudinal gradients, climate, and habitat heterogeneity. Before performing the multiple linear regressions, we checked for multicollinearity and dropped variables with lower predictive power in the univariate models for each pair of variables with  $|r| > 0.8$  (Appendix 4). We applied best-subsets regression, ranking models based on their adjusted  $R^2$ , with the *leaps* packages in *R* (Furnival and Wilson 2000) to obtain a subset of models that best explained species richness. 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 variable (Furnival and Wilson 2000; Miller 2002).

For the hierarchical partitioning analysis, we chose the best model according to the best subset regression for each guild and applied the *hier.part* package in *R* (Chevan and Sutherland 1991). In hierarchical partitioning regression, all possible combinations of explanatory variables are fitted in the model, and for each model the variable of interest is dropped and the model fitted

again. The importance of each explanatory variable is calculated as the average change in  $R^2$  (Chevan and Sutherland 1991).

## Results

### *Species richness and the Dynamic Habitat Indices*

Bird species richness strongly correlated with the different measures of the DHIs. The directions of the correlations were consistent with what ecological theory would predict. The species richness of birds in Thailand was highest where the cumulative annual productivity and annual minimum productivity were high, and seasonal variation in productivity was low. Among the three DHIs, cumulative annual productivity explained the most variability in univariate regression models, followed by minimum productivity, and seasonal variation in productivity. For functional guilds, the species richness of the resident bird guild derived from range maps had the strongest correlation with the cumulative annual productivity (Adjusted  $R^2 = 0.63$ ,  $P < 0.001$ ) (Table 1). The species richness of forest birds derived from species distribution prediction maps was also highly correlated with cumulative annual productivity (Adjusted  $R^2 = 0.60$ ,  $P < 0.001$ ) (Table 2). The models with the least predictive power were those for species richness pattern of the wetland guild derived from range maps, and species richness of the early-successional guild derived from species distribution model maps.

For multivariate models of the DHIs, the species richness of the resident guild derived from range maps had the strongest correlation to the composite DHI (Adjusted  $R^2 = 0.65$ ,  $P < 0.001$ ) (Table 3). The species richness of forest birds derived from species distribution prediction maps was also highly correlated with the DHIs (Adjusted  $R^2 = 0.61$ ,  $P < 0.001$ ) (Table 4). The poorest models were those for species richness pattern of the wetland guild derived from range maps, and species richness of the early-successional guild derived from species distribution

model prediction maps. Differences in the statistical significance for each of the DHI measures indicated that cumulative annual productivity, annual minimum productivity, and seasonal variation in productivity each provide unique and potentially complementary information explaining bird species richness.

#### *The relative importance of the DHIs and the environmental variables*

We found that species richness patterns for different functional guilds responded differently to environmental factors for both data sources (Table 5, Table 6). The DHIs outcompeted latitudinal gradients, climate, topography, habitat heterogeneity, and area in our multivariate models. The DHIs were the most important factor for explaining species richness pattern for all birds (58%), residents (60%), forest birds (44%), and migratory birds (33%). Climate (38%) and habitat heterogeneity (26%) played important, but secondary, roles in shaping the species richness patterns for most guilds. In contrast, topography (14%) and habitat area (13%) explained species richness the least for most guilds (Figure 4).

The relative importance of variables in explaining species richness was fairly similar for richness estimates based on range maps and species distribution models. The main difference was that climate emerged as the strongest factor, and the DHIs were the second most important factor, in explaining species richness patterns for most guilds derived from species distribution model prediction maps (Figure 5). These differences may be due to different numbers of bird species in each species richness map (Appendix 7).

## **Discussion**

Our study was the first to investigate the broad-scale relationships between bird species richness and dynamic patterns of primary productivity derived from the Dynamic Habitat Indices

in the tropics. The DHIs capture the variability of primary productivity throughout a year (i.e., energy availability) and explained species richness patterns of birds well. The DHIs were the most important factors in shaping species richness patterns of birds in Thailand, outcompeting latitudinal gradients, topography, climate, and habitat heterogeneity and area. However, DHIs and environmental variables were complementary. Among the three DHIs, the cumulative annual productivity explained the highest proportion of the variation in species richness patterns.

The DHIs explained bird species richness well and our results provide empirical evidence supporting species-energy hypothesis. Previous studies of bird richness and the DHIs in temperate ecosystems demonstrated that the DHIs can capture productivity dynamics for different bird guilds in the United States (Coops et al. 2009a) and Canada (Coops et al. 2009b). An important difference in the observed patterns of bird species richness and the DHIs in temperate and tropical regions is the relative importance of each DHI measure. In our results, species richness was most strongly correlated with cumulative annual productivity, and less correlated with seasonal variation in productivity. In contrast, seasonal variation in productivity is the most important factor for bird richness in the United States (Coops et al. 2009a), and cumulative annual productivity the least important factor. Minimum productivity was the most important factor explaining breeding bird species richness, in particular grassland birds in Ontario, Canada (Coops et al. 2009b), but minimum productivity was not as important in our results for the tropics. The differences between the DHIs' behavior in explaining bird species richness in temperate and tropical regions are likely due to less pronounced seasonal variation in tropical ecosystems.

Cumulative annual productivity explained the highest proportion of the variance in species richness for all bird species and for different functional guilds in the tropical ecosystems



of Thailand. The strong relationships between species richness patterns and the cumulative annual productivity suggest that birds in Thailand have the greatest richness in areas with the highest energy availability. However, we found that wetland bird guild showed weak correlations to the DHIs. The classification of wetland bird guild included reservoirs, and probably only permanent wetland, not seasonally dry wetland which may cause weak relationship between wetland birds and the DHIs. We expected that the cumulative annual productivity would be the most important factor because primary productivity strongly influences species richness in the subtropics and the tropics (Jetz et al. 2012; Rahbek 1997; Rahbek and Graves 2001), while ambient energy (i.e., temperature and related variables) constrains species richness in temperate regions (Hawkins et al. 2003). Minimum productivity and seasonal variation in productivity had moderate influence on the species richness pattern of birds in the tropics. Typically, tropical evergreen vegetation has a low seasonality and higher vegetation cover throughout the year, while tropical deciduous vegetation defoliates due to water stress (Trisurat et al. 2000). The dynamic patterns of primary productivity derived from the DHIs can disentangle the relationship between bird species richness and the variation in energy availability within a landscape (Coops et al. 2009a, b).

The combination of the DHIs and other environmental variables improved our models of species richness patterns of birds in the tropics. We found similar relationships as previous bird richness studies showing strong associations among primary productivity, topography, climate, habitat heterogeneity, and area in the tropics (Rahbek 1997; Rahbek et al. 2007). However, the relationships between bird species richness and environmental factors can vary widely among biogeographical regions and functional guilds. In the tropics, water and energy are the most important factors in shaping bird species richness patterns (Hawkins et al. 2003). For example,

across South America, climate explains bird species richness patterns best for birds with large species ranges (Rahbek et al. 2007). In the subtropics of Taiwan, productivity is the most important factor in shaping breeding bird species richness patterns (Koh et al. 2006; Lee et al. 2004). Climate and energy factors best explain elevational gradients of breeding bird species richness patterns in Hengduan mountains, China (Wu et al. 2013). For breeding bird species richness in the United States, seasonal variation in productivity and habitat heterogeneity are the most important factors (Hurlbert and Haskell 2003). Additionally, a global meta-analysis study of diversity drivers shows that productivity and climate are primary factors in shaping bird species richness patterns at broad scales (Field et al. 2009). Our results highlight the importance of dynamic productivity captured by the DHIs, and the ability of the DHIs in explaining species richness pattern of birds in tropical ecosystems, especially when combining the DHIs with other environmental variables.

In interpreting our results, it is important to highlight caveats of our analyses. First of all, range maps are inherently biased (Graham and Hijmans 2006), and tend to overestimate species occurrences and distributions (Rondinini et al. 2011). Therefore, we conducted our analysis based on both ranges maps, which allowed us to analyze more species, and maps from species distribution models, which are likely more accurate (Graham and Hijmans 2006; Pineda and Lobo 2012), and found similar results explaining richness based on either data source. One caveat of the accuracy of maps stemming from distribution models depends on the availability and the accuracy of occurrence data, and on the degree to which species interactions affect occurrences (Kadmon et al. 2004). We were reassured in that both richness maps showed very similar results. However, the observed difference in our results may be influenced by the different species pools.

We did not include some environmental variables, such as evolutionary history, disturbance regimes, and species interactions (Currie 1991; Gotelli and Colwell 2001) in our analyses of bird species richness in Thailand because these data were not available. While species richness patterns sometimes follow continental boundaries (a.k.a mid-domain effect, Colwell and Lees 2000), we did not include geometric constraints in our study either. According to the mid-domain effect definition, there can be a peak of species richness of endemic species in the middle of an area (Colwell and Lees 2000; Jetz and Rahbek 2001; Jetz et al. 2004). We did not observe this however, most likely because Thailand is home to few endemic bird species (Lekagul and Round 1991).

Our results highlight the effectiveness of the DHIs in capturing dynamic patterns of primary productivity for understanding species richness patterns in tropical ecosystems. We calculated the DHIs derived from fPAR MODIS satellite data and showed that the DHIs were the best variable explaining bird species richness patterns in the tropical ecosystems of Thailand. Additionally, the DHIs improved the explanatory power of models of species richness patterns when combined with other variables. As tropical regions are experiencing considerable economic development, causing rapid loss of natural habitat and biodiversity, there is a need for accurate and effective measures of biodiversity to support conservation efforts (Sutherland et al. 2009). The DHIs derived from remotely sensed data can quantify dynamic pattern of primary productivity, and advance the understanding of the patterns and drivers of biodiversity.

In summary, our study showed that the Dynamic Habitat Indices characterized dynamic patterns of primary productivity, and captured the nuanced species richness-energy relationships for birds and functional guilds in the tropics. The combination of the DHIs and other environmental variables provides insight into the factors shaping patterns of species richness in

the tropics. We suggest that future studies of tropical biodiversity could benefit from remotely sensed data thereby advancing the understanding of how tropical ecosystems are changing, and what effects this has on tropical bird diversity. The DHIs can serve as effective measures for broad-scale biodiversity assessments.

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## Tables

Table 1.  $R^2$  values for simple ordinary least squares models of species richness of different guilds derived from range maps and the DHIs: cumulative annual productivity, annual minimum productivity, and seasonal variation in productivity.

Guild	Cumulative productivity	Minimum productivity	Seasonal variation in productivity
All birds	0.58***	0.34***	-0.35***
Residents	0.63***	0.38***	-0.39***
Migratory birds	0.26***	0.09***	-0.10***
Forest birds	0.63***	0.38***	-0.38***
Early-successional birds	0.22***	0.10***	-0.10***
Farmland birds	-0.03***	-0.06***	0.07***
Wetland birds	NS	-0.01***	0.01***
Seacoast birds	0.07***	0.07***	-0.11***

\*\*\*  $P$ -value < 0.001, \*\*  $P$ -value < 0.01, \*  $P$ -value < 0.05, NS not significant.

Table 2.  $R^2$  values for simple ordinary least squares models of species richness of different guilds derived from species distribution model prediction maps and the DHIs: cumulative annual productivity, annual minimum productivity, and seasonal variation in productivity.

Guild	Cumulative productivity	Minimum productivity	Seasonal variation in productivity
All birds	0.53***	0.40***	-0.39***
Residents	0.57***	0.42***	-0.40***
Migratory birds	0.18***	0.10***	-0.13***
Forest birds	0.60***	0.46***	-0.42***
Early-successional birds	0.01**	NS	NS
Farmland birds	-0.02***	-0.06***	0.07***
Wetland birds	-0.30***	-0.25***	0.19***
Seacoast birds	-0.44***	0.05***	0.05***

\*\*\*  $P$ -value < 0.001, \*\*  $P$ -value < 0.01, \*  $P$ -value < 0.05, NS not significant.

Table 3. Parameter estimates of models of bird species richness based on range maps by different guilds for multivariate models that used the Dynamic Habitat Indices. Bold numbers are the parameters for each multiple regression model that was significant at  $P < 0.05$ .

Guild	Cumulative productivity	Minimum productivity	Seasonal variation in productivity	Adjusted $R^2$	$P$ -value
All birds	<b>0.2</b>	<b>-1.66</b>	-55.37	0.6	<0.001
Residents	<b>0.17</b>	<b>-1.22</b>	-24.35	0.65	<0.001
Migratory birds	<b>0.03</b>	<b>-0.49</b>	<b>-30.34</b>	0.26	<0.001
Forest birds	<b>0.18</b>	<b>-1.22</b>	-15.13	0.64	<0.001
Early-successional birds	<b>0.01</b>	<b>-0.08</b>	4.91	0.26	<0.001
Farmland birds	0	0	<b>17.38</b>	0.08	<0.001
Wetland birds	<b>0.01</b>	<b>-0.1</b>	8.41	0.03	<0.001
Seacoast birds	0	-0.24	<b>-67.35</b>	0.14	<0.001

Table 4. Parameter estimates of models of bird species richness based on species distribution model prediction maps by different guilds for multivariate models that used the Dynamic Habitat Indices. Bold numbers are the parameters for each multiple regression model that was significant at  $P < 0.05$ .

Guild	Cumulative productivity	Minimum productivity	Seasonal variation in productivity	Adjusted $R^2$	$P$ -value
All birds	<b>0.08</b>	-0.12	-13.67	0.53	<0.001
Residents	<b>0.08</b>	-0.01	23.53	0.57	<0.001
Migratory birds	<b>0.01</b>	<b>-0.21</b>	<b>-30.53</b>	0.2	<0.001
Forest birds	<b>0.1</b>	0.28	<b>78.06</b>	0.61	<0.001
Early-successional birds	<b>0</b>	0	1.03	0.01	<0.05
Farmland birds	<b>0</b>	-0.04	<b>13.43</b>	0.09	<0.001
Wetland birds	<b>-0.01</b>	<b>-0.3</b>	<b>-60.16</b>	0.33	<0.001
Seacoast birds	<b>0</b>	<b>-0.12</b>	<b>-31.28</b>	0.13	<0.001

Table 5. Adjusted  $R^2$  values of best models of bird species richness based on range maps by different guilds for multivariate models that used the combination of the DHIs, latitudinal gradients, topography, habitat heterogeneity, and habitat area.

Guild	#variables	Adjusted $R^2$	$P$ -value
All birds	7	0.74	< 0.001
Resident birds	8	0.76	< 0.001
Migratory birds	7	0.60	< 0.001
Forest birds	9	0.77	< 0.001
Early-successional birds	8	0.65	< 0.001
Farmland birds	8	0.84	< 0.001
Wetland birds	8	0.64	< 0.001
Seacoast birds	7	0.77	< 0.001

Table 6. Adjusted  $R^2$  values of best models of bird species richness based on species distribution prediction maps by different guilds for multivariate models that used the combination of the DHI, latitudinal gradients, topography, habitat heterogeneity, and habitat area.

Guild	#variables	Adjusted $R^2$	$P$ -value
All birds	7	0.83	< 0.001
Residents	8	0.83	< 0.001
Migratory birds	8	0.44	< 0.001
Forest birds	8	0.87	< 0.001
Early-successional birds	8	0.34	< 0.001
Farmland birds	5	0.77	< 0.001
Wetland birds	8	0.61	< 0.001
Seacoast birds	6	0.52	< 0.001



## Figures

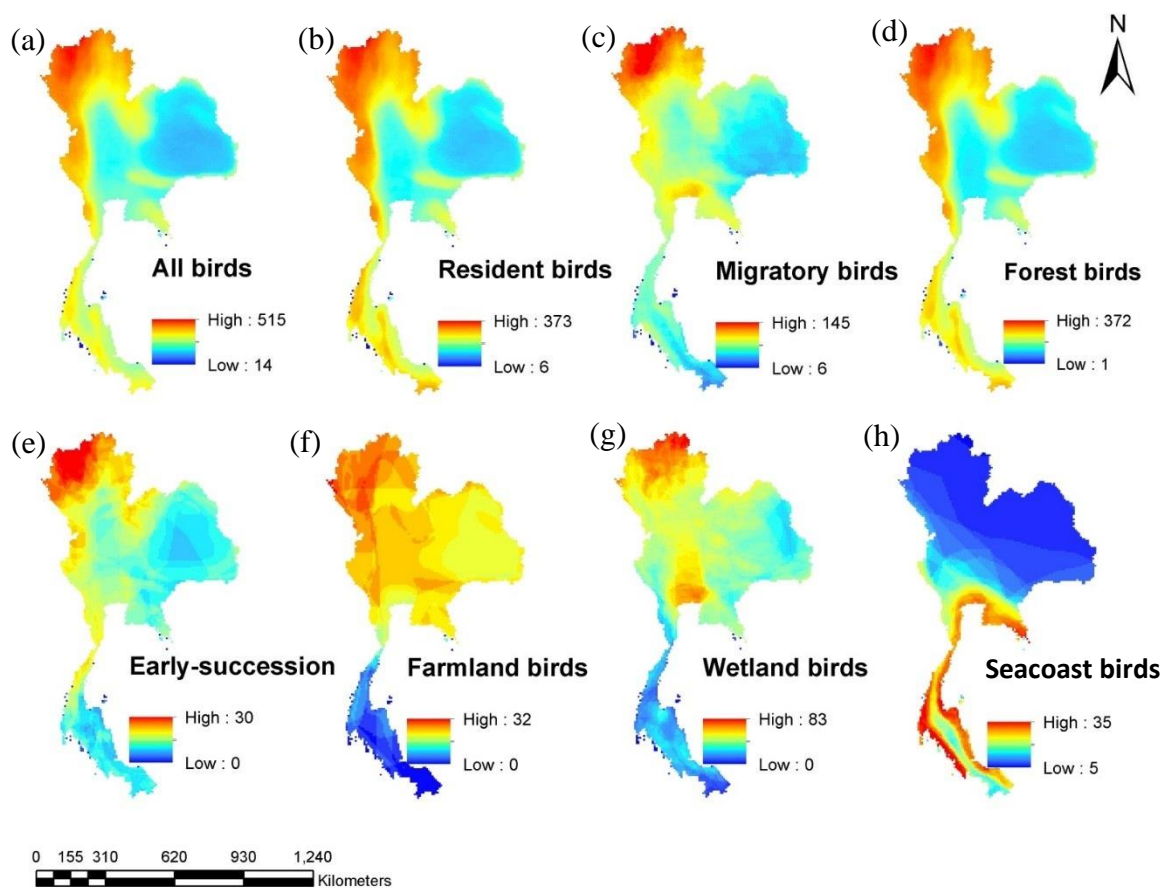


Figure 1. Species richness patterns for birds of Thailand derived from the range maps: (a) all birds ( $n = 888$  species), (b) resident birds ( $n = 664$  species), (c) migratory birds, (d) forest birds ( $n = 636$  species), (e) early-successional birds ( $n = 47$  species), (f) farmland birds ( $n = 35$  species), (g) wetland birds ( $n = 113$  species), and (h) seacoast birds ( $n = 57$  species).

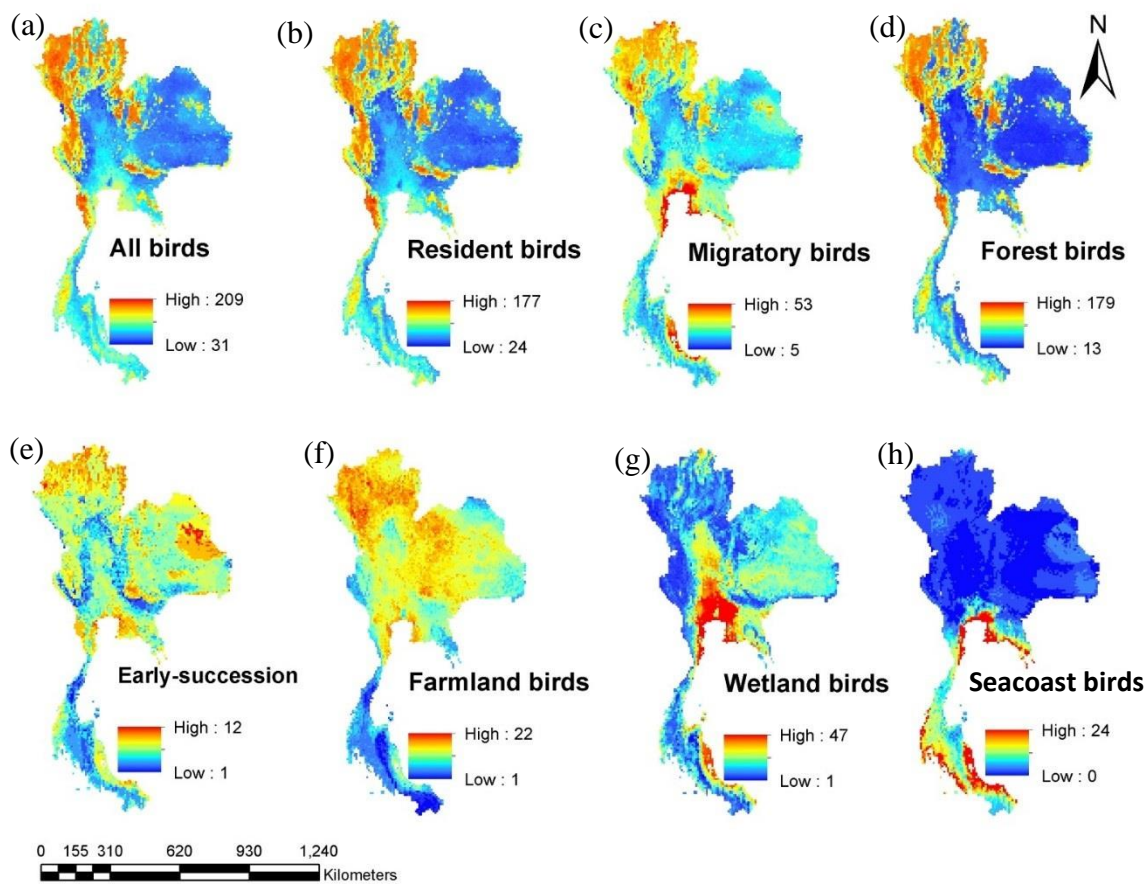


Figure 2. Species richness patterns for birds of Thailand derived from species distribution model prediction maps: (a) all birds ( $n = 336$  species), (b) resident birds ( $n = 261$  species), (c) migratory birds ( $n = 75$  species), (d) forest birds ( $n = 222$  species), (e) early-successional birds ( $n = 15$  species), (f) farmland birds ( $n = 26$  species), (g) wetland birds ( $n = 49$  species), and (h) seacoast birds ( $n = 24$  species).

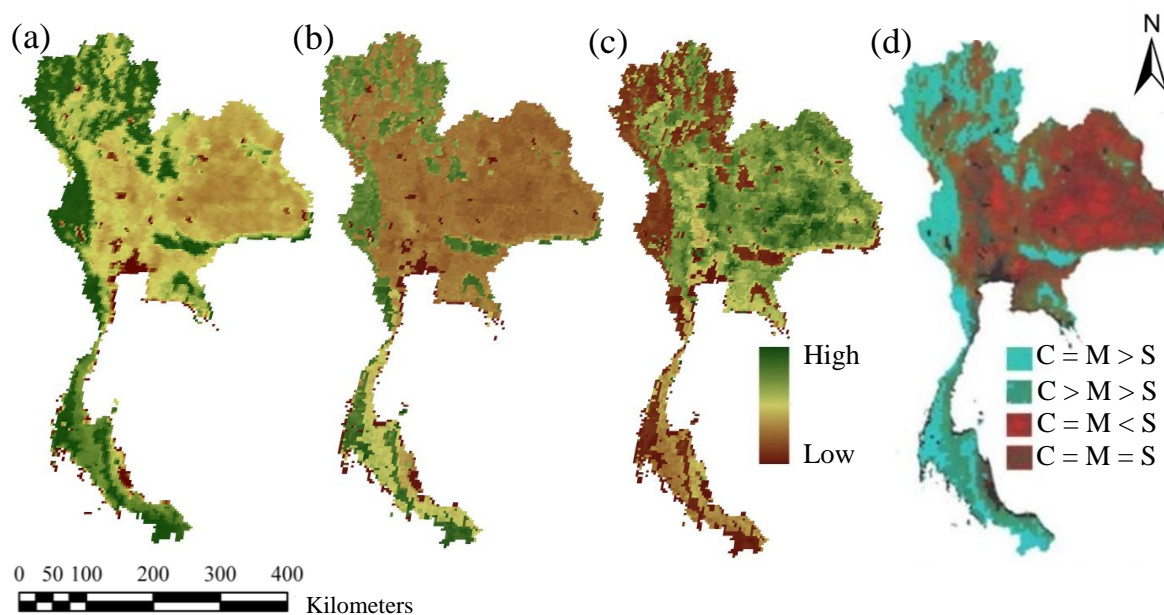


Figure 3. Individual measures of the Dynamic Habitat Indices (DHIs) for Thailand (a) cumulative annual productivity, (b) annual minimum productivity, (c) seasonal variation in productivity, and (d) the three DHIs from 2000-2009 1-km fPAR MODIS data in RGB. Bright green areas indicate consistent productivity throughout the year. Green areas represent high cumulative annual productivity, moderate annual minimum productivity, and low seasonality. Red areas have moderate productivity with high seasonality. Brown have low primary productivity in any part of the year. Abbreviations: C, cumulative annual productivity; M, annual minimum productivity; S, seasonal variation in productivity.

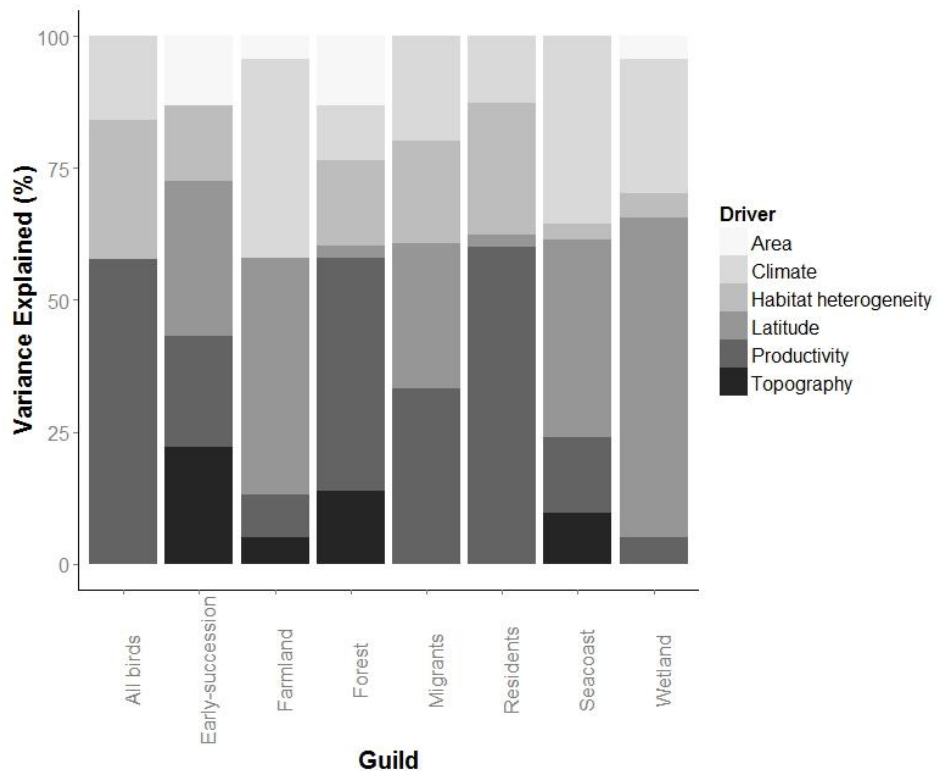


Figure 4. The percentage of independent contribution of variables in productivity, climate, topography, latitudinal, habitat heterogeneity, and habitat area to species richness for all birds, resident birds, migratory birds, forest birds, early-successional birds, farmland birds, wetland birds, and seacoast birds derived from range maps.

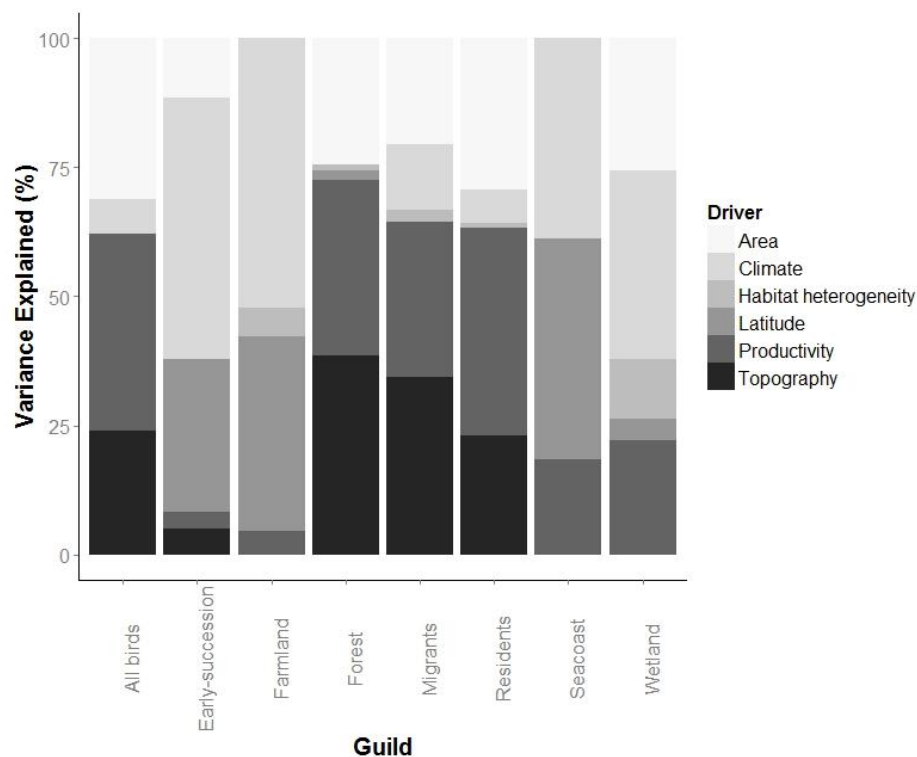


Figure 5. The percentage of independent contribution of variables in productivity, climate, topography, latitudinal, habitat heterogeneity, and habitat area to species richness for all birds, resident birds, migratory birds, forest birds, early-successional birds, farmland birds, wetland birds, and seacoast birds derived from species distribution model prediction maps. Values within each guild sum to 100.

## Appendices

Appendix 1. Bird species were classified into functional guilds based on habitat preference and migratory status. Abbreviation: R, resident birds; M, migratory birds; F, forest birds; E, early-successional birds; A, farmland birds; W, wetland birds; S, seacoast birds.

#	Scientific name	Common name	R	M	F	E	A	W	S
1	<i>Malacocincla abbotti</i>	Abbott's Babbler	x		x				
2	<i>Cettia flavolivacea</i>	Aberrant Bush-warbler	x		x				
3	<i>Sarkidiornis melanotos</i>	Comb Duck		x				x	
4	<i>Psittacula eupatria</i>	Alexandrine Parakeet	x		x				
5	<i>Seicercus soror</i>	Alstrom's Warbler		x	x				
6	<i>Falco amurensis</i>	Amur Falcon		x	x				
7	<i>Phylloscopus borealis</i>	Arctic Warbler		x	x				
8	<i>Hemixos flavala</i>	Ashy Bulbul	x		x				
9	<i>Dicrurus leucophaeus</i>	Ashy Drongo	x		x				
10	<i>Pericrocotus divaricatus</i>	Ashy Minivet		x	x				
11	<i>Orthotomus ruficeps</i>	Ashy Tailorbird	x		x				
12	<i>Columba pulchricollis</i>	Ashy Woodpigeon	x		x				
13	<i>Artamus fuscus</i>	Ashy Woodswallow	x				x		
14	<i>Phylloscopus maculipennis</i>	Ashy-throated Warbler	x		x				
15	<i>Glaucidium cuculoides</i>	Asian Barred Owlet	x				x		
16	<i>Hypsipetes leucocephalus</i>	Asian Black Bulbul	x		x				
17	<i>Muscicapa dauurica</i>	Asian Brown Flycatcher	x		x				
18	<i>Limnodromus semipalmatus</i>	Asian Dowitcher		x					x
19	<i>Chrysococcyx maculatus</i>	Asian Emerald Cuckoo	x		x				
20	<i>Irena puella</i>	Asian Fairy-bluebird	x		x				
21	<i>Aplonis panayensis</i>	Asian Glossy Starling	x		x				
22	<i>Ploceus hypoxanthus</i>	Asian Golden Weaver	x		x				
23	<i>Merops orientalis</i>	Asian Green Bee-eater	x				x		
24	<i>Calyptomena viridis</i>	Asian Green Broadbill	x		x				
25	<i>Delichon dasypus</i>	Asian House-martin		x	x				
26	<i>Anastomus oscitans</i>	Asian Openbill		x				x	
27	<i>Cypsiurus balasiensis</i>	Asian Palm-swift	x				x		
28	<i>Terpsiphone paradisi</i>	Asian Paradise-flycatcher	x		x				
29	<i>Sturnus contra</i>	Asian Pied Starling	x		x				
30	<i>Urosphena squameiceps</i>	Asian Stubtail		x	x				
31	<i>Ciconia episcopus</i>	Asian Woollyneck	x					x	

32	<i>Anorrhinus austeni</i>	Austen's Brown Hornbill	x		x				
33	<i>Mirafra javanica</i>	Australasian Lark	x					x	
34	<i>Aythya baeri</i>	Baer's Pochard		x				x	
35	<i>Zapornia pusilla</i>	Baillon's Crake		x				x	
36	<i>Gecinulus viridis</i>	Bamboo Woodpecker	x			x			
37	<i>Zapornia paykullii</i>	Band-bellied Crake		x				x	
38	<i>Cacomantis sonneratii</i>	Banded Bay Cuckoo	x		x				
39	<i>Eurylaimus javanicus</i>	Banded Broadbill	x		x				
40	<i>Lacedo pulchella</i>	Banded Kingfisher	x		x				
41	<i>Chrysophlegma miniaceum</i>	Banded Woodpecker	x		x				
42	<i>Arborophila brunneopectus</i>	Bar-backed Partridge	x		x				
43	<i>Coracina striata</i>	Bar-bellied Cuckooshrike	x		x				
44	<i>Pitta elliotii</i>	Bar-bellied Pitta	x		x				
45	<i>Hirundo rustica</i>	Barn Swallow		x				x	
46	<i>Turnix suscitator</i>	Barred Buttonquail	x					x	
47	<i>Macropygia unchall</i>	Barred Cuckoo-dove	x		x				
48	<i>Bubo sumatranus</i>	Barred Eagle-owl	x		x				
49	<i>Limosa lapponica</i>	Bar-tailed Godwit		x					x
50	<i>Hemipus picatus</i>	Bar-winged Flycatcher-shrike	x		x				
51	<i>Macheiramphus alcinus</i>	Bat Hawk	x		x				
52	<i>Blythipicus pyrrhotis</i>	Bay Woodpecker	x		x				
53	<i>Ploceus philippinus</i>	Baya Weaver	x			x			
54	<i>Esacus magnirostris</i>	Beach Thick-knee	x						x
55	<i>Sitta formosa</i>	Beautiful Nuthatch	x		x				
56	<i>Accipiter virgatus</i>	Besra	x		x				
57	<i>Seicercus valentini</i>	Bianchi's Warbler		x	x				
58	<i>Aviceda leuphotes</i>	Black Baza	x		x				
59	<i>Ixobrychus flavicollis</i>	Black Bittern	x					x	
60	<i>Dicrurus macrocercus</i>	Black Drongo	x					x	
61	<i>Ictinaetus malaiensis</i>	Black Eagle	x		x				
62	<i>Anthracoceros malayanus</i>	Black Hornbill	x		x				
63	<i>Milvus migrans</i>	Black Kite	x					x	
64	<i>Garrulax lugubris</i>	Black Laughingthrush	x		x				
65	<i>Platysmurus leucopterus</i>	Black Magpie	x			x			
66	<i>Melanoperdix niger</i>	Black Partridge	x		x				
67	<i>Ciconia nigra</i>	Black Stork		x				x	
68	<i>Meiglyptes jugularis</i>	Black-and-buff Woodpecker	x		x				
69	<i>Cymbirhynchus macrorhynchos</i>	Black-and-red Broadbill	x		x				
70	<i>Pycnonotus melanoleucos</i>	Black-and-white Bulbul	x		x				

71	<i>Eurylaimus ochromalus</i>	Black-and-yellow Broadbill	x		x				
72	<i>Enicurus immaculatus</i>	Black-backed Forktail	x		x				
73	<i>Ceyx erithaca</i>	Black-backed Kingfisher	x		x				
74	<i>Phaenicophaeus diardi</i>	Black-bellied Malkoha	x		x				
75	<i>Sterna acuticauda</i>	Black-bellied Tern	x					x	
76	<i>Pica pica</i>	Black-billed Magpie	x		x				
77	<i>Turdus dissimilis</i>	Black-breasted Thrush	x		x				
78	<i>Alcippe grotei</i>	Black-browed Fulvetta	x		x				
79	<i>Acrocephalus bistrigiceps</i>	Black-browed Reed-warbler		x				x	
80	<i>Pellorneum capistratum</i>	Black-capped Babbler	x		x				
81	<i>Halcyon pileata</i>	Black-capped Kingfisher		x				x	
82	<i>Sturnus nigricollis</i>	Black-collared Starling	x			x			
83	<i>Pycnonotus melanicterus</i>	Black-crested Bulbul	x		x				
84	<i>Nycticorax nycticorax</i>	Black-crowned Night-heron	x					x	
85	<i>Pteruthius melanotis</i>	Black-eared Shrike-babbler	x		x				
86	<i>Emberiza spodocephala</i>	Black-faced Bunting		x				x	
87	<i>Platalea minor</i>	Black-faced Spoonbill		x					x
88	<i>Pycnonotus atriceps</i>	Black-headed Bulbul	x		x				
89	<i>Carduelis ambigua</i>	Black-headed Greenfinch		x		x			
90	<i>Larus ridibundus</i>	Black-headed Gull		x					x
91	<i>Threskiornis melanocephalus</i>	Black-headed Ibis		x				x	
92	<i>Picus erythropygius</i>	Black-headed Woodpecker	x		x				
93	<i>Oriolus xanthonus</i>	Black-hooded Oriole	x			x			
94	<i>Hypothymis azurea</i>	Black-naped Monarch	x		x				
95	<i>Oriolus chinensis</i>	Black-naped Oriole		x	x				
96	<i>Sterna sumatrana</i>	Black-naped Tern	x						x
97	<i>Ephippiorhynchus asiaticus</i>	Black-necked Stork	x					x	
98	<i>Aerodramus maximus</i>	Black-nest Swiftlet	x		x				
99	<i>Zapornia bicolor</i>	Black-tailed Crake	x		x				
100	<i>Limosa limosa</i>	Black-tailed Godwit		x				x	
101	<i>Microhierax fringillarius</i>	Black-thighed Falconet	x		x				
102	<i>Stachyris nigricollis</i>	Black-throated Babbler	x		x				
103	<i>Garrulax chinensis</i>	Black-throated Laughingthrush	x		x				
104	<i>Paradoxornis nipalensis</i>	Black-throated Parrotbill	x		x				
105	<i>Aethopyga saturata</i>	Black-throated Sunbird	x		x				
106	<i>Aegithalos concinnus</i>	Black-throated Tit	x		x				
107	<i>Coracina melaschistos</i>	Black-winged Cuckooshrike	x		x				
108	<i>Hemipus hirundinaceus</i>	Black-winged Flycatcher-shrike	x		x				
109	<i>Elanus caeruleus</i>	Black-winged Kite	x				x		



110	<i>Himantopus himantopus</i>	Black-winged Stilt	x					x	
111	<i>Psittacula roseata</i>	Blossom-headed Parakeet	x		x				
112	<i>Urocissa erythrorhyncha</i>	Blue Magpie	x		x				
113	<i>Sitta azurea</i>	Blue Nuthatch	x		x				
114	<i>Pitta cyanea</i>	Blue Pitta	x		x				
115	<i>Monticola solitarius</i>	Blue Rock-thrush	x						x
116	<i>Myophonus caeruleus</i>	Blue Whistling-thrush	x		x				
117	<i>Nyctyornis athertoni</i>	Blue-bearded Bee-eater	x		x				
118	<i>Hierococcyx fugax</i>	Blue-breasted Quail	x			x			
119	<i>Loriculus galgulus</i>	Blue-crowned Hanging-parrot	x		x				
120	<i>Megalaima australis</i>	Blue-eared Barbet	x		x				
121	<i>Psittinus cyanurus</i>	Blue-eared Kingfisher	x		x				
122	<i>Megalaima asiatica</i>	Blue-fronted Redstart	x		x				
123	<i>Cinclidium frontale</i>	Blue-fronted Robin	x		x				
124	<i>Psittinus cyanurus</i>	Blue-rumped Parrot	x		x				
125	<i>Pitta soror</i>	Blue-rumped Pitta	x		x				
126	<i>Merops philippinus</i>	Blue-tailed Bee-eater	x		x				
127	<i>Luscinia svecica</i>	Bluethroat		x					x
128	<i>Megalaima asiatica</i>	Blue-throated Barbet	x		x				
129	<i>Merops viridis</i>	Blue-throated Bee-eater	x		x				
130	<i>Cyornis rubeculoides</i>	Blue-throated Flycatcher	x		x				
131	<i>Chloropsis cochinchinensis</i>	Blue-winged Leafbird	x		x				
132	<i>Minla cyanouoptera</i>	Blue-winged Minla	x		x				
133	<i>Pitta moluccensis</i>	Blue-winged Pitta	x		x				
134	<i>Acrocephalus concinens</i>	Blunt-winged Warbler		x					x
135	<i>Nisaetus alboniger</i>	Blyth's Hawk-eagle	x		x				
136	<i>Alcedo hercules</i>	Blyth's Kingfisher	x						x
137	<i>Merops viridis</i>	Bornean Crested Fireback	x		x				
138	<i>Haliastur indus</i>	Brahminy Kite	x						x
139	<i>Onychoprion anaethetus</i>	Bridled Tern	x						x
140	<i>Calidris falcinellus</i>	Broad-billed Sandpiper		x					x
141	<i>Dicrurus aeneus</i>	Bronzed Drongo	x		x				
142	<i>Metopidius indicus</i>	Bronze-winged Jacana	x						x
143	<i>Calorhamphus fuliginosus</i>	Brown Barbet	x		x				
144	<i>Ninox scutulata</i>	Brown Boobook	x		x				
145	<i>Sula leucogaster</i>	Brown Booby	x						x
146	<i>Bradypterus luteoventris</i>	Brown Bush-warbler	x			x			
147	<i>Cinclus pallasii</i>	Brown Dipper	x		x				
148	<i>Ketupa zeylonensis</i>	Brown Fish-owl	x		x				

149	<i>Alcippe brunneicauda</i>	Brown Fulvetta	x		x				
150	<i>Prinia polychroa</i>	Brown Prinia	x		x				
151	<i>Lanius cristatus</i>	Brown Shrike		x			x		
152	<i>Strix leptogrammica</i>	Brown Wood-owl	x		x				
153	<i>Hirundapus giganteus</i>	Brown-backed Needletail	x		x				
154	<i>Pycnonotus xanthorrhous</i>	Brown-breasted Bulbul	x		x				
155	<i>Muscicapa muttui</i>	Brown-breasted Flycatcher		x	x				
156	<i>Alcippe poioicephala</i>	Brown-cheeked Fulvetta	x		x				
157	<i>Larus brunnicephalus</i>	Brown-headed Gull		x					x
158	<i>Pericrocotus cantonensis</i>	Brown-rumped Minivet		x	x				
159	<i>Pelargopsis amauroptera</i>	Brown-winged Kingfisher	x		x				
160	<i>Phylloscopus pulcher</i>	Buff-barred Warbler		x	x				
161	<i>Trichastoma tickelli</i>	Buff-breasted babbler	x		x				
162	<i>Stachyris ambigua</i>	Buff-chested Babbler	x		x				
163	<i>Meiglyptes tukki</i>	Buff-necked Woodpecker	x		x				
164	<i>Chrysocolaptes lucidus</i>	Buff-spotted Flameback	x		x				
165	<i>Phylloscopus subaffinis</i>	Buff-throated Warbler	x				x		
166	<i>Iole olivacea</i>	Buff-vented Bulbul	x		x				
167	<i>Ketupa ketupu</i>	Buffy Fish-owl	x		x				
168	<i>Bulweria bulwerii</i>	Bulwer's Petrel		x					x
169	<i>Lanius collurioides</i>	Burmese Shrike	x		x				
170	<i>Yuhina humilis</i>	Burmese Yuhina	x		x				
171	<i>Anorrhinus galeritus</i>	Bushy-crested Hornbill	x		x				
172	<i>Bubulcus ibis</i>	Cattle Egret	x						x
173	<i>Nisaetus cirrhatus</i>	Changeable Hawk-eagle	x		x				
174	<i>Picus mentalis</i>	Checker-throated Woodpecker	x		x				
175	<i>Emberiza rutila</i>	Chestnut Bunting		x	x				
176	<i>Lonchura atricapilla</i>	Chestnut Munia	x		x				
177	<i>Turdus rubrocanus</i>	Chestnut Thrush	x		x				
178	<i>Pomatorhinus montanus</i>	Chestnut-backed Scimitar-babbler	x		x				
179	<i>Phaenicophaeus sumatranus</i>	Chestnut-bellied Malkoha	x		x				
180	<i>Sitta castanea</i>	Chestnut-bellied Nuthatch	x				x		
181	<i>Monticola rufiventris</i>	Chestnut-bellied Rock-thrush		x	x				
182	<i>Phaenicophaeus curvirostris</i>	Chestnut-breasted Malkoha	x		x				
183	<i>Timalia pileata</i>	Chestnut-capped Babbler	x		x				
184	<i>Garrulax mitratus</i>	Chestnut-capped Laughingthrush	x		x				
185	<i>Zoothera interpres</i>	Chestnut-capped Thrush	x		x				
186	<i>Cettia major</i>	Chestnut-crowned Bush-warbler		x			x		
187	<i>Seicercus castaniceps</i>	Chestnut-crowned Warbler	x		x				

188	<i>Emberiza fucata</i>	Chestnut-eared Bunting		x				x	
189	<i>Zosterops erythropleurus</i>	Chestnut-flanked White-eye		x	x				
190	<i>Pteruthius aenobarbus</i>	Chestnut-fronted Shrike-babbler	x		x				
191	<i>Merops leschenaulti</i>	Chestnut-headed Bee-eater	x		x				
192	<i>Arborophila cambodiana</i>	Chestnut-headed Partridge	x		x				
193	<i>Tesia castaneocoronata</i>	Chestnut-headed Tesia	x		x				
194	<i>Enicurus ruficapillus</i>	Chestnut-naped Forktail	x		x				
195	<i>Arborophila charltonii</i>	Chestnut-necklaced Partridge	x		x				
196	<i>Stachyris maculata</i>	Chestnut-rumped Babbler	x		x				
197	<i>Minla strigula</i>	Chestnut-tailed Minla	x		x				
198	<i>Sturnus malabaricus</i>	Chestnut-tailed Starling	x				x		
199	<i>Sitta nagaensis</i>	Chestnut-vented Nuthatch	x		x				
200	<i>Stachyris erythroptera</i>	Chestnut-winged Babbler	x		x				
201	<i>Clamator coromandus</i>	Chestnut-winged Cuckoo		x	x				
202	<i>Bradypterus tacsanowskii</i>	Chinese Bush-warbler		x				x	
203	<i>Egretta eulophotes</i>	Chinese Egret		x					x
204	<i>Francolinus pintadeanus</i>	Chinese Francolin	x		x				
205	<i>Phylloscopus yunnanensis</i>	Chinese Leaf-warbler		x	x				
206	<i>Ardeola bacchus</i>	Chinese Pond-heron		x				x	
207	<i>Accipiter soloensis</i>	Chinese Sparrowhawk		x			x		
208	<i>Anas zonorhyncha</i>	Chinese Spot-billed Duck		x				x	
209	<i>Fregata andrewsi</i>	Christmas Frigatebird	x						x
210	<i>Ixobrychus cinnamomeus</i>	Cinnamon Bittern	x					x	
211	<i>Treron fulvicollis</i>	Cinnamon-headed Green-pigeon	x		x				
212	<i>Harpactes orrhophaeus</i>	Cinnamon-rumped Trogon	x		x				
213	<i>Motacilla citreola</i>	Citrine Wagtail		x				x	
214	<i>Acrocephalus stentoreus</i>	Clamorous Reed-warbler		x				x	
215	<i>Gampsorhynchus torquatus</i>	Collared Babbler	x		x				
216	<i>Microhierax caerulescens</i>	Collared Falconet	x		x				
217	<i>Mycerobas affinis</i>	Collared Grosbeak	x		x				
218	<i>Todiramphus chloris</i>	Collared Kingfisher	x						x
219	<i>Glaucidium brodiei</i>	Collared Owlet	x		x				
220	<i>Otus bakkamoena</i>	Collared Scops-owl	x				x		
221	<i>Tyto alba</i>	Common Barn-owl	x		x				
222	<i>Turnix sylvaticus</i>	Common Buttonquail	x					x	
223	<i>Fulica atra</i>	Common Coot		x				x	
224	<i>Grus grus</i>	Common Crane		x				x	
225	<i>Dinopium javanense</i>	Common Flameback	x		x				
226	<i>Tringa nebularia</i>	Common Greenshank		x					x

227	<i>Sterna nilotica</i>	Gull-billed Tern		x					x
228	<i>Upupa epops</i>	Common Hoopoe	x				x		
229	<i>Aegithina tiphia</i>	Common Iora	x		x				
230	<i>Falco tinnunculus</i>	Common Kestrel		x			x		
231	<i>Alcedo atthis</i>	Common Kingfisher	x		x				
232	<i>Gallinula chloropus</i>	Common Moorhen	x					x	
233	<i>Acridotheres tristis</i>	Common Myna	x		x				
234	<i>Aythya ferina</i>	Common Pochard		x				x	
235	<i>Carpodacus erythrinus</i>	Common Rosefinch		x			x		
236	<i>Actitis hypoleucos</i>	Common Sandpiper		x				x	
237	<i>Gallinago gallinago</i>	Common Snipe		x				x	
238	<i>Saxicola torquatus</i>	Common Stonechat		x	x				
239	<i>Orthotomus sutorius</i>	Common Tailorbird	x		x				
240	<i>Anas crecca</i>	Common Teal		x				x	
241	<i>Sterna hirundo</i>	Common Tern		x					x
242	<i>Tephrodornis pondicerianus</i>	Common Woodshrike	x		x				
243	<i>Psilopogon haemacephalus</i>	Coppersmith Barbet	x				x		
244	<i>Nectarinia calcostetha</i>	Copper-throated Sunbird	x		x				
245	<i>Carpococcyx renauldi</i>	Coral-billed Ground-cuckoo	x		x				
246	<i>Pomatorhinus ferruginosus</i>	Coral-billed Scimitar-babbler	x		x				
247	<i>Nettapus coromandelianus</i>	Cotton Pygmy-goose	x					x	
248	<i>Dromas ardeola</i>	Crab-plover		x					x
249	<i>Pycnonotus simplex</i>	Cream-vented Bulbul	x		x				
250	<i>Melophus lathamii</i>	Crested Bunting	x			x			
251	<i>Spizixos canifrons</i>	Crested Finchbill	x		x				
252	<i>Accipiter trivirgatus</i>	Crested Goshawk	x		x				
253	<i>Platylophus galericulatus</i>	Crested Jay	x		x				
254	<i>Megaceryle lugubris</i>	Crested Kingfisher	x		x				
255	<i>Rollulus rouloul</i>	Crested Partridge	x		x				
256	<i>Spilornis cheela</i>	Crested Serpent-eagle	x		x				
257	<i>Hemiprocne coronata</i>	Crested Treeswift	x		x				
258	<i>Aethopyga siparaja</i>	Crimson Sunbird	x		x				
259	<i>Prionochilus percussus</i>	Crimson-breasted Flowerpecker	x		x				
260	<i>Picoides cathpharius</i>	Crimson-breasted Woodpecker	x		x				
261	<i>Picus puniceus</i>	Crimson-winged Woodpecker	x		x				
262	<i>Dicrurus annectans</i>	Crow-billed Drongo		x	x				
263	<i>Calidris ferruginea</i>	Curlew Sandpiper		x					x
264	<i>Heterophasia melanoleuca</i>	Dark-backed Sibia	x		x				
265	<i>Orthotomus atrogularis</i>	Dark-necked Tailorbird	x		x				

266	<i>Apus acuticauda</i>	Dark-rumped Swift		x	x				
267	<i>Muscicapa sibirica</i>	Dark-sided Flycatcher		x	x				
268	<i>Zoothera marginata</i>	Dark-sided Thrush	x		x				
269	<i>Oriolus xanthonotus</i>	Dark-throated Oriole	x		x				
270	<i>Phoenicurus aureoreus</i>	Daurian Redstart		x	x				
271	<i>Bradypterus davidi</i>	David's Bush-warbler		x		x			
272	<i>Phylloscopus davisoni</i>	Davison's Leaf-warbler	x		x				
273	<i>Harpactes diardii</i>	Diard's Trogon	x		x				
274	<i>Corydon sumatranus</i>	Dusky Broadbill	x		x				
275	<i>Hirundo concolor</i>	Dusky Crag-martin	x		x				
276	<i>Bubo coromandus</i>	Dusky Eagle-owl	x		x				
277	<i>Turdus naumanni</i>	Dusky Thrush		x	x				
278	<i>Phylloscopus fuscatus</i>	Dusky Warbler		x			x		
279	<i>Pitta phayrei</i>	Eared Pitta	x		x				
280	<i>Phylloscopus coronatus</i>	Eastern Crowned Warbler		x	x				
281	<i>Tyto longimembris</i>	Eastern Grass-owl	x					x	
282	<i>Aquila heliaca</i>	Eastern Imperial Eagle		x					
283	<i>Circus spilonotus</i>	Eastern Marsh-harrier		x				x	
284	<i>Stigmatopelia chinensis</i>	Eastern Spotted Dove	x		x				
285	<i>Botaurus stellaris</i>	Eurasian Bittern		x				x	
286	<i>Buteo buteo</i>	Eurasian Buzzard		x	x				
287	<i>Numenius arquata</i>	Eurasian Curlew		x					x
288	<i>Falco subbuteo</i>	Eurasian Hobby		x		x			
289	<i>Garrulus glandarius</i>	Eurasian Jay	x		x				
290	<i>Zoothera dauma</i>	Eurasian Scaly Thrush		x	x				
291	<i>Accipiter nisus</i>	Eurasian Sparrowhawk		x		x			
292	<i>Burhinus oedicephalus</i>	Eurasian Thick-knee		x				x	
293	<i>Passer montanus</i>	Eurasian Tree Sparrow	x				x		
294	<i>Mareca penelope</i>	Eurasian Wigeon		x				x	
295	<i>Scolopax rusticola</i>	Eurasian Woodcock		x	x				
296	<i>Jynx torquilla</i>	Eurasian Wryneck		x			x		
297	<i>Zosterops everetti</i>	Everett's White-eye	x		x				
298	<i>Turdus obscurus</i>	Eyebrowed Thrush		x	x				
299	<i>Napothera epilepidota</i>	Eyebrowed Wren-babbler	x		x				
300	<i>Mareca falcata</i>	Falcated Duck		x				x	
301	<i>Trichastoma bicolor</i>	Ferruginous Babbler	x		x				
302	<i>Aythya nyroca</i>	Ferruginous Duck		x				x	
303	<i>Muscicapa ferruginea</i>	Ferruginous Flycatcher		x	x				
304	<i>Caloperdix ocellus</i>	Ferruginous Partridge	x		x				

305	<i>Pericrocotus igneus</i>	Fiery Minivet	x		x				
306	<i>Alophoixus finschii</i>	Finsch's Bulbul	x		x				
307	<i>Dicaeum ignipectus</i>	Fire-breasted Flowerpecker	x		x				
308	<i>Cephalopyrus flammiceps</i>	Fire-capped Tit		x	x				
309	<i>Psilopogon pyrolophus</i>	Fire-tufted Barbet	x		x				
310	<i>Pycnonotus flavescens</i>	Flavescent Bulbul	x		x				
311	<i>Macronous ptilosus</i>	Fluffy-backed Tit-babbler	x		x				
312	<i>Dendronanthus indicus</i>	Forest Wagtail		x	x				
313	<i>Niltava davidi</i>	Fujian Niltava	x		x				
314	<i>Dendrocopos macei</i>	Fulvous-breasted Woodpecker	x			x			
315	<i>Rhinomyias olivaceus</i>	Fulvous-chested Jungle-flycatcher	x		x				
316	<i>Spatula querquedula</i>	Garganey		x				x	
317	<i>Pitta granatina</i>	Garnet Pitta	x		x				
318	<i>Collocalia germani</i>	Germain's swiftlet	x						x
319	<i>Thaumatibis gigantea</i>	Giant Ibis	x					x	
320	<i>Sitta magna</i>	Giant Nuthatch	x		x				
321	<i>Pitta caerulea</i>	Giant Pitta	x		x				
322	<i>Plegadis falcinellus</i>	Glossy Ibis		x				x	
323	<i>Collocalia esculenta</i>	Glossy Swiftlet	x		x				
324	<i>Stachyris chrysaea</i>	Golden Babbler	x		x				
325	<i>Tarsiger chrysaeus</i>	Golden Bush-robin		x	x				
326	<i>Gerygone sulphurea</i>	Golden-bellied Gerygone	x						x
327	<i>Ampeliceps coronatus</i>	Golden-crested Myna	x		x				
328	<i>Chloropsis aurifrons</i>	Golden-fronted Leafbird	x		x				
329	<i>Cisticola exilis</i>	Golden-headed Cisticola	x		x				
330	<i>Megalaima franklinii</i>	Golden-throated Barbet	x		x				
331	<i>Psilopogon chrysopogon</i>	Gold-whiskered Barbet	x		x				
332	<i>Batrachostomus stellatus</i>	Gould's Frogmouth	x		x				
333	<i>Aethopyga gouldiae</i>	Gould's Sunbird		x	x				
334	<i>Argusianus argus</i>	Great Argus	x		x				
335	<i>Psilopogon virens</i>	Great Barbet	x		x				
336	<i>Phalacrocorax carbo</i>	Great Cormorant		x				x	
337	<i>Eurostopodus macrotis</i>	Great eared nightjar	x				x		
338	<i>Lyncornis macrotis</i>	Great Eared-nightjar	x		x				
339	<i>Fregata minor</i>	Great Frigatebird	x						x
340	<i>Buceros bicornis</i>	Great Hornbill	x		x				
341	<i>Aegithina lafresnayei</i>	Great Iora	x		x				
342	<i>Calidris tenuirostris</i>	Great Knot		x					x
343	<i>Acrocephalus arundinaceus</i>	Great Reed-warbler		x				x	

344	<i>Mulleripicus pulverulentus</i>	Great Slaty Woodpecker	x		x				
345	<i>Esacus recurvirostris</i>	Great Thick-knee	x					x	
346	<i>Parus major</i>	Great Tit	x		x				
347	<i>Ardea alba</i>	Great White Egret	x					x	
348	<i>Ardea sumatrana</i>	Great-billed Heron	x						x
349	<i>Leptoptilos dubius</i>	Greater Adjutant		x				x	
350	<i>Centropus sinensis</i>	Greater Coucal	x		x				
351	<i>Thalasseus bergii</i>	Greater Crested Tern	x						x
352	<i>Chloropsis sonnerati</i>	Greater Green Leafbird	x		x				
353	<i>Garrulax pectoralis</i>	Greater Necklaced Laughingthrush	x		x				
354	<i>Rostratula benghalensis</i>	Greater Painted-snipe	x					x	
355	<i>Dicrurus paradiseus</i>	Greater Racket-tailed Drongo	x		x				
356	<i>Charadrius leschenaultii</i>	Greater Sandplover		x					x
357	<i>Clanga clanga</i>	Greater Spotted Eagle		x				x	
358	<i>Chrysophlegma flavinucha</i>	Greater Yellownappe	x		x				
359	<i>Cochoa viridis</i>	Green Cochoa	x		x				
360	<i>Ducula aenea</i>	Green Imperial-pigeon	x		x				
361	<i>Aegithina viridissima</i>	Green Iora	x		x				
362	<i>Cissa chinensis</i>	Green Magpie	x		x				
363	<i>Pavo muticus</i>	Green Peafowl	x		x				
364	<i>Tringa ochropus</i>	Green Sandpiper		x				x	
365	<i>Butorides striata</i>	Green-backed Heron	x		x				
366	<i>Phaenicophaeus tristis</i>	Green-billed Malkoha	x		x				
367	<i>Psilopogon faiostriatus</i>	Green-eared Barbet	x		x				
368	<i>Phylloscopus trochiloides</i>	Greenish Warbler		x	x				
369	<i>Arborophila chloropus</i>	Green-legged Partridge	x		x				
370	<i>Aethopyga nipalensis</i>	Green-tailed Sunbird	x		x				
371	<i>Saxicola ferreus</i>	Grey Bushchat	x		x				
372	<i>Ardea cinerea</i>	Grey Heron		x				x	
373	<i>Caprimulgus indicus</i>	Grey Nightjar	x		x				
374	<i>Polyplectron bicalcaratum</i>	Grey Peacock-pheasant	x		x				
375	<i>Pluvialis squatarola</i>	Grey Plover		x					x
376	<i>Dendrocitta formosae</i>	Grey Treepie	x		x				
377	<i>Motacilla cinerea</i>	Grey Wagtail		x	x				
378	<i>Lanius tephronotus</i>	Grey-backed Shrike		x				x	
379	<i>Pycnonotus cyaniventris</i>	Grey-bellied Bulbul	x		x				
380	<i>Tesia cyaniventer</i>	Grey-bellied Tesia	x		x				
381	<i>Prinia hodgsonii</i>	Grey-breasted Prinia	x					x	
382	<i>Arachnothera affinis</i>	Grey-breasted Spiderhunter	x		x				

383	<i>Chalcophaps indica</i>	Grey-capped Emerald Dove	x		x				
384	<i>Picoides canicapillus</i>	Grey-capped Woodpecker	x		x				
385	<i>Alophoixus bres</i>	Grey-cheeked Bulbul	x		x				
386	<i>Alcippe morrisonia</i>	Grey-cheeked Fulvetta	x		x				
387	<i>Seicercus poliogenys</i>	Grey-cheeked Warbler	x		x				
388	<i>Rhinomyias umbratilis</i>	Grey-chested Jungle-flycatcher	x		x				
389	<i>Pericrocotus solaris</i>	Grey-chinned Minivet	x		x				
390	<i>Seicercus tephrocephalus</i>	Grey-crowned Warbler		x	x				
391	<i>Iole propinqua</i>	Grey-eyed Bulbul	x		x				
392	<i>Macronous kelleyi</i>	Grey-faced Tit-babbler	x		x				
393	<i>Picus canus</i>	Grey-faced Woodpecker	x		x				
394	<i>Stachyris poliocephala</i>	Grey-headed Babbler	x		x				
395	<i>Pyrrhula erythaca</i>	Grey-headed Bullfinch	x			x			
396	<i>Culicicapa ceylonensis</i>	Grey-headed Canary-flycatcher	x		x				
397	<i>Icthyophaga ichthyaetus</i>	Grey-headed Fish-eagle	x		x				
398	<i>Vanellus cinereus</i>	Grey-headed Lapwing		x				x	
399	<i>Psittacula finschii</i>	Grey-headed Parakeet	x		x				
400	<i>Paradoxornis gularis</i>	Grey-headed Parrotbill	x		x				
401	<i>Hemiprocne longipennis</i>	Grey-rumped Treeswift	x		x				
402	<i>Turdus feae</i>	Grey-sided Thrush		x	x				
403	<i>Tringa brevipes</i>	Grey-tailed Tattler		x					x
404	<i>Stachyris nigriceps</i>	Grey-throated Babbler	x		x				
405	<i>Turdus boulboul</i>	Grey-winged Blackbird	x		x				
406	<i>Pitta gurneyi</i>	Gurney's Pitta	x		x				
407	<i>Cyornis hainanus</i>	Hainan Blue-flycatcher	x		x				
408	<i>Dicrurus hottentottus</i>	Hair-crested Drongo	x		x				
409	<i>Tricholestes criniger</i>	Hairy-backed Bulbul	x		x				
410	<i>Hemicircus canente</i>	Heart-spotted Woodpecker	x		x				
411	<i>Rhinoplax vigil</i>	Helmeted Hornbill	x		x				
412	<i>Circus cyaneus</i>	Hen Harrier		x				x	
413	<i>Cyornis banyumas</i>	Hill Blue-flycatcher	x		x				
414	<i>Gracula religiosa</i>	Hill Myna	x		x				
415	<i>Prinia atrogularis</i>	Hill Prinia	x		x				
416	<i>Cutia nipalensis</i>	Himalayan Cutia	x		x				
417	<i>Collocalia brevirostris</i>	Himalayan Swiftlet	x		x				
418	<i>Batrachostomus hodgsoni</i>	Hodgson's Frogmouth	x		x				
419	<i>Pitta sordida</i>	Hooded Pitta	x		x				
420	<i>Malacocincla sepiaria</i>	Horsfield's Babbler	x		x				
421	<i>Corvus splendens</i>	House Crow	x			x			



422	<i>Apus nipalensis</i>	House Swift	x		x				
423	<i>Phylloscopus humei</i>	Hume's Leaf-warbler		x	x				
424	<i>Phalacrocorax fuscicollis</i>	Indian Cormorant	x					x	
425	<i>Cuculus micropterus</i>	Indian Cuckoo		x	x				
426	<i>Caprimulgus asiaticus</i>	Indian Nightjar	x				x		
427	<i>Coracias benghalensis</i>	Indian Roller	x		x				
428	<i>Mirafra erythrocephala</i>	Indochinese Bushlark	x		x				
429	<i>Coracina polioptera</i>	Indochinese Cuckooshrike	x		x				
430	<i>Yuhina torqueola</i>	Indochinese Yuhina	x		x				
431	<i>Phylloscopus inornatus</i>	Inornate Warbler		x	x				
432	<i>Ardea intermedia</i>	Intermediate egret	x					x	
433	<i>Lymnocyptes minimus</i>	Jack Snipe		x				x	
434	<i>Ramphiculus jambu</i>	Jambu Fruit-dove	x		x				
435	<i>Terpsiphone atrocaudata</i>	Japanese Paradise-flycatcher		x	x				
436	<i>Coturnix japonica</i>	Japanese Quail		x			x		
437	<i>Accipiter gularis</i>	Japanese Sparrowhawk		x	x				
438	<i>Zosterops japonicus</i>	Japanese White-eye		x	x				
439	<i>Alcedo euryzona</i>	Javan Blue-banded Kingfisher	x		x				
440	<i>Batrachostomus affinis</i>	Javan Frogmouth	x		x				
441	<i>Ardeola speciosa</i>	Javan Pond-heron	x					x	
442	<i>Aviceda jerdoni</i>	Jerdon's Baza	x		x				
443	<i>Saxicola jerdoni</i>	Jerdon's Bushchat	x		x				
444	<i>Corvus levaillantii</i>	Jungle Crow	x				x		
445	<i>Acridotheres fuscus</i>	Jungle Myna	x		x				
446	<i>Lophura leucomelanos</i>	Kalij Pheasant	x		x				
447	<i>Charadrius alexandrinus</i>	Kentish Plover		x					x
448	<i>Phylloscopus ogilviegranti</i>	Kloss's Leaf-warbler	x		x				
449	<i>Picus vittatus</i>	Laced Woodpecker	x		x				
450	<i>Locustella lanceolata</i>	Lanceolated Warbler		x	x				
451	<i>Cyornis magnirostris</i>	Large Blue-flycatcher		x	x				
452	<i>Coracina macei</i>	Large Cuckooshrike	x		x				
453	<i>Batrachostomus auritus</i>	Large Frogmouth	x		x				
454	<i>Treron capellei</i>	Large Green-pigeon	x		x				
455	<i>Hierococcyx sparverioides</i>	Large Hawk-cuckoo	x		x				
456	<i>Niltava grandis</i>	Large Niltava	x		x				
457	<i>Pomatorhinus hypoleucos</i>	Large Scimitar-babbler	x		x				
458	<i>Tephrodornis gularis</i>	Large Woodshrike	x		x				
459	<i>Turdinus macrodactylus</i>	Large Wren-babbler	x		x				
460	<i>Corvus macrorhynchos</i>	Large-billed Crow	x					x	

461	<i>Acrocephalus orinus</i>	Large-billed Reed-warbler		x				x	
462	<i>Caprimulgus macrurus</i>	Large-tailed Nightjar	x		x				
463	<i>Phylloscopus proregulus</i>	Lemon-rumped Warbler		x	x				
464	<i>Leptoptilos javanicus</i>	Lesser Adjutant	x		x				
465	<i>Centropus bengalensis</i>	Lesser Coucal	x		x				
466	<i>Thalasseus bengalensis</i>	Lesser Crested Tern		x					x
467	<i>Coracina fimbriata</i>	Lesser Cuckooshrike	x		x				
468	<i>Icthyophaga humilis</i>	Lesser Fish-eagle	x		x				
469	<i>Fregata ariel</i>	Lesser Frigatebird	x						x
470	<i>Chloropsis cyanopogon</i>	Lesser Green Leafbird	x		x				
471	<i>Garrulax monileger</i>	Lesser Necklaced Laughingthrush	x		x				
472	<i>Dicrurus remifer</i>	Lesser Racket-tailed Drongo	x		x				
473	<i>Charadrius mongolus</i>	Lesser Sandplover		x					x
474	<i>Brachypteryx leucophrys</i>	Lesser Shortwing	x		x				
475	<i>Dendrocygna javanica</i>	Lesser Whistling-duck	x					x	
476	<i>Picus chlorolophus</i>	Lesser Yellownape	x		x				
477	<i>Pycnonotus sinensis</i>	Light-vented Bulbul		x		x			
478	<i>Gypsophila crispifrons</i>	Limestone Wren-babbler	x		x				
479	<i>Psilopogon lineatus</i>	Lineated Barbet	x		x				
480	<i>Chrysococcyx minutillus</i>	Little Bronze-cuckoo	x		x				
481	<i>Emberiza pusilla</i>	Little Bunting		x		x			
482	<i>Microcarbo niger</i>	Little Cormorant	x					x	
483	<i>Macropygia ruficeps</i>	Little Cuckoo-dove	x		x				
484	<i>Egretta garzetta</i>	Little Egret	x					x	
485	<i>Tachybaptus ruficollis</i>	Little Grebe	x					x	
486	<i>Treron olax</i>	Little Green-pigeon		x	x				
487	<i>Ficedula westermanni</i>	Little Pied Flycatcher	x		x				
488	<i>Glareola lactea</i>	Little Pratincole	x					x	
489	<i>Charadrius dubius</i>	Little Ringed Plover		x				x	
490	<i>Arachnothera longirostra</i>	Little Spiderhunter	x		x				
491	<i>Sternula albifrons</i>	Little Tern	x						x
492	<i>Rhizothera longirostris</i>	Long-billed Partridge	x		x				
493	<i>Charadrius placidus</i>	Long-billed Plover		x				x	
494	<i>Arachnothera robusta</i>	Long-billed Spiderhunter	x		x				
495	<i>Psarisomus dalhousiae</i>	Long-tailed Broadbill	x		x				
496	<i>Pericrocotus ethologus</i>	Long-tailed Minivet	x		x				
497	<i>Lanius schach</i>	Long-tailed Shrike	x		x				
498	<i>Heterophasia picaoides</i>	Long-tailed Sibia	x		x				
499	<i>Zoothera dixonii</i>	Long-tailed Thrush	x		x				

500	<i>Calidris subminuta</i>	Long-toed Stint		x					x	
501	<i>Lophura erythrophthalma</i>	Malay Crestless Fireback	x		x					
502	<i>Lyncornis temminckii</i>	Malay Eared-nightjar	x		x					
503	<i>Cuculus fugax</i>	Malay Hawk-cuckoo	x		x					
504	<i>Indicator archipelagicus</i>	Malay Honeyguide	x		x					
505	<i>Gorsachius melanolophus</i>	Malay Night-heron	x						x	
506	<i>Polyplectron malacense</i>	Malay Peacock-pheasant	x		x					
507	<i>Charadrius peronii</i>	Malay Plover	x							x
508	<i>Pitta irena</i>	Malayan Banded Pitta	x		x					
509	<i>Garrulax peninsulæ</i>	Malayan Laughingthrush	x		x					
510	<i>Cyornis turcosus</i>	Malaysian Blue-flycatcher	x		x					
511	<i>Cettia canturians</i>	Manchurian Bush-warbler		x			x			
512	<i>Acrocephalus tangorum</i>	Manchurian Reed-warbler		x					x	
513	<i>Pitta megarhyncha</i>	Mangrove Pitta	x		x					
514	<i>Pachycephala grisola</i>	Mangrove Whistler	x							x
515	<i>Certhia manipurensis</i>	Manipur Treecreeper	x		x					
516	<i>Turdinus marmorata</i>	Marbled Wren-babbler	x		x					
517	<i>Oriolus traillii</i>	Maroon Oriole	x		x					
518	<i>Blythipicus rubiginosus</i>	Maroon Woodpecker	x		x					
519	<i>Philentoma velata</i>	Maroon-breasted Philentoma	x		x					
520	<i>Tringa stagnatilis</i>	Marsh Sandpiper		x						x
521	<i>Seicercus omeiensis</i>	Martens's Warbler		x	x					
522	<i>Heliopais personatus</i>	Masked Finfoot	x		x					
523	<i>Bambusicola fytchii</i>	Mountain Bamboo-partridge	x		x					
524	<i>Hypsipetes mcclllandii</i>	Mountain Bulbul	x		x					
525	<i>Alcippe peracensis</i>	Mountain Fulvetta	x		x					
526	<i>Ducula badia</i>	Mountain Imperial-pigeon	x		x					
527	<i>Phylloscopus trivirgatus</i>	Mountain Leaf-warbler	x		x					
528	<i>Otus spilocephalus</i>	Mountain Scops-owl	x		x					
529	<i>Orthotomus cuculatus</i>	Mountain Tailorbird	x		x					
530	<i>Malacopteron magnirostre</i>	Moustached Babbler	x		x					
531	<i>Psilopogon incognitus</i>	Moustached Barbet	x		x					
532	<i>Hierococcyx vagans</i>	Moustached Hawk-cuckoo	x		x					
533	<i>Syrmaicus humiae</i>	Mrs Hume's Pheasant	x		x					
534	<i>Ficedula mugimaki</i>	Mugimaki Flycatcher		x	x					
535	<i>Ficedula narcissina</i>	Narcissus Flycatcher		x	x					
536	<i>Accipiter gentilis</i>	Northern Goshawk		x	x					
537	<i>Delichon urbicum</i>	Northern House-martin		x			x			
538	<i>Vanellus vanellus</i>	Northern Lapwing		x					x	

539	<i>Anas acuta</i>	Northern Pintail		x				x	
540	<i>Spatula clypeata</i>	Northern Shoveler		x				x	
541	<i>Alophoixus ochraceus</i>	Ochraceous Bulbul	x		x				
542	<i>Iole virescens</i>	Olive Bulbul	x		x				
543	<i>Anthus hodgsoni</i>	Olive-backed Pipit		x			x		
544	<i>Nectarinia jugularis</i>	Olive-backed Sunbird	x		x				
545	<i>Dinopium rafflesii</i>	Olive-backed Woodpecker	x		x				
546	<i>Pycnonotus plumosus</i>	Olive-winged Bulbul	x		x				
547	<i>Chrysocolaptes validus</i>	Orange-backed Woodpecker	x		x				
548	<i>Dicaeum trigonostigma</i>	Orange-bellied Flowerpecker	x		x				
549	<i>Chloropsis hardwickii</i>	Orange-bellied Leafbird	x		x				
550	<i>Treron bicinctus</i>	Orange-breasted Green-pigeon	x		x				
551	<i>Harpactes oreskios</i>	Orange-breasted Trogon	x		x				
552	<i>Tarsiger cyanurus</i>	Orange-flanked Bush-robin		x	x				
553	<i>Zoothera citrina</i>	Orange-headed Thrush		x	x				
554	<i>Phodilus badius</i>	Oriental Bay-owl	x		x				
555	<i>Cuculus saturatus</i>	Oriental Cuckoo		x			x		
556	<i>Anhinga melanogaster</i>	Oriental Darter	x					x	
557	<i>Eurystomus orientalis</i>	Oriental Dollarbird	x		x				
558	<i>Falco severus</i>	Oriental Hobby		x	x				
559	<i>Pernis ptilorhynchus</i>	Oriental Honey-buzzard	x		x				
560	<i>Copsychus saularis</i>	Oriental Magpie-robin	x				x		
561	<i>Anthracoceros albirostris</i>	Oriental Pied Hornbill	x		x				
562	<i>Glareola maldivarum</i>	Oriental Pratincole	x					x	
563	<i>Otus sunia</i>	Oriental Scops-owl		x	x				
564	<i>Alauda gulgula</i>	Oriental Skylark		x	x				
565	<i>Streptopelia orientalis</i>	Oriental Turtle-dove	x		x				
566	<i>Zosterops palpebrosus</i>	Oriental White-eye	x		x				
567	<i>Pandion haliaetus</i>	Osprey		x					x
568	<i>Pluvialis fulva</i>	Pacific Golden Plover		x				x	
569	<i>Egretta sacra</i>	Pacific Reef-egret	x						x
570	<i>Hirundo tahitica</i>	Pacific Swallow	x						x
571	<i>Apus pacificus</i>	Pacific Swift		x	x				
572	<i>Anthus rufulus</i>	Paddyfield Pipit	x				x		
573	<i>Mycteria leucocephala</i>	Painted Stork		x				x	
574	<i>Cyornis unicolor</i>	Pale Blue-flycatcher	x		x				
575	<i>Paradoxornis atrosuperciliaris</i>	Pale-billed Parrotbill	x				x		
576	<i>Columba punicea</i>	Pale-capped Pigeon	x		x				
577	<i>Cettia pallidipes</i>	Pale-footed Bush-warbler	x		x				

578	<i>Gecinulus grantia</i>	Pale-headed Woodpecker	x		x				
579	<i>Phylloscopus tenellipes</i>	Pale-legged Leaf-warbler		x	x				
580	<i>Locustella certhiola</i>	Pallas's Grasshopper-warbler		x				x	
581	<i>Larus ichthyaetus</i>	Pallas's Gull		x					x
582	<i>Falco peregrinus</i>	Peregrine Falcon	x		x				
583	<i>Hydrophasianus chirurgus</i>	Pheasant-tailed Jacana	x					x	
584	<i>Saxicola caprata</i>	Pied Bushchat	x			x			
585	<i>Rhipidura javanica</i>	Pied Fantail	x			x			
586	<i>Circus melanoleucos</i>	Pied Harrier		x				x	
587	<i>Ducula bicolor</i>	Pied Imperial-pigeon	x						x
588	<i>Ceryle rudis</i>	Pied Kingfisher	x		x				
589	<i>Lalage nigra</i>	Pied Triller	x		x				
590	<i>Treron vernans</i>	Pink-necked Green-pigeon	x		x				
591	<i>Macronous gularis</i>	Pin-striped Tit-babbler	x		x				
592	<i>Gallinago stenura</i>	Pintail Snipe		x				x	
593	<i>Treron apicauda</i>	Pin-tailed Green-pigeon		x	x				
594	<i>Erythrura prasina</i>	Pin-tailed Parrotfinch	x			x			
595	<i>Dicaeum concolor</i>	Plain Flowerpecker	x		x				
596	<i>Riparia paludicola</i>	Plain Martin	x		x				
597	<i>Prinia inornata</i>	Plain Prinia	x					x	
598	<i>Antheptes simplex</i>	Plain Sunbird	x		x				
599	<i>Passer flaveolus</i>	Plain-backed Sparrow	x		x				
600	<i>Rhyticeros subruficollis</i>	Plain-pouched Hornbill	x		x				
601	<i>Antheptes malacensis</i>	Plain-throated Sunbird	x		x				
602	<i>Cacomantis merulinus</i>	Plaintive Cuckoo		x	x				
603	<i>Rhyacornis fuliginosa</i>	Plumbeous Water-redstart	x			x			
604	<i>Stercorarius pomarinus</i>	Pomarine Jaeger		x					x
605	<i>Pycnonotus eutilotus</i>	Puff-backed Bulbul	x		x				
606	<i>Pellorneum ruficeps</i>	Puff-throated Babbler	x		x				
607	<i>Alophoixus pallidus</i>	Puff-throated Bulbul	x		x				
608	<i>Cochoa purpurea</i>	Purple Cochoa	x		x				
609	<i>Ardea purpurea</i>	Purple Heron		x				x	
610	<i>Nectarinia asiatica</i>	Purple Sunbird	x		x				
611	<i>Porphyrio porphyrio</i>	Purple Swampphen	x					x	
612	<i>Sturnus sturninus</i>	Purple-backed Starling		x		x			
613	<i>Hypogramma hypogrammicum</i>	Purple-naped Sunbird	x		x				
614	<i>Nectarinia sperata</i>	Purple-throated Sunbird	x		x				
615	<i>Muscicapella hodgsoni</i>	Pygmy Blue-flycatcher	x		x				
616	<i>Pnoepyga pusilla</i>	Pygmy Wren-babbler	x		x				

617	<i>Crypsirina temia</i>	Racket-tailed Treepie	x			x			
618	<i>Phylloscopus schwarzi</i>	Radde's Warbler		x	x				
619	<i>Rhinorhiza chlorophaea</i>	Raffles's Malkoha	x		x				
620	<i>Eupetes macrocerus</i>	Rail-babbler	x		x				
621	<i>Coturnix coromandelica</i>	Rain Quail	x		x				
622	<i>Temnurus temnurus</i>	Ratchet-tailed Treepie	x		x				
623	<i>Amandava amandava</i>	Red Avadavat	x		x				
624	<i>Gallus gallus</i>	Red Junglefowl	x		x				
625	<i>Streptopelia tranquebarica</i>	Red Turtle-dove	x		x				
626	<i>Nyctornis amictus</i>	Red-bearded Bee-eater	x		x				
627	<i>Zanclostomus javanicus</i>	Red-billed Malkoha	x		x				
628	<i>Pomatorhinus ochraceiceps</i>	Red-billed Scimitar-babbler	x		x				
629	<i>Psittacula alexandri</i>	Red-breasted Parakeet	x		x				
630	<i>Picus rabieri</i>	Red-collared Woodpecker	x		x				
631	<i>Hemicircus concretus</i>	Red-crested Woodpecker	x		x				
632	<i>Psilopogon rafflesii</i>	Red-crowned Barbet	x		x				
633	<i>Otus rufescens</i>	Reddish Scops-owl	x		x				
634	<i>Pycnonotus brunneus</i>	Red-eyed Bulbul	x		x				
635	<i>Liocichla phoenicea</i>	Red-faced Liocichla	x		x				
636	<i>Harpactes erythrocephalus</i>	Red-headed Trogon	x		x				
637	<i>Sarcogyps calvus</i>	Red-headed Vulture	x		x				
638	<i>Rallina fasciata</i>	Red-legged Crake	x		x				
639	<i>Harpactes kasumba</i>	Red-naped Trogon	x		x				
640	<i>Calidris ruficollis</i>	Red-necked Stint		x					x
641	<i>Hirundo daurica</i>	Red-rumped Swallow	x				x		
642	<i>Garrulax milnei</i>	Red-tailed Laughingthrush	x		x				
643	<i>Psilopogon mystacophanos</i>	Red-throated Barbet	x		x				
644	<i>Anthus cervinus</i>	Red-throated Pipit		x				x	
645	<i>Anthreptes rhodolaemus</i>	Red-throated Sunbird	x		x				
646	<i>Pycnonotus cafer</i>	Red-vented Bulbul	x				x		
647	<i>Vanellus indicus</i>	Red-wattled Lapwing	x			x			
648	<i>Pycnonotus jocosus</i>	Red-whiskered Bulbul	x		x				
649	<i>Buceros rhinoceros</i>	Rhinoceros Hornbill	x		x				
650	<i>Anthus richardi</i>	Richard's Pipit		x			x		
651	<i>Vanellus duvaucelii</i>	River Lapwing	x					x	
652	<i>Sterna aurantia</i>	River Tern	x					x	
653	<i>Sterna dougallii</i>	Roseate Tern	x						x
654	<i>Pericrocotus roseus</i>	Rosy Minivet		x	x				
655	<i>Anthreptes singalensis</i>	Ruby-cheeked Sunbird	x		x				

656	<i>Halcyon coromanda</i>	Ruddy Kingfisher		x	x				
657	<i>Tadorna ferruginea</i>	Ruddy Shelduck		x				x	
658	<i>Arenaria interpres</i>	Ruddy Turnstone		x				x	
659	<i>Zapornia fusca</i>	Ruddy-breasted Crake	x					x	
660	<i>Prinia rufescens</i>	Rufescent Prinia	x		x				
661	<i>Calidris pugnax</i>	Ruff		x				x	
662	<i>Sasia abnormis</i>	Rufous Piculet	x		x				
663	<i>Dendrocitta vagabunda</i>	Rufous Treepie	x		x				
664	<i>Micropternus brachyurus</i>	Rufous Woodpecker	x		x				
665	<i>Ceyx rufidorsa</i>	Rufous-backed Kingfisher	x		x				
666	<i>Heterophasia annectens</i>	Rufous-backed Sibia	x		x				
667	<i>Lophotriorchis kienerii</i>	Rufous-bellied Eagle	x		x				
668	<i>Niltava sundara</i>	Rufous-bellied Niltava		x	x				
669	<i>Dendrocopos hyperythrus</i>	Rufous-bellied Woodpecker		x	x				
670	<i>Ficedula solitaria</i>	Rufous-browed Flycatcher	x		x				
671	<i>Stachyris ruficeps</i>	Rufous-capped Babbler	x		x				
672	<i>Ficedula dumetoria</i>	Rufous-chested Flycatcher	x		x				
673	<i>Actenoides concretus</i>	Rufous-collared Kingfisher	x		x				
674	<i>Malacopteron magnum</i>	Rufous-crowned Babbler	x		x				
675	<i>Abroscopus albogularis</i>	Rufous-faced Warbler	x		x				
676	<i>Stachyris rufifrons</i>	Rufous-fronted Babbler	x		x				
677	<i>Ficedula strophciata</i>	Rufous-gorgeted Flycatcher		x	x				
678	<i>Aceros nipalensis</i>	Rufous-necked Hornbill	x		x				
679	<i>Graminicola bengalensis</i>	Rufous-rumped Grassbird	x		x				
680	<i>Luscinia sibilans</i>	Rufous-tailed Robin		x	x				
681	<i>Trichixos pyrropygus</i>	Rufous-tailed Shama	x		x				
682	<i>Orthotomus sericeus</i>	Rufous-tailed Tailorbird	x		x				
683	<i>Alcippe rufogularis</i>	Rufous-throated Fulvetta	x		x				
684	<i>Arborophila rufogularis</i>	Rufous-throated Partridge	x		x				
685	<i>Butastur liventer</i>	Rufous-winged Buzzard	x		x				
686	<i>Alcippe castaneiceps</i>	Rufous-winged Fulvetta	x		x				
687	<i>Mirafra assamica</i>	Rufous-winged Lark	x					x	
688	<i>Philentoma pyrhoptera</i>	Rufous-winged Philentoma	x		x				
689	<i>Bradypterus mandelli</i>	Russet Bush-warbler	x		x				
690	<i>Passer rutilans</i>	Russet Sparrow	x					x	
691	<i>Cacomantis sepulcralis</i>	Rusty-breasted Cuckoo	x		x				
692	<i>Alcippe dubia</i>	Rusty-capped Fulvetta	x		x				
693	<i>Pomatorhinus erythrogenys</i>	Rusty-cheeked Scimitar-babbler	x		x				
694	<i>Pitta oatesi</i>	Rusty-naped Pitta	x		x				

695	<i>Riparia riparia</i>	Sand Martin		x				x	
696	<i>Calidris alba</i>	Sanderling		x					x
697	<i>Ficedula sapphira</i>	Sapphire Flycatcher	x		x				
698	<i>Caprimulgus affinis</i>	Savanna Nightjar	x		x				
699	<i>Pycnonotus squamatus</i>	Scaly-breasted Bulbul	x		x				
700	<i>Lonchura punctulata</i>	Scaly-breasted Munia	x		x				
701	<i>Malacopteron cinereum</i>	Scaly-crowned Babbler	x		x				
702	<i>Mergus squamatus</i>	Scaly-sided Merganser		x	x				
703	<i>Haematospiza sipahi</i>	Scarlet Finch	x		x				
704	<i>Pericrocotus flammeus</i>	Scarlet Minivet	x		x				
705	<i>Aethopyga mystacalis</i>	Scarlet Sunbird	x		x				
706	<i>Dicaeum cruentatum</i>	Scarlet-backed Flowerpecker	x		x				
707	<i>Prionochilus thoracicus</i>	Scarlet-breasted Flowerpecker	x		x				
708	<i>Harpactes duvaucelii</i>	Scarlet-rumped Trogon	x		x				
709	<i>Ixobrychus eurhythmus</i>	Schrenck's Bittern		x	x				
710	<i>Accipiter badius</i>	Shikra	x		x				
711	<i>Pericrocotus brevirostris</i>	Short-billed Minivet	x		x				
712	<i>Asio flammeus</i>	Short-eared Owl		x				x	
713	<i>Malacocincla malaccensis</i>	Short-tailed Babbler	x		x				
714	<i>Batrachostomus poliophus</i>	Short-tailed Frogmouth	x		x				
715	<i>Paradoxornis davidianus</i>	Short-tailed Parrotbill	x			x			
716	<i>Centropus rectunguis</i>	Short-toed Coucal	x		x				
717	<i>Lophura diardi</i>	Siamese Fireback	x		x				
718	<i>Luscinia cyane</i>	Siberian Blue Robin		x	x				
719	<i>Luscinia calliope</i>	Siberian Rubythroat		x			x		
720	<i>Zoothera sibirica</i>	Siberian Thrush		x	x				
721	<i>Phylloscopus forresti</i>	Sichuan Leaf-warbler	x		x				
722	<i>Oriolus mellianus</i>	Silver Oriole		x	x				
723	<i>Lophura nycthemera</i>	Silver Pheasant	x		x				
724	<i>Hirundapus cochinchinensis</i>	Silver-backed Needletail		x	x				
725	<i>Serilophus lunatus</i>	Silver-breasted Broadbill	x		x				
726	<i>Garrulax melanostigma</i>	Silver-eared Laughingthrush	x		x				
727	<i>Leiothrix argentauris</i>	Silver-eared Mesia	x		x				
728	<i>Rhaphidura leucopygialis</i>	Silver-rumped Spinetail	x		x				
729	<i>Ficedula hodgsonii</i>	Slaty-backed Flycatcher		x	x				
730	<i>Enicurus schistaceus</i>	Slaty-backed Forktail	x		x				
731	<i>Tesia olivea</i>	Slaty-bellied Tesia	x		x				
732	<i>Ficedula tricolor</i>	Slaty-blue Flycatcher	x		x				
733	<i>Lewinia striata</i>	Slaty-breasted Rail	x		x				



734	<i>Rallina eurizonoides</i>	Slaty-legged Crake		x	x				
735	<i>Oriolus tenuirostris</i>	Slender-billed Oriole		x	x				
736	<i>Gyps tenuirostris</i>	Slender-billed Vulture	x		x				
737	<i>Pericrocotus cinnamomeus</i>	Small Minivet	x		x				
738	<i>Niltava macgrigoriae</i>	Small Niltava	x		x				
739	<i>Ficedula hyperythra</i>	Snowy-browed Flycatcher	x		x				
740	<i>Onychoprion fuscatus</i>	Sooty Tern		x					x
741	<i>Malacopteron affine</i>	Sooty-capped Babbler	x		x				
742	<i>Pycnonotus aurigaster</i>	Sooty-headed Bulbul	x				x		
743	<i>Phylloscopus reguloides</i>	Southern Blyth's Leaf-warbler		x	x				
744	<i>Picumnus innominatus</i>	Speckled Piculet	x				x		
745	<i>Columba hodgsonii</i>	Speckled Woodpigeon		x	x				
746	<i>Actinodura ramsayi</i>	Spectacled Barwing	x		x				
747	<i>Pycnonotus erythroptalmos</i>	Spectacled Bulbul	x		x				
748	<i>Arachnothera flavigaster</i>	Spectacled Spiderhunter	x		x				
749	<i>Calidris pygmaea</i>	Spoon-billed Sandpiper		x					x
750	<i>Bubo nipalensis</i>	Spot-bellied Eagle-owl	x		x				
751	<i>Pelecanus philippensis</i>	Spot-billed Pelican		x				x	
752	<i>Garrulax merulinus</i>	Spot-breasted Laughingthrush	x		x				
753	<i>Paradoxornis guttaticollis</i>	Spot-breasted Parrotbill	x				x		
754	<i>Stachyris striolata</i>	Spot-necked Babbler	x		x				
755	<i>Rhipidura perlata</i>	Spotted Fantail	x		x				
756	<i>Tringa guttifer</i>	Spotted Greenshank		x					x
757	<i>Athene brama</i>	Spotted Owlet	x		x				
758	<i>Tringa erythropus</i>	Spotted Redshank		x				x	
759	<i>Strix seloputo</i>	Spotted Wood-owl	x		x				
760	<i>Pellorneum albiventre</i>	Spot-throated Babbler	x		x				
761	<i>Mycerobas melanozanthos</i>	Spot-winged Grosbeak	x				x		
762	<i>Saroglossa spiloptera</i>	Spot-winged Starling		x			x		
763	<i>Surniculus lugubris</i>	Square-tailed Drongo-cuckoo	x		x				
764	<i>Treron pompadora</i>	Sri Lanka Green-pigeon	x		x				
765	<i>Aquila nipalensis</i>	Steppe Eagle		x	x				
766	<i>Pelargopsis capensis</i>	Stork-billed Kingfisher	x		x				
767	<i>Ciconia stormi</i>	Storm's Stork	x		x				
768	<i>Pycnonotus zeylanicus</i>	Straw-headed Bulbul	x		x				
769	<i>Pomatorhinus ruficollis</i>	Streak-breasted Scimitar-babbler	x		x				
770	<i>Picus viridanus</i>	Streak-breasted Woodpecker	x		x				
771	<i>Pycnonotus blanfordi</i>	Streak-eared Bulbul	x		x				
772	<i>Ixos malaccensis</i>	Streaked Bulbul	x		x				

773	<i>Arachnothera magna</i>	Streaked Spiderhunter	x		x				
774	<i>Ploceus manyar</i>	Streaked Weaver	x		x				
775	<i>Napothera brevicaudata</i>	Streaked Wren-babbler	x		x				
776	<i>Picus xanthopygaeus</i>	Streak-throated Woodpecker	x		x				
777	<i>Pycnonotus striatus</i>	Striated Bulbul	x		x				
778	<i>Megalurus palustris</i>	Striated Grassbird	x		x				
779	<i>Yuhina castaniceps</i>	Striated Yuhina	x		x				
780	<i>Dendrocopos atratus</i>	Stripe-breasted Woodpecker	x		x				
781	<i>Kenopia striata</i>	Striped Wren-babbler	x		x				
782	<i>Pycnonotus finlaysoni</i>	Stripe-throated Bulbul	x		x				
783	<i>Phylloscopus ricketti</i>	Sulphur-breasted Warbler		x	x				
784	<i>Melanochlora sultanea</i>	Sultan Tit	x		x				
785	<i>Anser cygnoides</i>	Swan Goose		x				x	
786	<i>Hydrobates monorhis</i>	Swinhoe's Storm-petrel	x						x
787	<i>Ficedula albicilla</i>	Taiga Flycatcher		x			x		
788	<i>Calidris temminckii</i>	Temminck's Stint		x				x	
789	<i>Xenus cinereus</i>	Terek Sandpiper		x					x
790	<i>Dicaeum agile</i>	Thick-billed Flowerpecker	x		x				
791	<i>Treron curvirostra</i>	Thick-billed Green-pigeon	x		x				
792	<i>Arachnothera crassirostris</i>	Thick-billed Spiderhunter	x		x				
793	<i>Acrocephalus aedon</i>	Thick-billed Warbler		x	x				
794	<i>Cyornis tickelliae</i>	Tickell's Blue-flycatcher	x		x				
795	<i>Anorrhinus tickelli</i>	Tickell's Brown Hornbill	x		x				
796	<i>Phylloscopus affinis</i>	Tickell's Leaf-warbler		x	x				
797	<i>Lanius tigrinus</i>	Tiger Shrike		x	x				
798	<i>Ficedula superciliaris</i>	Ultramarine Flycatcher		x	x				
799	<i>Sitta frontalis</i>	Velvet-fronted Nuthatch	x		x				
800	<i>Eumyias thalassinus</i>	Verditer Flycatcher	x		x				
801	<i>Loriculus vernalis</i>	Vernal Hanging-parrot	x		x				
802	<i>Sturnus burmannicus</i>	Vinous-breasted Starling	x		x				
803	<i>Chrysococcyx xanthorhynchus</i>	Violet Cuckoo		x	x				
804	<i>Niltava vivida</i>	Vivid Niltava	x		x				
805	<i>Nisaetus nanus</i>	Wallace's Hawk-eagle	x		x				
806	<i>Gallicrex cinerea</i>	Watercock	x					x	
807	<i>Hydrochous gigas</i>	Waterfall Swift	x		x				
808	<i>Treron sphenurus</i>	Wedge-tailed Green-pigeon	x		x				
809	<i>Eudynamis scolopaceus</i>	Western Koel	x		x				
810	<i>Rallus aquaticus</i>	Western Water Rail		x				x	
811	<i>Numenius phaeopus</i>	Whimbrel		x					x

812	<i>Chlidonias hybrida</i>	Whiskered Tern		x					x
813	<i>Hemiprocne comata</i>	Whiskered Treeswift	x		x				
814	<i>Yuhina flavicollis</i>	Whiskered Yuhina	x		x				
815	<i>Motacilla alba</i>	White Wagtail		x				x	
816	<i>Treron sieboldii</i>	White-bellied Green-pigeon		x	x				
817	<i>Lonchura leucogastra</i>	White-bellied Munia	x		x				
818	<i>Hodgsonius phaenicuroides</i>	White-bellied Redstart	x			x			
819	<i>Haliaeetus leucogaster</i>	White-bellied Sea-eagle	x						x
820	<i>Dryocopus javensis</i>	White-bellied Woodpecker	x		x				
821	<i>Erpornis zantholeuca</i>	White-bellied Yuhina	x		x				
822	<i>Halcyon smyrnensis</i>	White-breasted Kingfisher	x			x			
823	<i>Amaurornis phoenicurus</i>	White-breasted Waterhen	x		x				
824	<i>Amaurornis cinerea</i>	White-browed Crake	x		x				
825	<i>Rhipidura aureola</i>	White-browed Fantail	x		x				
826	<i>Garrulax sannio</i>	White-browed Laughingthrush	x		x				
827	<i>Sasia ochracea</i>	White-browed Piculet	x			x			
828	<i>Pomatorhinus schisticeps</i>	White-browed Scimitar-babbler	x		x				
829	<i>Brachypteryx montana</i>	White-browed Shortwing	x		x				
830	<i>Pteruthius flaviscapis</i>	White-browed Shrike-babbler	x		x				
831	<i>Trichastoma rostratum</i>	White-chested Babbler	x		x				
832	<i>Garrulax leucolophus</i>	White-crested Laughingthrush	x		x				
833	<i>Enicurus leschenaulti</i>	White-crowned Forktail	x		x				
834	<i>Berenicornis comatus</i>	White-crowned Hornbill	x		x				
835	<i>Butastur teesa</i>	White-eyed Buzzard	x				x		
836	<i>Eurochelidon sirintarae</i>	White-eyed River-martin		x				x	
837	<i>Otus sagittatus</i>	White-fronted Scops-owl	x		x				
838	<i>Ficedula monileger</i>	White-gorgeted Flycatcher	x		x				
839	<i>Hypsipetes thompsoni</i>	White-headed Bulbul	x		x				
840	<i>Lonchura maja</i>	White-headed Munia	x		x				
841	<i>Stachyris leucotis</i>	White-necked Babbler	x		x				
842	<i>Garrulax strepitans</i>	White-necked Laughingthrush	x		x				
843	<i>Lonchura striata</i>	White-rumped Munia	x		x				
844	<i>Polihierax insignis</i>	White-rumped Pygmy-falcon	x		x				
845	<i>Copsychus malabaricus</i>	White-rumped Shama	x		x				
846	<i>Gyps bengalensis</i>	White-rumped Vulture	x		x				
847	<i>Meiglyptes tristis</i>	White-rumped Woodpecker	x			x			
848	<i>Sturnus sinensis</i>	White-shouldered Starling		x			x		
849	<i>Cyornis concretus</i>	White-tailed Flycatcher	x		x				
850	<i>Cinclidium leucurum</i>	White-tailed Robin	x		x				

851	<i>Alophoixus flaveolus</i>	White-throated Bulbul	x		x				
852	<i>Rhipidura albicollis</i>	White-throated Fantail	x		x				
853	<i>Monticola gularis</i>	White-throated Rock-thrush		x	x				
854	<i>Acridotheres grandis</i>	White-vented Myna	x		x				
855	<i>Asarcornis scutulata</i>	White-winged Duck	x					x	
856	<i>Chlidonias leucopterus</i>	White-winged Tern		x					x
857	<i>Hirundo smithii</i>	Wire-tailed Swallow	x					x	
858	<i>Tringa glareola</i>	Wood Sandpiper		x				x	
859	<i>Gallinago nemoricola</i>	Wood Snipe		x	x				
860	<i>Rhyticeros undulatus</i>	Wreathed Hornbill	x		x				
861	<i>Rhabdotorrhinus corrugatus</i>	Wrinkled Hornbill	x		x				
862	<i>Ixobrychus sinensis</i>	Yellow Bittern	x					x	
863	<i>Motacilla flava</i>	Yellow Wagtail		x			x		
864	<i>Alophoixus phaeocephalus</i>	Yellow-bellied Bulbul	x		x				
865	<i>Rhipidura hypoxantha</i>	Yellow-bellied Fantail	x		x				
866	<i>Dicaeum melanoxanthum</i>	Yellow-bellied Flowerpecker	x		x				
867	<i>Prinia flaviventris</i>	Yellow-bellied Prinia	x		x				
868	<i>Abroscopus superciliaris</i>	Yellow-bellied Warbler	x		x				
869	<i>Eophona migratoria</i>	Yellow-billed Grosbeak		x		x			
870	<i>Emberiza aureola</i>	Yellow-breasted Bunting		x				x	
871	<i>Prionochilus maculatus</i>	Yellow-breasted Flowerpecker	x		x				
872	<i>Cissa hypoleuca</i>	Yellow-breasted Magpie	x		x				
873	<i>Sylviparus modestus</i>	Yellow-browed Tit	x		x				
874	<i>Parus spilonotus</i>	Yellow-cheeked Tit	x		x				
875	<i>Psilopogon henricii</i>	Yellow-crowned Barbet	x		x				
876	<i>Leiopicus mahrattensis</i>	Yellow-crowned Woodpecker	x		x				
877	<i>Arachnothera chrysogenys</i>	Yellow-eared Spiderhunter	x		x				
878	<i>Chrysomma sinense</i>	Yellow-eyed Babbler	x		x				
879	<i>Treron phoenicopterus</i>	Yellow-footed Green-pigeon	x		x				
880	<i>Turnix tanki</i>	Yellow-legged Buttonquail		x	x				
881	<i>Ficedula zanthopygia</i>	Yellow-rumped Flycatcher		x	x				
882	<i>Phylloscopus armandii</i>	Yellow-streaked Warbler		x	x				
883	<i>Pycnonotus goiavier</i>	Yellow-vented Bulbul	x			x			
884	<i>Dicaeum chrysorrheum</i>	Yellow-vented Flowerpecker	x		x				
885	<i>Treron seimundi</i>	Yellow-vented Green-pigeon	x		x				
886	<i>Phylloscopus cantator</i>	Yellow-vented Warbler	x		x				
887	<i>Geopelia striata</i>	Zebra Dove	x		x				
888	<i>Cisticola juncidis</i>	Zitting Cisticola	x					x	

Appendix 2. Results for species distribution models for 336 bird species in Thailand. The occurrence of each species is indicated as “#Record”. The AUC values of species distribution models are indicated by “AUC”. Fitted 95% C.I. AUC values for the biased corrected null-model are indicated by “95% C.I. Bias”. All 336 species distribution models are significantly deviating from biased corrected null-models ( $P < 0.05$ ).

#	Scientific name	Common name	Record	AUC	95% C.I. Bias
1	<i>Malacocincla abbotti</i>	Abbott's Babbler	28	0.953	0.819
2	<i>Phylloscopus borealis</i>	Arctic Warbler	45	0.953	0.733
3	<i>Hemixos flavala</i>	Ashy Bulbul	38	0.939	0.766
4	<i>Dicrurus leucophaeus</i>	Ashy Drongo	154	0.804	0.597
5	<i>Pericrocotus divaricatus</i>	Ashy Minivet	34	0.870	0.771
6	<i>Artamus fuscus</i>	Ashy Woodswallow	141	0.710	0.601
7	<i>Glaucidium cuculoides</i>	Asian Barred Owlet	84	0.828	0.652
8	<i>Hypsipetes leucocephalus</i>	Asian Black Bulbul	29	0.971	0.807
9	<i>Muscicapa dauurica</i>	Asian Brown Flycatcher	118	0.756	0.620
10	<i>Chrysococcyx maculatus</i>	Asian Emerald Cuckoo	23	0.945	0.829
11	<i>Irena puella</i>	Asian Fairy-bluebird	69	0.927	0.669
12	<i>Aplonis panayensis</i>	Asian Glossy Starling	40	0.960	0.710
13	<i>Merops orientalis</i>	Asian Green Bee-eater	81	0.768	0.656
14	<i>Delichon dasypus</i>	Asian House-martin	33	0.939	0.776
15	<i>Anastomus oscitans</i>	Asian Openbill	118	0.861	0.620
16	<i>Cypsiurus balasiensis</i>	Asian Palm-swift	241	0.616	0.551
17	<i>Terpsiphone paradisi</i>	Asian Paradise-flycatcher	49	0.864	0.714
18	<i>Sturnus contra</i>	Asian Pied Starling	100	0.875	0.629
19	<i>Cacomantis sonneratii</i>	Banded Bay Cuckoo	22	0.944	0.830
20	<i>Eurylaimus javanicus</i>	Banded Broadbill	21	0.930	0.825
21	<i>Lacedo pulchella</i>	Banded Kingfisher	26	0.969	0.844
22	<i>Hirundo rustica</i>	Barn Swallow	278	0.638	0.538
23	<i>Macropygia unchall</i>	Barred Cuckoo-dove	20	0.972	0.811
24	<i>Hemipus picatus</i>	Bar-winged Flycatcher-shrike	71	0.814	0.672
25	<i>Ploceus philippinus</i>	Baya Weaver	40	0.892	0.710
26	<i>Accipiter virgatus</i>	Besra	22	0.902	0.830
27	<i>Aviceda lephotes</i>	Black Baza	38	0.845	0.766
28	<i>Ixobrychus flavicollis</i>	Black Bittern	20	0.967	0.811

29	<i>Dicrurus macrocercus</i>	Black Drongo	228	0.641	0.557
30	<i>Milvus migrans</i>	Black Kite	46	0.913	0.620
31	<i>Acrocephalus bistrigiceps</i>	Black-browed Reed-Warbler	27	0.941	0.831
32	<i>Halcyon pileata</i>	Black-capped Kingfisher	91	0.858	0.634
33	<i>Sturnus nigricollis</i>	Black-collared Starling	98	0.687	0.456
34	<i>Pycnonotus melanicterus</i>	Black-crested Bulbul	185	0.824	0.579
35	<i>Nycticorax nycticorax</i>	Black-crowned Night-heron	51	0.939	0.698
36	<i>Pycnonotus atriceps</i>	Black-headed Bulbul	75	0.879	0.664
37	<i>Oriolus xanthonus</i>	Black-hooded Oriole	36	0.927	0.785
38	<i>Hypothymis azurea</i>	Black-naped Monarch	97	0.856	0.637
39	<i>Oriolus chinensis</i>	Black-naped Oriole	106	0.752	0.616
40	<i>Garrulax chinensis</i>	Black-throated Laughingthrush	29	0.943	0.807
41	<i>Aethopyga saturata</i>	Black-throated Sunbird	45	0.901	0.733
42	<i>Coracina melaschistos</i>	Black-winged Cuckooshrike	37	0.933	0.748
43	<i>Elanus caeruleus</i>	Black-winged Kite	92	0.822	0.632
44	<i>Himantopus himantopus</i>	Black-winged Stilt	81	0.890	0.656
45	<i>Pitta cyanea</i>	Blue Pitta	20	0.968	0.811
46	<i>Monticola solitarius</i>	Blue Rock-thrush	63	0.888	0.675
47	<i>Myophonus caeruleus</i>	Blue Whistling-thrush	77	0.921	0.534
48	<i>Nyctyornis athertoni</i>	Blue-bearded Bee-eater	34	0.965	0.771
49	<i>Psilopogon cyanotis</i>	Blue-eared barbet	41	0.929	0.726
50	<i>Merops philippinus</i>	Blue-tailed Bee-eater	55	0.814	0.724
51	<i>Psilopogon asiaticus</i>	Blue-throated barbet	62	0.949	0.673
52	<i>Cyornis rubeculoides</i>	Blue-throated Flycatcher	28	0.838	0.819
53	<i>Chloropsis cochinchinensis</i>	Blue-winged Leafbird	71	0.883	0.672
54	<i>Minla cyanouroptera</i>	Blue-winged Minla	20	0.971	0.811
55	<i>Haliastur indus</i>	Brahminy Kite	110	0.896	0.624
56	<i>Dicrurus aeneus</i>	Bronzed Drongo	79	0.840	0.657
57	<i>Metopidius indicus</i>	Bronze-winged Jacana	43	0.891	0.722
58	<i>Ninox scutulata</i>	Brown Boobook	22	0.964	0.830
59	<i>Lanius cristatus</i>	Brown Shrike	182	0.597	0.580
60	<i>Hirundapus giganteus</i>	Brown-backed Needletail	38	0.938	0.766
61	<i>Alcippe poioicephala</i>	Brown-cheeked Fulvetta	33	0.938	0.776
62	<i>Larus brunnicephalus</i>	Brown-headed Gull	29	0.980	0.807
63	<i>Pelargopsis amauroptera</i>	Brown-winged Kingfisher	23	0.989	0.829
64	<i>Trichastoma tickelli</i>	Buff-breasted babbler	23	0.949	0.829
65	<i>Iole olivacea</i>	Buff-vented Bulbul	22	0.975	0.830
66	<i>Lanius colluriooides</i>	Burmese Shrike	27	0.924	0.831
67	<i>Bubulcus ibis</i>	Cattle Ibis	173	0.667	0.582

68	<i>Nisaetus cirrhatus</i>	Changeable Hawk-eagle	20	0.937	0.811
69	<i>Phaenicophaeus curvirostris</i>	Chestnut-breasted Malkoha	21	0.986	0.825
70	<i>Timalia pileata</i>	Chestnut-capped Babbler	21	0.873	0.825
71	<i>Zosterops erythropleurus</i>	Chestnut-flanked White-eye	20	0.938	0.811
72	<i>Merops leschenaulti</i>	Chestnut-headed Bee-eater	78	0.818	0.649
73	<i>Minla strigula</i>	Chestnut-tailed Minla	24	0.995	0.808
74	<i>Sturnus malabaricus</i>	Chestnut-tailed Starling	32	0.815	0.752
75	<i>Sitta nagaensis</i>	Chestnut-vented Nuthatch	23	0.989	0.829
76	<i>Ardeola bacchus</i>	Chinese Pond-heron	215	0.658	0.563
77	<i>Ixobrychus cinnamomeus</i>	Cinnamon Bittern	34	0.862	0.771
78	<i>Todiramphus chloris</i>	Collared Kingfisher	66	0.914	0.680
79	<i>Glaucidium brodiei</i>	Collared Owlet	44	0.947	0.737
80	<i>Otus lettia</i>	Collared Scops-owl	30	0.818	0.762
81	<i>Dinopium javanense</i>	Common Flameback	30	0.946	0.762
82	<i>Tringa nebularia</i>	Common Greenshank	45	0.953	0.733
83	<i>Upupa epops</i>	Common Hoopoe	64	0.743	0.680
84	<i>Aegithina tiphia</i>	Common Iora	144	0.706	0.620
85	<i>Falco tinnunculus</i>	Common Kestrel	31	0.779	0.758
86	<i>Alcedo atthis</i>	Common Kingfisher	126	0.800	0.610
87	<i>Gallinula chloropus</i>	Common Moorhen	53	0.814	0.710
88	<i>Acridotheres tristis</i>	Common Myna	419	0.664	0.500
89	<i>Tringa totanus</i>	Common Redshank	31	0.944	0.758
90	<i>Carpodacus erythrinus</i>	Common Rosefinch	20	0.950	0.811
91	<i>Actitis hypoleucos</i>	Common Sandpiper	113	0.881	0.620
92	<i>Gallinago gallinago</i>	Common Snipe	32	0.946	0.752
93	<i>Saxicola torquatus</i>	Common Stonechat	95	0.769	0.644
94	<i>Orthotomus sutorius</i>	Common Tailorbird	178	0.632	0.585
95	<i>Sterna hirundo</i>	Common Tern	28	0.967	0.819
96	<i>Psilopogon haemacephalus</i>	Coppersmith barbet	181	0.711	0.576
97	<i>Nettapus coromandelianus</i>	Cotton Pygmy-goose	23	0.838	0.829
98	<i>Accipiter trivirgatus</i>	Crested Goshawk	34	0.900	0.771
99	<i>Spilornis cheela</i>	Crested Serpent-eagle	66	0.894	0.680
100	<i>Hemiprocne coronata</i>	Crested Treeswift	37	0.917	0.748
101	<i>Aethopyga siparaja</i>	Crimson Sunbird	40	0.951	0.710
102	<i>Dicrurus annectans</i>	Crow-billed Drongo	27	0.933	0.831
103	<i>Calidris ferruginea</i>	Curlew Sandpiper	21	0.991	0.825
104	<i>Heterophasia melanoleuca</i>	Dark-backed Sibia	30	0.983	0.762
105	<i>Orthotomus atrogularis</i>	Dark-necked Tailorbird	81	0.753	0.656
106	<i>Muscicapa sibirica</i>	Dark-sided Flycatcher	29	0.891	0.807

107	<i>Phylloscopus davisoni</i>	Davison's Leaf-warbler	26	0.977	0.844
108	<i>Hirundo concolor</i>	Dusky Crag-martin	20	0.839	0.811
109	<i>Phylloscopus fuscatus</i>	Dusky Warbler	47	0.876	0.732
110	<i>Phylloscopus coronatus</i>	Eastern Crowned Warbler	22	0.932	0.830
111	<i>Circus spilonotus</i>	Eastern Marsh-harrier	26	0.939	0.844
112	<i>Spilopelia chinensis</i>	Eastern Spotted Dove	347	0.539	0.521
113	<i>Buteo buteo</i>	Eurasian Buzzard	26	0.943	0.844
114	<i>Garrulus glandarius</i>	Eurasian Jay	37	0.944	0.748
115	<i>Passer montanus</i>	Eurasian Tree Sparrow	338	0.640	0.519
116	<i>Turdus obscurus</i>	Eyebrowed Thrush	26	0.977	0.844
117	<i>Dicaeum ignipectus</i>	Fire-breasted Flowerpecker	33	0.952	0.776
118	<i>Pycnonotus flavescens</i>	Flavescent Bulbul	54	0.954	0.703
119	<i>Dendronanthus indicus</i>	Forest Wagtail	34	0.898	0.771
120	<i>Aerodramus germani</i>	Germain's swiftlet	80	0.868	0.443
121	<i>Stachyris chrysaea</i>	Golden Babbler	26	0.989	0.844
122	<i>Gerygone sulphurea</i>	Golden-bellied Gerygone	27	0.986	0.831
123	<i>Chloropsis aurifrons</i>	Golden-fronted Leafbird	57	0.877	0.697
124	<i>Megalaima franklinii</i>	Golden-throated Barbet	29	0.987	0.807
125	<i>Aethopyga gouldiae</i>	Gould's Sunbird	26	0.988	0.844
126	<i>Psilopogon virens</i>	Great Barbet	39	0.942	0.780
127	<i>Lyncornis macrotis</i>	Great Eared-nightjar	21	0.973	0.825
128	<i>Buceros bicornis</i>	Great Hornbill	43	0.977	0.722
129	<i>Aegithina lafresnayei</i>	Great Iora	35	0.913	0.758
130	<i>Parus major</i>	Great Tit	30	0.990	0.762
131	<i>Ardea alba</i>	Great White Egret	135	0.791	0.607
132	<i>Centropus sinensis</i>	Greater Coucal	222	0.643	0.563
133	<i>Chrysocolaptes guttacristatus</i>	Greater Flameback	35	0.944	0.758
134	<i>Chloropsis sonnerati</i>	Greater Green Leafbird	32	0.926	0.752
135	<i>Garrulax pectoralis</i>	Greater Necklaced Laughingthrush	22	0.957	0.830
136	<i>Dicrurus paradiseus</i>	Greater Racket-tailed Drongo	133	0.807	0.608
137	<i>Charadrius leschenaultii</i>	Greater Sandplover	26	0.957	0.844
138	<i>Picus flavinucha</i>	Greater Yellownape	24	0.901	0.808
139	<i>Aegithina viridissima</i>	Green Iora	20	0.984	0.811
140	<i>Cissa chinensis</i>	Green Magpie	29	0.952	0.807
141	<i>Tringa ochropus</i>	Green Sandpiper	27	0.941	0.831
142	<i>Butorides striata</i>	Green-backed Heron	101	0.784	0.631
143	<i>Phaenicophaeus tristis</i>	Green-billed Malkoha	126	0.732	0.610
144	<i>Psilopogon faiostrictus</i>	Green-eared barbet	30	0.981	0.762
145	<i>Phylloscopus trochiloides</i>	Greenish Warbler	44	0.891	0.737



146	<i>Arborophila chloropus</i>	Green-legged Partridge	24	0.971	0.808
147	<i>Aethopyga nipalensis</i>	Green-tailed Sunbird	25	0.991	0.823
148	<i>Saxicola ferreus</i>	Grey Bushchat	35	0.946	0.758
149	<i>Ardea cinerea</i>	Grey Heron	67	0.906	0.680
150	<i>Pluvialis squatarola</i>	Grey Plover	24	0.995	0.808
151	<i>Dendrocitta formosae</i>	Grey Treepie	20	0.975	0.811
152	<i>Motacilla cinerea</i>	Grey Wagtail	83	0.896	0.646
153	<i>Lanius tephronotus</i>	Grey-backed Shrike	42	0.961	0.733
154	<i>Prinia hodgsonii</i>	Grey-breasted Prinia	48	0.865	0.718
155	<i>Chalcophaps indica</i>	Grey-capped Emerald Dove	56	0.854	0.713
156	<i>Picooides canicapillus</i>	Grey-capped Woodpecker	51	0.883	0.698
157	<i>Alcippe morrisonia</i>	Grey-cheeked Fulvetta	38	0.968	0.766
158	<i>Pericrocotus solaris</i>	Grey-chinned Minivet	32	0.964	0.752
159	<i>Seicercus tephrocephalus</i>	Grey-crowned Warbler	35	0.976	0.758
160	<i>Iole propinqua</i>	Grey-eyed Bulbul	61	0.847	0.687
161	<i>Culicicapa ceylonensis</i>	Grey-headed Canary-flycatcher	90	0.873	0.645
162	<i>Vanellus cinereus</i>	Grey-headed Lapwing	31	0.868	0.758
163	<i>Hemiprocne longipennis</i>	Grey-rumped Treeswift	25	0.951	0.823
164	<i>Stachyris nigriceps</i>	Grey-throated Babbler	31	0.955	0.758
165	<i>Cyornis hainanus</i>	Hainan Blue-flycatcher	28	0.973	0.819
166	<i>Dicrurus hottentottus</i>	Hair-crested Drongo	76	0.890	0.517
167	<i>Cyornis banyumas</i>	Hill Blue-flycatcher	53	0.883	0.710
168	<i>Gracula religiosa</i>	Hill Myna	45	0.934	0.733
169	<i>Prinia atrogularis</i>	Hill Prinia	21	0.984	0.825
170	<i>Aerodramus brevirostris</i>	Himalayan Swiftlet	42	0.885	0.733
171	<i>Passer domesticus</i>	House Sparrow	56	0.945	0.713
172	<i>Apus nipalensis</i>	House Swift	112	0.751	0.616
173	<i>Phalacrocorax fuscicollis</i>	Indian Cormorant	39	0.947	0.780
174	<i>Coracias benghalensis</i>	Indian Roller	195	0.673	0.571
175	<i>Mirafra erythrocephala</i>	Indochinese Bushlark	34	0.916	0.771
176	<i>Phylloscopus inornatus</i>	Inornate Warbler	130	0.751	0.605
177	<i>Ardea intermedia</i>	Intermediate egret	73	0.911	0.664
178	<i>Accipiter gularis</i>	Japanese Sparrowhawk	26	0.948	0.844
179	<i>Zosterops japonicus</i>	Japanese White-eye	42	0.957	0.733
180	<i>Ardeola speciosa</i>	Javan Pond-heron	92	0.881	0.632
181	<i>Charadrius alexandrinus</i>	Kentish Plover	31	0.950	0.758
182	<i>Coracina macei</i>	Large Cuckooshrike	26	0.993	0.844
183	<i>Hierococyx sparverioides</i>	Large Hawk-cuckoo	26	0.941	0.844
184	<i>Niltava grandis</i>	Large Niltava	21	0.978	0.825

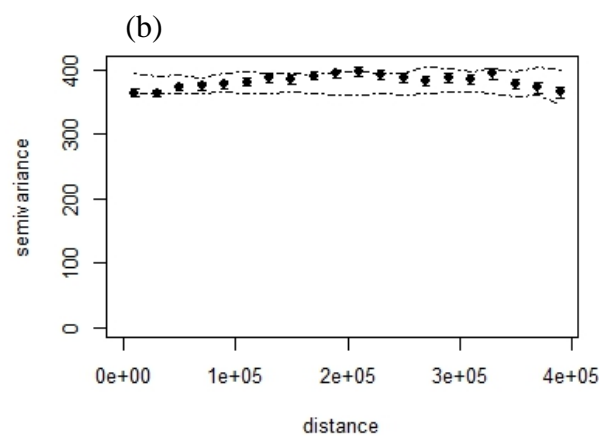
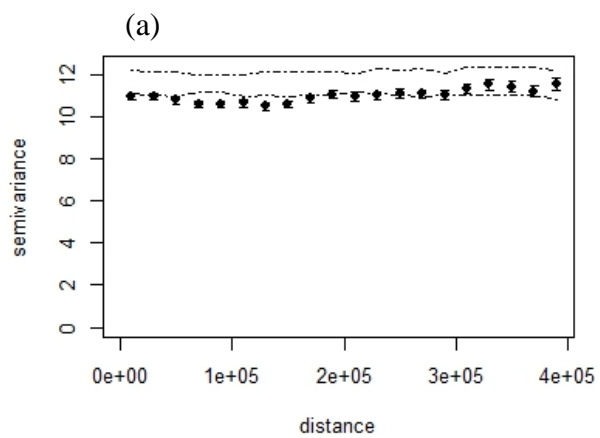
185	<i>Tephrodornis gularis</i>	Large Woodshrike	33	0.960	0.776
186	<i>Corvus macrorhynchos</i>	Large-billed Crow	226	0.701	0.557
187	<i>Caprimulgus macrurus</i>	Large-tailed Nightjar	34	0.912	0.771
188	<i>Centropus bengalensis</i>	Lesser Coucal	59	0.730	0.699
189	<i>Garrulax monileger</i>	Lesser Necklaced Laughingthrush	32	0.953	0.752
190	<i>Dicrurus remifer</i>	Lesser Racket-tailed Drongo	52	0.933	0.690
191	<i>Charadrius mongolus</i>	Lesser Sandplover	40	0.951	0.710
192	<i>Dendrocygna javanica</i>	Lesser Whistling-duck	80	0.719	0.443
193	<i>Picus chlorolophus</i>	Lesser Yellownape	24	0.927	0.808
194	<i>Psilopogon lineatus</i>	Lineated barbet	54	0.797	0.703
195	<i>Microcarbo niger</i>	Little Cormorant	131	0.872	0.605
196	<i>Egretta garzetta</i>	Little Egret	234	0.735	0.553
197	<i>Tachybaptus ruficollis</i>	Little Grebe	68	0.884	0.667
198	<i>Ficedula westermanni</i>	Little Pied Flycatcher	28	0.968	0.819
199	<i>Charadrius dubius</i>	Little Ringed Plover	47	0.948	0.732
200	<i>Arachnothera longirostra</i>	Little Spiderhunter	69	0.897	0.669
201	<i>Sternula albifrons</i>	Little Tern	32	0.982	0.752
202	<i>Psarisomus dalhousiae</i>	Long-tailed Broadbill	33	0.939	0.776
203	<i>Pericrocotus ethologus</i>	Long-tailed Minivet	30	0.976	0.762
204	<i>Lanius schach</i>	Long-tailed Shrike	72	0.814	0.657
205	<i>Calidris subminuta</i>	Long-toed Stint	30	0.976	0.762
206	<i>Oriolus traillii</i>	Maroon Oriole	22	0.983	0.830
207	<i>Tringa stagnatilis</i>	Marsh Sandpiper	34	0.989	0.771
208	<i>Hypsipetes mccllellandii</i>	Mountain Bulbul	47	0.949	0.732
209	<i>Ducula badia</i>	Mountain Imperial-pigeon	42	0.960	0.733
210	<i>Orthotomus cuculatus</i>	Mountain Tailorbird	24	0.987	0.808
211	<i>Psilopogon incognitus</i>	Moustached barbet	28	0.991	0.819
212	<i>Alophoixus ochraceus</i>	Ochraceous Bulbul	46	0.950	0.620
213	<i>Anthus hodgsoni</i>	Olive-backed Pipit	60	0.901	0.620
214	<i>Nectarinia jugularis</i>	Olive-backed Sunbird	195	0.742	0.571
215	<i>Dicaeum trigonostigma</i>	Orange-bellied Flowerpecker	36	0.944	0.785
216	<i>Harpactes oreskios</i>	Orange-breasted Trogon	29	0.956	0.807
217	<i>Eurystomus orientalis</i>	Oriental Dollarbird	62	0.869	0.673
218	<i>Pernis ptilorhynchus</i>	Oriental Honey-buzzard	69	0.860	0.669
219	<i>Copsychus saularis</i>	Oriental Magpie-robin	301	0.639	0.530
220	<i>Anthracoceros albirostris</i>	Oriental Pied Hornbill	52	0.959	0.690
221	<i>Glareola maldivarum</i>	Oriental Pratincole	39	0.939	0.780
222	<i>Acrocephalus orientalis</i>	Oriental Reed Warbler	34	0.938	0.771
223	<i>Streptopelia orientalis</i>	Oriental Turtle-dove	20	0.936	0.811

224	<i>Zosterops palpebrosus</i>	Oriental White-eye	61	0.880	0.687
225	<i>Pandion haliaetus</i>	Osprey	31	0.966	0.758
226	<i>Pluvialis fulva</i>	Pacific Golden Plover	38	0.971	0.766
227	<i>Egretta sacra</i>	Pacific Reef-egret	37	0.934	0.748
228	<i>Hirundo tahitica</i>	Pacific Swallow	77	0.920	0.534
229	<i>Apus pacificus</i>	Pacific Swift	46	0.914	0.620
230	<i>Anthus rufulus</i>	Paddyfield Pipit	85	0.796	0.653
231	<i>Mycteria leucocephala</i>	Painted Stork	28	0.989	0.819
232	<i>Phylloscopus tenellipes</i>	Pale-legged Leaf-warbler	31	0.936	0.758
233	<i>Falco peregrinus</i>	Peregrine Falcon	25	0.945	0.823
234	<i>Hydrophasianus chirurgus</i>	Pheasant-tailed Jacana	25	0.943	0.823
235	<i>Saxicola caprata</i>	Pied Bushchat	81	0.889	0.656
236	<i>Rhipidura javanica</i>	Pied Fantail	164	0.811	0.587
237	<i>Circus melanoleucos</i>	Pied Harrier	26	0.920	0.844
238	<i>Treron vernans</i>	Pink-necked Green-pigeon	24	0.934	0.808
239	<i>Macronous gularis</i>	Pin-striped tit-babbler	87	0.896	0.637
240	<i>Gallinago stenura</i>	Pintail Snipe	39	0.830	0.780
241	<i>Dicaeum concolor</i>	Plain flowerpecker	31	0.932	0.758
242	<i>Prinia inornata</i>	Plain Prinia	98	0.898	0.456
243	<i>Passer flaveolus</i>	Plain-backed Sparrow	81	0.874	0.656
244	<i>Anthreptes malacensis</i>	Plain-throated Sunbird	75	0.776	0.664
245	<i>Pellorneum ruficeps</i>	Puff-throated Babbler	72	0.874	0.657
246	<i>Alophoixus pallidus</i>	Puff-throated Bulbul	53	0.932	0.710
247	<i>Ardea purpurea</i>	Purple Heron	38	0.853	0.766
248	<i>Cinnyris asiatica</i>	Purple Sunbird	44	0.912	0.737
249	<i>Porphyrio porphyrio</i>	Purple Swampphen	28	0.982	0.819
250	<i>Crypsirina temia</i>	Racket-tailed Treepie	54	0.877	0.703
251	<i>Phylloscopus schwarzi</i>	Radde's Warbler	38	0.928	0.766
252	<i>Gallus gallus</i>	Red Junglefowl	73	0.869	0.664
253	<i>Streptopelia tranquebarica</i>	Red turtle dove	151	0.802	0.591
254	<i>Pycnonotus brunneus</i>	Red-eyed Bulbul	30	0.965	0.762
255	<i>Harpactes erythrocephalus</i>	Red-headed Trogon	31	0.962	0.758
256	<i>Calidris ruficollis</i>	Red-necked Stint	30	0.980	0.762
257	<i>Hirundo daurica</i>	Red-rumped Swallow	77	0.691	0.534
258	<i>Psilopogon mystacophanos</i>	Red-throated Barbet	26	0.979	0.844
259	<i>Vanellus indicus</i>	Red-wattled Lapwing	144	0.808	0.620
260	<i>Pycnonotus jocosus</i>	Red-whiskered Bulbul	157	0.831	0.586
261	<i>Anthus richardi</i>	Richard's Pipit	47	0.835	0.732
262	<i>Columba livia</i>	Rock Dove	256	0.736	0.549

263	<i>Pericrocotus roseus</i>	Rosy Minivet	29	0.959	0.807
264	<i>Anthreptes singalensis</i>	Ruby-cheeked Sunbird	63	0.918	0.675
265	<i>Zapornia fusca</i>	Ruddy-breasted crake	28	0.962	0.819
266	<i>Prinia rufescens</i>	Rufescent Prinia	54	0.840	0.703
267	<i>Dendrocitta vagabunda</i>	Rufous Treepie	21	0.933	0.825
268	<i>Niltava sundara</i>	Rufous-bellied Niltava	20	0.983	0.811
269	<i>Stachyris rufifrons</i>	Rufous-fronted babbler	36	0.957	0.785
270	<i>Alcippe castaneiceps</i>	Rufous-winged Fulvetta	28	0.991	0.819
271	<i>Riparia riparia</i>	Sand Martin	28	0.952	0.819
272	<i>Lonchura punctulata</i>	Scaly-breasted Munia	149	0.673	0.601
273	<i>Pericrocotus flammeus</i>	Scarlet Minivet	88	0.881	0.653
274	<i>Dicaeum cruentatum</i>	Scarlet-backed Flowerpecker	161	0.705	0.588
275	<i>Accipiter badius</i>	Shikra	67	0.811	0.680
276	<i>Pericrocotus brevirostris</i>	Short-billed Minivet	21	0.973	0.825
277	<i>Luscinia cyane</i>	Siberian Blue Robin	32	0.882	0.752
278	<i>Luscinia calliope</i>	Siberian Rubythroat	28	0.943	0.819
279	<i>Serilophus lunatus</i>	Silver-breasted Broadbill	29	0.914	0.807
280	<i>Garrulax melanostigma</i>	Silver-eared Laughingthrush	23	0.993	0.829
281	<i>Leiothrix argentauris</i>	Silver-eared Mesia	23	0.972	0.829
282	<i>Enicurus schistaceus</i>	Slaty-backed Forktail	26	0.991	0.844
283	<i>Pericrocotus cinnamomeus</i>	Small Minivet	27	0.965	0.831
284	<i>Pycnonotus aurigaster</i>	Sooty-headed Bulbul	146	0.819	0.597
285	<i>Phylloscopus reguloides</i>	Southern Blyth's Leaf-warbler	41	0.970	0.726
286	<i>Picumnus innominatus</i>	Speckled Piculet	24	0.944	0.808
287	<i>Athene brama</i>	Spotted Owlet	24	0.952	0.808
288	<i>Tringa erythropus</i>	Spotted Redshank	22	0.988	0.830
289	<i>Surniculus lugubris</i>	Square-tailed Drongo-cuckoo	30	0.876	0.762
290	<i>Pelargopsis capensis</i>	Stork-billed Kingfisher	20	0.985	0.811
291	<i>Pycnonotus blanfordi</i>	Streak-eared Bulbul	229	0.707	0.565
292	<i>Arachnothera magna</i>	Streaked Spiderhunter	52	0.908	0.690
293	<i>Hirundo striolata</i>	striated swallow	57	0.868	0.697
294	<i>Pycnonotus finlaysoni</i>	Stripe-throated Bulbul	83	0.896	0.646
295	<i>Melanochloa sultanea</i>	Sultan Tit	33	0.899	0.776
296	<i>Ficedula albicilla</i>	Taiga Flycatcher	116	0.770	0.616
297	<i>Calidris temminckii</i>	Temminck's Stint	21	0.977	0.825
298	<i>Treron curvirostra</i>	Thick-billed Green-pigeon	42	0.905	0.733
299	<i>Cyornis tickelliae</i>	Tickell's Blue-flycatcher	31	0.854	0.758
300	<i>Sitta frontalis</i>	Velvet-fronted Nuthatch	54	0.885	0.703
301	<i>Eumyias thalassinus</i>	Verditer Flycatcher	61	0.900	0.687

302	<i>Loriculus vernalis</i>	Vernal Hanging-parrot	53	0.942	0.710
303	<i>Sturnus burmannicus</i>	Vinous-breasted Starling	20	0.985	0.811
304	<i>Gallixrex cinerea</i>	Watercock	22	0.883	0.830
305	<i>Eudynamys scolopaceus</i>	Western Koel	192	0.717	0.581
306	<i>Numenius phaeopus</i>	Whimbrel	28	0.957	0.819
307	<i>Chlidonias hybrida</i>	Whiskered Tern	40	0.959	0.710
308	<i>Motacilla alba</i>	White Wagtail	77	0.860	0.534
309	<i>Haliaeetus leucogaster</i>	White-bellied Sea-eagle	37	0.925	0.748
310	<i>Erpornis zantholeuca</i>	White-bellied Yuhina	43	0.946	0.722
311	<i>Halcyon smyrnensis</i>	White-breasted Kingfisher	194	0.650	0.568
312	<i>Amaurornis phoenicurus</i>	White-breasted Waterhen	130	0.674	0.605
313	<i>Sasia ochracea</i>	White-browed Piculet	24	0.981	0.808
314	<i>Pomatorhinus schisticeps</i>	White-browed Scimitar-babbler	39	0.949	0.780
315	<i>Pteruthius flaviscapis</i>	White-browed shrike-babbler	41	0.963	0.726
316	<i>Garrulax leucolophus</i>	White-crested Laughingthrush	51	0.890	0.698
317	<i>Enicurus leschenaulti</i>	White-crowned Forktail	24	0.978	0.808
318	<i>Lonchura striata</i>	White-rumped Munia	74	0.808	0.658
319	<i>Copsychus malabaricus</i>	White-rumped Shama	113	0.857	0.620
320	<i>Rhipidura albicollis</i>	White-throated Fantail	54	0.946	0.703
321	<i>Acridotheres grandis</i>	White-vented Myna	260	0.694	0.549
322	<i>Chlidonias leucopterus</i>	White-winged Tern	20	0.979	0.811
323	<i>Hirundo smithii</i>	Wire-tailed Swallow	30	0.925	0.762
324	<i>Tringa glareola</i>	Wood Sandpiper	58	0.939	0.703
325	<i>Rhyticeros undulatus</i>	Wreathed Hornbill	28	0.977	0.819
326	<i>Ixobrychus sinensis</i>	Yellow Bittern	54	0.898	0.703
327	<i>Motacilla flava</i>	Yellow Wagtail	51	0.854	0.698
328	<i>Rhipidura hypoxantha</i>	Yellow-bellied Fantail	21	0.993	0.825
329	<i>Prinia flaviventris</i>	Yellow-bellied Prinia	45	0.846	0.733
330	<i>Abroscopus superciliaris</i>	Yellow-bellied Warbler	38	0.959	0.766
331	<i>Parus spilonotus</i>	Yellow-cheeked Tit	34	0.982	0.771
332	<i>Chrysomma sinense</i>	Yellow-eyed Babbler	20	0.945	0.811
333	<i>Pycnonotus goiavier</i>	Yellow-vented Bulbul	121	0.824	0.620
334	<i>Dicaeum chrysorrheum</i>	Yellow-vented Flowerpecker	27	0.964	0.831
335	<i>Geopelia striata</i>	Zebra Dove	206	0.698	0.563
336	<i>Cisticola juncidis</i>	Zitting Cisticola	46	0.914	0.620

Appendix 3. Semivariograms were used to examine the spatial autocorrelation in model residuals for all bird species richness based on (a) range maps and (b) species distribution model prediction maps



Appendix 4. Pearson's correlation coefficients for 11 selected environmental variables used in multivariate models for the species richness pattern of birds in Thailand.

Variable*	Latitude	C	M	S	MAT	MATR	AP	Elevation	TR	Area
Latitude										
C	-0.006									
M	-0.157	0.739								
S	0.292	-0.400	-0.657							
MAT	-0.070	-0.031	-0.006	0.378						
MATR	0.586	0.261	0.178	0.277	0.576					
AP	-0.503	0.138	0.270	-0.145	0.388	-0.043				
Elevation	0.426	0.528	0.495	-0.363	-0.323	0.391	-0.202			
TR	0.094	0.592	0.609	-0.505	-0.231	0.235	0.020	0.753		
Area	0.247	0.590	0.648	-0.499	-0.180	0.344	-0.034	0.758	0.791	
LCR	0.367	0.093	0.039	0.130	0.098	0.405	-0.055	0.254	0.244	0.290

\*C, cumulative annual productivity; M, annual minimum productivity; S, seasonal variation in productivity; MAT, mean annual temperature; MART, mean annual temperature range; AP, annual precipitation; TR, topographic relief; LCR, land cover richness.

Appendix 5.  $R^2$  values for simple ordinary least squares models of species richness for different guilds derived from range maps and 14 environmental variables. Sign indicates direction of relationship. Bolded variable names indicate variables included for subsequent analysis due to correlations with bird species richness guilds ( $R^2$  values  $> 0.05$ ) and less collinearity among variables based on Pearson's correlation coefficients  $|r| < 0.8$ . C, cumulative annual productivity; M, annual minimum productivity; S, seasonal variation in productivity; MAT, mean annual temperature; MART, mean annual temperature range; AP, annual precipitation; TR, topographic relief; LCR, land cover richness.

Variable	All birds	Resident birds	Migratory birds	Forest birds	Early-successional birds	Farmland birds	Wetland birds	Seacoast birds
<b>Latitude</b>	0.02***	0.01**	0.23***	0.01***	0.28***	0.78***	0.56***	-0.67***
<b>C</b>	0.58***	0.63***	0.26***	0.63***	0.22***	-0.03***	NS	0.07***
<b>M</b>	0.34***	0.38***	0.09***	0.38***	0.10***	-0.06***	-0.01***	0.07***
<b>S</b>	-0.35***	-0.39***	-0.10***	-0.38***	-0.10***	0.07***	0.01***	-0.11***
<b>MAT</b>	-0.43***	-0.42***	-0.32***	-0.45***	-0.40***	-0.06***	-0.06***	0.07***
<b>MATR</b>	0.17***	0.13***	0.28***	0.15***	0.36***	0.50***	0.46***	-0.58***
<b>MAP</b>	NS	NS	-0.05***	NS	0.08***	-0.43***	-0.28***	0.32***
<b>Elevation</b>	0.48***	0.47***	0.38***	0.49***	0.46***	0.12***	0.13***	0.09***
<b>TR</b>	0.53***	0.57***	0.28***	0.56***	0.31***	0.01**	0.02***	NS
<b>LCR</b>	0.02***	0.02***	0.03***	0.02***	0.04***	0.11***	0.02***	-0.13***
<b>Area of forest</b>	0.50***	0.51***	0.31***	0.52***	0.35***	0.06***	0.05***	-0.01***
Area of scrub	0.03***	0.04***	0.02***	0.04***	0.02***	0.01**	NS	NS
Area of agriculture	-0.49***	-0.50***	-0.30***	-0.51***	-0.34***	-0.07***	-0.05***	0.02***
Area of wetland	-0.02***	-0.02***	-0.01**	-0.02***	-0.01***	NS	NS	-0.01*
Area of coast	NS	NS	NS	NS	NS	0.01**	NS	0.01*

\*\*\*  $P$ -value  $< 0.001$ , \*\*  $P$ -value  $< 0.01$ , \*  $P$ -value  $< 0.05$ , NS, not significant.



Appendix 6.  $R^2$  values for simple ordinary least squares models of species richness for different guilds derived from species distribution model prediction maps and 14 environmental variables. Sign indicates direction of relationship. Bolded variable names indicate variables included for subsequent analysis due to correlations with bird species richness guilds ( $R^2$  values  $> 0.05$ ) and less collinearity among variables based on Pearson's correlation coefficients  $|r| < 0.8$ . C, cumulative annual productivity; M, annual minimum productivity; S, seasonal variation in productivity; MAT, mean annual temperature; MART, mean annual temperature range; AP, annual precipitation; TR, topographic relief; LCR, land cover richness.

Variable	All birds	Residents	Migratory birds	Forest birds	Early-successional birds	Farmland birds	Wetland birds	Seacoast birds
<b>Latitude</b>	0.03***	0.02***	0.04***	0.02***	0.18***	<b>0.55***</b>	-0.03***	<b>-0.44***</b>
<b>C</b>	<b>0.53***</b>	<b>0.57***</b>	<b>0.18***</b>	<b>0.60***</b>	0.01**	-0.02***	<b>-0.30***</b>	0.05***
<b>M</b>	<b>0.40***</b>	<b>0.42***</b>	<b>0.10***</b>	<b>0.46***</b>	NS	<b>-0.06***</b>	<b>-0.25***</b>	0.05***
<b>S</b>	<b>-0.39***</b>	<b>-0.40***</b>	<b>-0.13***</b>	<b>-0.42***</b>	NS	<b>0.07***</b>	<b>0.19***</b>	<b>-0.09***</b>
<b>MAT</b>	<b>-0.32***</b>	<b>-0.48***</b>	<b>-0.24***</b>	<b>-0.53***</b>	<b>-0.14***</b>	-0.04	<b>0.38***</b>	0.02***
<b>MATR</b>	<b>0.18***</b>	<b>0.12***</b>	<b>0.06***</b>	<b>0.13</b>	<b>0.08***</b>	<b>0.50***</b>	<b>-0.15***</b>	<b>-0.36***</b>
<b>MAP</b>	-0.01***	-0.01***	-0.04***	-0.00*	-0.07***	-0.65***	-0.01*	<b>0.20***</b>
<b>Elevation</b>	<b>0.63***</b>	<b>0.62***</b>	<b>0.31***</b>	<b>0.67***</b>	<b>0.14***</b>	<b>0.10***</b>	<b>-0.39***</b>	-0.05***
<b>TR</b>	<b>0.62***</b>	<b>0.63***</b>	<b>0.19***</b>	<b>0.67***</b>	0.02***	0.01*	-0.42***	NS
<b>LCR</b>	0.03***	0.02***	NS	0.03***	0.04***	<b>0.11***</b>	<b>-0.14***</b>	<b>-0.07***</b>
<b>Area of forest</b>	<b>0.73***</b>	<b>0.73***</b>	<b>0.26***</b>	<b>0.77***</b>	<b>0.08***</b>	0.04***	<b>-0.44***</b>	-0.01**
Area of scrub	0.05***	0.05***	0.00*	0.05***	NS	NS	-0.05***	NS
Area of agriculture	-0.72***	-0.72***	-0.25***	-0.76***	-0.07***	-0.03***	0.44***	0.01**
Area of wetland	-0.01***	-0.02***	-0.01***	-0.02***	NS	NS	NS	-0.01*
Area of coast	NS	NS	0.01**	NS	NS	NS	NS	0.03***

\*\*\*  $P$ -value  $< 0.001$ , \*\*  $P$ -value  $< 0.01$ , \*  $P$ -value  $< 0.05$ , NS, not significant.

Appendix 7. Pearson's correlation coefficients ( $r$ ) between species richness for each guild derived from range maps and species distribution model prediction maps.

Species distribution model prediction map (#species)	All birds (336)	Resident birds (261)	Migratory birds (75)	Forest birds (222)	Early-Successional birds (15)	Farmland birds (26)	Wetland birds (49)	Seacoast birds (24)
Rang map (#species)								
All birds (888)	0.74							
Resident birds (664)	0.74	0.75						
Migratory birds (224)	0.63	0.61	0.62					
Forest birds (636)	0.75	0.75	0.52	0.77				
Early-Successional birds (47)	0.64	0.63	0.57	0.62	0.25			
Farmland birds (35)	0.19	0.18	0.24	0.16	0.33	0.74		
Wetland birds (113)	0.26	0.24	0.40	0.20	0.28	0.66	0.15	
Seacoast birds (57)	0.04	0.03	0.08	0.00	-0.30	-0.58	-0.39	0.75

## **Chapter 2: The effects of habitat heterogeneity, as measured by satellite image texture, on tropical forest bird distributions**

### **Abstract**

Habitat heterogeneity is a key landscape characteristic influencing species distributions and diversity patterns. However, assessments of habitat heterogeneity at broad-scales are difficult and therefore limited. Our goal was to evaluate the performance of satellite image texture measures as an indicator of habitat heterogeneity for predicting tropical forest bird distributions over broad areas with varying levels of vertical forest habitat structure. We calculated a suite of texture measures from satellite-derived productivity data (1-km fPAR MODIS data) over only forested areas across Thailand. We evaluated these texture measures in terms of their ability to provide within-class habitat heterogeneity in species distribution models for 86 tropical forest bird species. We tested the predictive power of these models against models with landscape metrics derived from categorical land cover data. Measures of texture were effective in predicting occurrences of tropical forest birds, and homogeneity was the best predictor among texture measures. However, by themselves, both habitat composition-only and fragmentation-only measures were better predictors of species distributions than texture-only measures. Combining texture measures with habitat composition-only data significantly improved model accuracy though, and that combination performed better than habitat composition-only plus fragmentation measures. Based on our results, we suggest that satellite texture measures can predict species distributions at broad scales in regions with complex habitat heterogeneity such as tropical forests. Incorporating texture measures into broad-scale species distribution models may contribute to a better understanding of the mechanisms underlying species distributions and to more accurate predictions of range shifts due to land use and climate change.

## Introduction

Combating the crisis of biodiversity loss due to human activities and climate change requires efficient and accurate assessments of broad-scale patterns of biodiversity (Pereira et al. 2013; Scholes et al. 2008; Sutherland et al. 2009). Remotely sensed data are increasingly used to model and understand species diversity and distributions at relevant temporal and spatial scales (Kerr and Ostrovsky 2003; Turner 2014; Turner et al. 2003). The challenge is how to quantify habitat features that are ecologically relevant to the species or taxa of interest. The use of satellite image texture has proved to be useful in capturing heterogeneity of land cover and vegetation (Culbert et al. 2009; Haralick et al. 1973; Wood et al. 2012). However, broad-scale assessments of species diversity-heterogeneity patterns have been conducted almost exclusively in temperate ecosystems (Culbert et al. 2012; Hepinstall and Sader 1997; St-Louis et al. 2009). Incomplete assessments of species diversity-heterogeneity patterns in tropical ecosystems continues to hamper understanding of the underlying mechanisms shaping such patterns, hindering conservation efforts (Tuanmu and Jetz 2015). Measures of habitat heterogeneity designed to predict biodiversity at scales relevant to conservation planning and the specific mechanisms underlying biodiversity patterns are needed to improve conservation and habitat management in the tropics.

Habitat heterogeneity is an important landscape attribute influencing species and ecosystem functions (Kerr and Packer 1997; Macarthur and Macarthur 1961; Stein et al. 2014), and essential for mapping and monitoring broad-scale patterns of biodiversity (Culbert et al. 2012; St-Louis et al. 2014b). Spatial heterogeneity of habitat affects metapopulations and communities by influencing movement patterns of individuals, intra- and interspecific interactions among organisms, and exposure to physical structure of habitats such as edge effects

(Benton et al. 2003; Fahrig 2003). Species perceive heterogeneity of their habitats at multiple scales throughout their life history (Morrison et al. 2006). At fine scales, heterogeneity of vegetation structure strongly influences bird assemblages (Bersier and Meyer 1994). Species may select habitat for nesting and foraging in association with heterogeneity in vertical and horizontal vegetation structure (Martin 1993). At broad scales, habitat heterogeneity influences the spatial patterns of species richness and distributions (Bellis et al. 2008; Culbert et al. 2012). Species may respond to heterogeneity in landscapes, such as forest fragmentation, depending on their habitat area requirement and ability to cross gaps (Dale et al. 1994). While the effects of habitat heterogeneity on species distribution patterns are well documented in temperate regions (Hepinstall and Sader 1997; Tuttle et al. 2006), its effects on species distributions at broad scales in tropical ecosystems is not. This knowledge gap is unfortunate because a better understanding of the effects of habitat heterogeneity on current patterns of species distributions is essential for biodiversity conservation and habitat management.

The habitat heterogeneity hypothesis predicts that more varied habitat can support greater numbers of species because more heterogeneous habitat structure provides more foraging niches thereby allowing more species to co-exist (Hutchinson and MacArthur 1959; MacArthur and MacArthur 1961). However, the positive species-heterogeneity relationship is not universally true (Bar-Massada and Wood 2014; Tews et al. 2004). However, the strength of relationship varies, and can be positive, negative, unimodal, or flat depending on ecological characteristics of species or the taxonomic group (Bellis et al. 2008; Hepinstall and Sader 1997), scales (Bar-Massada et al. 2012), habitat type (Estes et al. 2010), biodiversity indices (e.g., species richness, abundance, or distribution) (St-Louis et al. 2014b).

Modeling broad-scale patterns of species-heterogeneity benefits greatly from the use of remotely sensed data (Bellis et al. 2008; St-Louis et al. 2014b; Tuanmu and Jetz 2015). Direct field measures of habitat heterogeneity, while effective in explaining species distributions and diversity patterns, are time consuming and labor intensive. Consequently, field-based studies of habitat heterogeneity and diversity are typically limited to small areas (Innes and Koch 1998). The advantages of spatially continuous coverage by satellite data, have prompted many broad-scale studies to employ satellite imagery, and heterogeneity measures derived from, for example, elevation or categorical land cover data (Kerr and Packer 1997; Rahbek et al. 2007). However, land-cover-based and elevation-based heterogeneity measures have shortcomings. Land cover classification gives some information on spatial and temporal dynamics of habitat types, but ignores within-class habitat heterogeneity (St-Louis et al. 2006). Elevation-based data, on the other hand, do not capture vegetation patterns directly, and is only one of many factors determining habitat heterogeneity. Recently, using high-spectral and spatial satellite data from space-borne systems, such as Light Detection and Ranging (LiDAR) and Synthetic Aperture Radar (SAR) have gained importance as effective approaches to detect heterogeneity of vegetation structure, but data from these active sensors is not widely available (Nagendra and Rocchini 2008).

Image texture has high potential for characterizing habitat, and thus for improving upon methods for mapping and monitoring biodiversity. The texture of a satellite image contains information about the spatial and structural arrangement of objects (Haralick et al. 1973). Image texture quantifies the pattern of brightness variations or grey-levels within an image or region within an image. There are two classes of texture measures: first-order (occurrence) and second-order measures (co-occurrence) (Haralick et al. 1973). First-order texture measures are based on

the frequency distribution of pixel values (i.e., cumulative annual fPAR) in a defined neighborhood within an image, typically implemented as a moving window. Second-order texture measures are based on the differences in spectral values among neighboring pixels (i.e., the grey-level co-occurrence matrix, GLCM) (Haralick et al. 1973). The first-order measures are based on individual pixel values which reflect their compositional variability, whereas the second-order measures are determined by the interaction or co-occurrence of pixel values which reflect their spatial arrangement and dependence. Characteristics of different texture measures relate to spatial and spectral variation in a satellite image. Additionally, texture measures reflect heterogeneity among land cover classes, such as sharp transitions between forest and pasture (Haralick 1979). Therefore, texture measures are useful for characterizing land cover (Franklin et al., 2000; 2001), and habitat modeling (Bellis et al. 2008; Estes et al. 2008; Tuttle et al. 2006).

Satellite observations provide a suite of vegetation indices to calculate texture measures in order to assess habitat heterogeneity at broad scales. The challenge is how to derive measures of texture that are most relevant for species distributions. For example, NDVI-based texture derived from Landsat imagery can predict species distributions of birds in the northeastern United States (Hepinstall and Sader 1997), and species richness of birds in the desert Southwest (St-Louis et al. 2009) and the Midwestern United States (Culbert et al. 2012; Wood et al. 2013). EVI – based texture derived from Moderate Resolution Imaging Spectroradiometer (MODIS) can explain bird species richness patterns in the United States (Tuanmu and Jetz 2015). Texture measures can also be assessed based on spatial data on the fraction of light absorbed by the vegetation (fPAR) imagery from MODIS data. MODIS fPAR is grounded in species-energy availability theory, and, as a measure of available energy, has successfully predicted biodiversity patterns for fauna in the temperate regions (Coops et al. 2009a; Coops et al. 2009b). So far

MODIS fPAR data has not been used to derive texture measures for species distribution modeling. This is unfortunate, because MODIS fPAR data are available at high temporal resolution and over broad scales, thus providing a potentially greater opportunity to develop relevant, consistent, and applicable texture measures for biodiversity assessments (Coops et al. 2008). However, the use of MODIS fPAR data as texture measures to capture within-class habitat heterogeneity across broad spatial extents has not been tested.

Texture measures derived from remotely sensed data have successfully predicted species distributions and richness patterns of species at broad scales. Texture–species relationships have been studied for multiple taxa in a variety of habitat types, such as bird species richness in North American desert shrub land and grassland (St-Louis et al. 2009; St-Louis et al. 2014a), Wisconsin grassland, savanna, and woodland (Wood et al. 2013), Midwestern ecoregions (Culbert et al. 2012), the United States (Tuanmu and Jetz 2015), and South American highland forests (Bellis et al. 2015). The relationship between species distribution patterns and habitat heterogeneity has been demonstrated for mountain bongo in east African montane forest (Estes et al. 2008; Estes et al. 2010), the red tail monkey (Stickler and Southworth 2008), the Greater Rhea in grassland Argentina (Bellis et al. 2008), and bird distributions in Maine (Hepinstall and Sader 1997). Studies of bird distributions in Maine and Argentina show the association with heterogeneous habitats (Bellis et al. 2008; Hepinstall and Sader 1997). To our knowledge, the species distribution–heterogeneity relationship for tropical forest birds has not yet been evaluated. Birds, in particular, respond to a variety of habitat features, and capturing the breadth of those features using remotely sensed data is challenging. Thus, it still remains unclear whether texture measures derived from MODIS fPAR data can predict broad-scale species distribution



patterns of forest birds in structurally complex, closed-canopy habitat such as tropical forest ecosystems.

Our goal was to evaluate the ability of satellite image texture measures derived from MODIS fPAR to predict tropical bird species distributions. Our specific objectives were to test: (1) if texture measures can predict distributions of tropical forest bird specialists across broad scales, and (2) how these models based on texture measures compare with models based on measures of habitat availability and habitat fragmentation, and can these variables complement each other to improve species distribution modeling of tropical birds. We hypothesize that texture measures can describe broad-scale distributions of species utilizing forest habitats with complex vertical and horizontal habitat structure, and perform particularly well for species with large body size and that nest in tree cavities or canopies, compared to species with smaller body size that utilize simple vertical and horizontal structure and nest on the ground or in the understory. We hypothesize that including texture measures would improve model performance for predicting tropical bird distributions because landscape metrics derived from land cover classification ignore within-habitat variability, whereas texture measures capture both within and between habitat heterogeneity. Furthermore, we expected that texture measures would complement measures of habitat composition and fragmentation in particular for area- and edge-sensitive species.

## Methods

### *Study area*

Our study area was the tropical forest ecosystems of Thailand covering 163,391 km<sup>2</sup> (32% of the country total area, RFD 2013) (Figure 6). The climate is seasonal with monsoons, a rainy and a dry season. Annual precipitation ranges between 1000 mm and 4000 from May to October in the rainy season. The average annual temperature is approximately 26-29 °C, and the highest temperature is approximately 40 °C in April (TMD 2010). The study area consists of two major diverse types of tropical forest: broad-leaved evergreen forest and broad-leaved deciduous forest. The tropical broad-leaved evergreen forest contains multiple forest habitat types including montane evergreen forest, dry evergreen forest, rain forest, pine forest, swamp forest, mangrove forest, and beach forest. The tropical broad-leaved deciduous forest includes mixed deciduous forest and dry dipterocarp forest (RFD 2013). Thailand is a global biodiversity hotspot (Myers et al. 2000) , and is home to more than 1,000 bird species (Bird Conservation Society of Thailand Records Committee 2012). However, Thailand is facing extensive forest loss and fragmentation which has led to a decline in forest bird diversity (Pattanaivibool and Dearden 2002; Round and Gale 2008; Woodruff 2013).

### *Study species and occurrence data*

To evaluate the utility of texture measures for species modelling, we obtained data on bird species occurrences from the Global Biodiversity Information Facility (GBIF) (<http://www.gbif.org/>). The bird GBIF data for Thailand is mainly based on opportunistic observations and some field survey data. For the purpose of our study, we focused on resident forest bird species to investigate the ability of texture measures in predicting bird distributions utilizing different forest habitat types all year round. We analyzed all georeferenced records

collected from 2000-2015, to temporally coincide with texture and landscape metric data. We included all species with greater than 30 unique localities as the minimum sample size required for species distribution modeling (Hernandez et al. 2006; Pearson et al. 2007). We assembled 86 forest specialist bird species of 5 taxonomic orders and 28 families with a total of 12,858 georeferenced records (Table 7). All samples were georeferenced to the spatial resolution of the environmental data that we used (1 km<sup>2</sup>).

#### *Texture measure data*

To characterize texture, we calculated a suite of texture measures (Table 8) based on the 1-km MODIS fPAR data from the MOD15A2. We acquired 8-day mosaics of Collection 5 data from 2003-2014. We analyzed a 12-year time period to balance potential land-cover changes and a sufficient number of cloud-free fPAR values to characterize the greenness. To characterize the greenness throughout a year, we extracted the MODIS fPAR value for the 15<sup>th</sup> of each month, and calculated the cumulative annual productivity by summing monthly MODIS observations for each year (Coops et al. 2009a; Coops et al. 2008). To exclude artificially low fPAR values over water, we masked the pixels covered by water, and we selected the median value of the 12-year time series for each date to exclude low values due to sensor errors or missing data. Details about the way the fPAR composite image was derived can be found in Radeloff et al (in preparation).

We calculated three first-order texture measures: entropy, mean, and variance in a 3×3 moving window. We also calculated eight second-order texture measures: angular second moment, contrast, correlation, dissimilarity, entropy, homogeneity, mean, and variance (Haralick et al. 1973). We selected these texture measures based on their ability to characterize vegetation structure, and therefore be relevant measures for bird species distributions (Bellis et al. 2008; Hepinstall and Sader 1997; Wood et al. 2012). We quantized the imagery to 64 values to limit

the size of the GLCM and avoid matrices that are too sparsely populated (Culbert et al. 2012). We calculated the texture measures for adjacent pixels as the mean of the four possible directional GLCMs (0°, 45°, 90° and 135°) (Haralick et al. 1973). We calculated texture measures using ENVI software (Exelis Visual Information Solutions, Boulder, Colorado). The texture data were projected to the WGS84 geographic coordinate system with UTM47N using bilinear convolution (Figure 7). Many texture measures are correlated (Culbert et al. 2012) and we applied a Pearson's correlation coefficient threshold ( $|r| > 0.7$ ) to exclude collinear variables (Dormann et al. 2013), which reduced the eleven texture measures to five measures: first-order coefficient of variation, second-order homogeneity, correlation, contrast, and entropy (Appendix 9).

#### *Habitat composition data*

We generated habitat composition at 1-km resolution based on categorical land-cover data. These measures are commonly used to predict bird species distributions in broad-scale studies (Jetz and Rahbek 2002; Kerr and Packer 1997; Kreft and Jetz 2007). We calculated habitat composition from the 2000 Thailand land cover map with a 30-m resolution, derived from Landsat TM, ETM+. To quantify habitat composition measures, we calculated the proportion of habitat area within a 1-km grid cell for six forest habitat types: montane evergreen forest, dry evergreen forest, lowland evergreen forest, mixed deciduous forest, dry dipterocarp forest, and secondary-growth forest.

#### *Habitat fragmentation data*

We also calculated five fragmentation measures of forest habitat from the 2000 Thailand land cover map for core, edge, perforation, bridge, and loop with the Morphological Spatial Pattern Analysis (MSPA) implemented in GUIDOS analytical tool (Vogt et al. 2007). The

MSPA is based on morphological image segmentation allowing an automated per-pixel classification and description of the geometry, pattern, fragmentation, and connectivity of a landscape (Soille and Vogt 2009; Vogt et al. 2007). We selected five fragmentation metrics, (1) core is defined as forest pixels whose distance to the non-forested areas is greater than the edge width, and is considered as the focal habitat area for birds, (2) 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, (3) perforation is similar to edge, but it corresponds to the inner boundary of a core forest area, (4) bridge is a set of contiguous non-core forest pixels connecting at least two forest patches, (5) loop is a group of pixels that connect different parts of the same forest patch (Saura et al. 2011; Soille and Vogt 2009).

### *Species distribution models*

We used logistic regression models (GLMs, McCullagh and Nelder, 1989) to (1) evaluate whether MODIS fPAR texture can predict bird species distributions, (2) evaluate whether combining measures of texture with habitat composition and fragmentation derived from land cover classifications can improve model performance for species distributions.

We fitted all possible combinations of (i) texture, (ii) composition, (iii) fragmentation, (iv) texture + composition, (v) fragmentation + composition, and (vi) texture + fragmentation + composition. To assess multicollinearity among the 16 texture, habitat composition, and fragmentation variables, we applied Pearson's correlation coefficients ( $|r| > 0.7$ ) and found that there was no collinearity among them (Appendix 10). To address potential nonlinearities in the relationship between species distributions and predictors, we included both linear and quadratic forms of predictors in the models. The best approximating model was then selected based on the Akaike Information criterion (AIC) with the best fitting model having the lowest AIC (Burnham

and Anderson, 2002). The GLM modeling algorithm requires binary or background data, so we generated pseudo-absences by randomly sampling 1-km grid cells within forested areas. Generating pseudo-absences from environmental regions further away from the optimum established by presence data may lead to over-prediction of the model (Bateman et al. 2012; VanDerWal et al. 2009). For each model run, we constructed two sets of pseudo-absences, each chosen at random to obtain more reliable distribution model outputs (Thuiller et al. 2009). We generated pseudo-absences as ten times the number of presence records (Barbet-Massin et al. 2012).

To evaluate model performance, we used 10-fold cross-validation with a split random sample of 90% of presence data used for calibration (training data) and the remaining 10% for evaluation (testing data) (Elith et al. 2011). During the calibration process, we gave equal weighting to presence data and pseudo-absence data. For each species, we used 10-fold cross validation on the two pseudoabsence replicates, for a total of 20 replicates each. We used AUC values to test model performance, and initially considered values above 0.7 to be indicative of useful models (Elith et al. 2006; Swets 1988).

The importance of each variable for each species was calculated using a randomization procedure as one minus the Pearson's correlation coefficients between the standard prediction and the prediction where the considered variables was randomly permuted. If the correlation is high (i.e., there is a small difference between the two predictions), the variable permuted is considered not important for the model. Therefore, one minus the correlation coefficient represents, for a given variable, the probability that the coefficient can contribute to the model. The higher the probability, the higher a variable contributes in predicting the pattern (Thuiller et al. 2009).

### *Model comparison*

To determine whether including texture measures are important in predicting current distributions of tropical forest birds in Thailand, we compared estimators of model performance (i.e., AUC) between composition and texture, and between composition and texture + composition, and between composition and texture + fragmentation + composition. We used Wilcoxon signed-rank tests for related samples to test the significant difference among models. Additionally, we examined whether the texture + composition + fragmentation models for all bird species consistently select the texture measures (Araujo and Luoto 2007; Bateman et al. 2012).

For each species, we calculated the relative difference of AUC values of the composition, texture + composition, fragmentation + composition, and texture + fragmentation + composition ( $\Delta$  AUC). Large relative values of  $\Delta$  AUC indicate that one model scenario performed substantially better than the other, whereas  $\Delta$  AUC values close to zero indicate that the two model scenarios performed equally well. All statistical analyses were conducted in R (R Core Team 2015). GLMs were fitted within the BIOMOD2 package (Thuiller 2003; Thuiller et al. 2009).

## **Results**

### *Texture measures as predictors of species distributions*

Texture measures effectively predicted species distributions for 86 tropical forest birds with an average AUC value of 0.80 (AUC > 0.7 is a fair model, Swets 1988) (Table 9). However, the predictive accuracies of models varied across species and taxonomic orders. Of all species modelled, Tickell's Brown Hornbill (*Anorrhinus tickelli*) had the highest AUC values of 0.94 (Appendix 8). Among different taxonomic orders, Bucerotiformes (i.e., hornbill species)

had the highest AUC values with an average AUC value of 0.87. On the other hand, the forest bird species in Passeriformes and Piciformes taxonomic groups had the lowest AUC values with an average AUC value of 0.79 (Figure 8). As we expected, texture measures derived from 1-km MODIS fPAR well predicted large body size-forest bird species, such as hornbill species because hornbill species perceive and utilize forest structure at larger scales than smaller species, and thus are influenced more by heterogeneity of forest structure.

In comparison to habitat composition and fragmentation, the composition models outperformed fragmentation models ( $P < 0.001$ ), and texture models ( $P < 0.001$ ). However, the texture + composition models were significantly better than the fragmentation + composition models ( $P < 0.001$ ) (Figure 8), indicating the complementarity of information carried by measures of texture. We found that there was considerable variation in AUC values among species and the AUC values of the composition models were not higher in all species. Texture measures better predicted Grey Peacock Pheasant, Yellow-vented Flowerpecker, Greater Necklaced Laughingthrush, Lesser Necklaced Laughingthrush, and Buff-vented Bulbul distributions than measures of composition and fragmentation (Appendix 8). At the taxonomic level, forest bird species in Bucerotiformes showed no significant difference in AUC values between texture models and fragmentation models ( $P = 0.875$ ) (Figure 8), indicating that this group of species may perceive habitat heterogeneity as habitat fragmentation due to their large home range size.

#### *The incorporation of texture measures with habitat composition and fragmentation*

The incorporation of texture measures significantly improved species distribution models for tropical forest birds. The texture + composition + fragmentation models for all bird species consistently selected the texture measures, especially homogeneity and contrast (results not



shown). The incorporation of texture measures into the models for tropical forest birds significantly improved the AUC values from 0.889 ( $\pm 0.057$  SD), for the composition models to 0.927 ( $\pm 0.0576$  SD) for the texture + composition + fragmentation models (Table 9) with relative gains up to 39% in Bar-backed Partridge (results not shown) and average 10% in Galliformes ( $P < 0.001$ ) (Figure 9). Likewise, including texture or fragmentation significantly improved model performance compared with composition models ( $P < 0.001$ ). Galliformes showed the highest increase of the relative AUC values. However, Bucerotiformes and Cuculiformes taxonomic groups showed no difference in the relative AUC values after including fragmentation into texture + composition models (Figure 9). While confirming the importance of habitat composition and fragmentation, these results also highlight the importance of including texture measures to predict the distributions of tropical forest bird at the broad-scales.

#### *Variable importance of texture measures*

Second-order homogeneity was the best predictor for overall bird species distributions when using texture measure alone (Figure 10). At the taxonomic level, Bucerotiformes, Cuculiformes, Passeriforme, and Piciformes were strongly associated with second-order homogeneity whereas Galliformes was highly associated with second-order entropy. Second-order homogeneity, and contrast were the best complement to habitat composition and fragmentation for modeling species distributions, highlighting their relevance for capturing habitat characteristics. The relationships of texture measures and species distributions varied, sometimes positive, negative, and nonlinear depending on species and taxonomic groups. Almost all texture measures showed nonlinear relationships in the most parsimonious model for each species (lowest AIC) (results not shown). We thus chose Tickell's brown hornbill with the highest model accuracy to investigate the strength of the relationships. We found that the

probability of occurrences of Tickell's brown hornbill increased as homogeneity and correlation values increased but not linearly, while the probability of occurrences decreased as coefficient of variation and contrast increased. The probability of occurrences was higher at the middle level of entropy values. These results indicated that the probability of occurrences for Tickell's brown hornbill were high in highly homogeneous areas (Figure 11).

### *Habitat suitability maps*

To validate that the distribution models from the texture + fragmentation + composition improved the predictions from the habitat composition models, we investigated the suitability maps of the brown hornbill. We selected brown hornbill because this species is an IUCN non-threatened concern facing serious threat from human activities, such as deforestation, and illegal poaching (Poonswad et al. 2013; Round 1988). A visual inspection of the predicted potential geographic distributions of Brown Hornbills derived from both models showed a broad agreement with the currently known distribution from 15 protected areas across Thailand that covers the extent of dry and montane evergreen forest biomes with elevation ranges of 500-1500 m (Poonswad 1993; Round et al. 2003). However, the texture + fragmentation + composition model (Figure 12a) agreed better with the known range whereas the habitat composition model over-predicted suitable areas (Figure 12b).

## **Discussion**

We evaluated the ability of image texture measures, a proxy of within-class habitat heterogeneity, to predict distributions of tropical forest birds at broad scales. We found that image texture measures derived from 1-km MODIS fPAR effectively predicted the distributions of tropical forest birds across Thailand. As expected, texture measures strongly associated with broad-scale distributions of forest bird species utilizing forest habitats with complex vertical and

horizontal structure such as those nesting in old-growth tree cavities, compared to species utilizing forest habitats with simpler vertical and horizontal structure, such as ground-nesting species. Texture measures complemented measures of habitat composition well, and more so than fragmentation metrics. Our results suggest that texture measures successfully captured habitat heterogeneity and provide detailed information which can complement measures of habitat composition when predicting patterns of species distributions. Given this, we suggest that texture-based MODIS fPAR measures can contribute to a better understanding of patterns of species distributions and diversity at broad temporal and spatial scales.

Our results support previous studies modeling species distributions based on image texture, for example the Greater Rhea, a grassland bird species of central Argentina (Bellis et al. 2008), and temperate birds in Maine (Hepinstall and Sader 1997) as well as bird richness patterns in savanna, grassland, and woodland (Wood et al. 2013), desert-scrub (St-Louis et al. 2009; St-Louis et al. 2014a; St-Louis et al. 2006), North American ecosystems (Culbert et al. 2012; Tuanmu and Jetz 2015), and South American highland forests (Bellis et al. 2015). While modeling bird distribution patterns has been effective in habitats with low vertical structure, such as grassland (Bellis et al. 2008), and among habitat generalists (Hepinstall and Sader 1997), we showed that image textured derived from MODIS fPAR can capture within-class habitat heterogeneity and successfully predict species distribution patterns even in habitats with highly complex habitat structure as is common in tropical forest ecosystems.

As we expected, texture measures predict distributions for species with large body size utilizing complex vertical and horizontal habitat structure better, than those of smaller body size species utilizing understory vegetation structure. Specifically, tropical forest birds in Bucerotiformes taxonomic group, such as hornbills strongly associated with texture measures.

Hornbills are large-size frugivorous bird species ( Poonswad et al. 1998; Lekagul and Round 1991; Kitamura et al. 2004) with approximately body mass of 0.9 – 3 kg (Dunning 2008), and with an average home range size of 3.7 - 10 km<sup>2</sup> for the breeding season and 14.7 - 28 km<sup>2</sup> for the non-breeding season in Thailand (Poonswad and Tsuji 1994). Hornbills nest in tree cavities and gather to feed in fruiting trees, and thus require old-growth evergreen forests and mixed deciduous forests (Poonswad 1995; Poonswad et al. 2005). In contrast, smaller body size, canopy or understory foraging and nesting bird species had lower associations with texture measures. These taxonomic groups, such as pheasant, cuckoo, flycatcher, and piculet may perceive habitat heterogeneity at different scales, causing texture measures to have lower predictive power (Robson 2000; Round 1988). While satellite imagery is generally not well suited to measure the structure of understory vegetation in forests (Gottschalk et al. 2005), understory mapping can be successful when structural characteristics are correlated with canopy features (Estes et al. 2010).

The combined texture with habitat composition and fragmentation models yielded the highest model accuracies compared to models derived from habitat composition, and predicted more accurate suitable habitat for tropical forest bird species. The best models included a relatively even mix of texture, fragmentation, and habitat composition because each measure is important and contributes to different aspects that shape species distributions, richness, and abundance differently, and species may respond to those factors differently. We expected that including texture measures into distribution models would improve model performance more because texture measures capture additional characteristics of heterogeneity of forest structure that are useful in predicting distribution patterns. Texture measures capture the between and within heterogeneity of a given forest type, whereas habitat composition and fragmentation based on land cover classification do not provide within land cover class heterogeneity (Estes et

al. 2010). This explains the complementary information of texture measures with commonly used habitat composition and fragmentation measures in predicting species distributions. Surprisingly though, model accuracies for hornbill and cuckoo species showed no improvement of model accuracies after including fragmentation measures into the combined texture and habitat models. This highlights the importance of habitat heterogeneity for canopy-species. Previous studies also showed that the combination of texture, productivity, landscape metrics, and human disturbance resulted in a better understanding of the relationships between bird species richness in Midwest temperate ecosystems (Culbert et al. 2012), Southwest desert-scrub (St-Louis et al. 2014b; St-Louis et al. 2006), and across the United States (Tuanmu and Jetz 2015) as well as bird distributions in Argentinian grassland (Bellis et al. 2008).

A few image texture measures were most important in predicting bird distribution at broad-scales. Although species-heterogeneity predicts a positive relationship where more heterogeneity results in higher species diversity (Macarthur and Macarthur 1961), most of texture measures in our study had a nonlinear relationship. Theoretical and empirical studies have suggested that a trade-off between the positive effect of high habitat heterogeneity and the negative effect of small habitat areas on species diversity may cause an unimodal species-heterogeneity relationship (Allouche et al. 2012; Kadmon and Allouche 2007). Second-order homogeneity was the most important factor in predicting tropical forest bird distributions but exhibited nonlinear relationships with most species. Second-order homogeneity is a measure of uniformity and is high when adjacent pixels have similar reflectance values, suggesting that tropical bird occurrences are more likely in homogeneous habitats. The reason for this may be that among different forest types, evergreen forests are generally more homogenous than deciduous forests and secondary-growth forests (Appendix 11). Most of our study species

occupy evergreen forests, which is why homogeneity of habitat may be more important than other texture measures. In contrast, we found that second-order entropy was the most important factor in predicting ground foraging and nesting species, such as pheasants and partridge. This taxonomic group utilizes a variety of forest habitat structure from evergreen to scrub and forage a variety of diet such as invertebrate, grains, buds, seeds, and fallen fruits. This may make Galliformes respond positively to higher heterogeneity. Our findings are supported by a previous study on bird species richness patterns with texture based MODIS EVI showing that the texture measures sensitive to low levels of heterogeneous habitat (e.g., entropy) are useful for homogeneous areas, such as forest ecosystem, while measures that have similar sensitivity across heterogeneity levels (e.g., homogeneity) are useful for diverse habitat types (Tuanmu and Jetz 2015). This is likely the reason why homogeneity and entropy were the most useful measures for capturing spatial heterogeneity in forest ecosystems.

When we compared species distribution models based on texture versus habitat composition versus fragmentation, we found that both sets of habitat measures outperformed texture-only measures. This supports the theory that habitat heterogeneity of vegetation structure is more important in explaining species diversity at small- scales, but spatial patterns of landscape elements are more important at broad-scales (Hutto 1985). The only exception was the hornbill, which showed no significant difference in model accuracy when modeling with texture-only variables or fragmentation-only variables. We speculate that this is due to that fact that because of its large body size, hornbill species perceive within-forest structure as fragmentation of habitat.

Texture measure derived from MODIS fPAR improved model predictions for tropical bird distributions, but many texture measures are difficult to interpret in terms of their

relationships with individual species and ecological processes (Culbert et al. 2012). We developed texture measures based on fPAR rather than individual spectral bands of remote sensing images in previous studies (Estes et al. 2010). Texture measures from MODIS fPAR can be conceptualized as a measure of spatial variability and spatial arrangement of vegetation productivity (i.e., availability of energy within a landscape). This makes texture measures more ecologically meaningful and thus more applicable for biodiversity modelling at broad-scales (Coops et al. 2009a; Coops et al. 2009b). However, the interpretation of texture based on 1-km MODIS fPAR is different than texture measures derived from higher resolution remote sensing images, such as 30-m Landsat data, which capture both vertical and horizontal complexity of vegetation structure (Wood et al. 2012). MODIS' 1-km spatial resolution may not be relevant to some smaller body size species utilizing understory habitat, and thus limit the use of MODIS fPAR for connecting them to their specific ecological functions. However, the lower temporal frequency of Landsat images can make it challenging to acquire cloud free imagery at the same phenological stage over broad-scales (Culbert et al. 2009).

In summary, our study shows that texture measures are effective variables in predicting tropical forest bird species distribution patterns at broad-scales. Texture measures derived from MODIS fPAR captured habitat heterogeneity for several taxonomic groups, and across varied forest habitats, ranging from secondary-growth forests to moist evergreen forests. The incorporation of texture measures and landscape metrics improved model performance because texture measures provide more ecologically relevant information and may enhance understanding of the relationship between heterogeneity and species distributions and underlying mechanisms. The successful applications of texture based MODIS fPAR indicate broader applications for biodiversity assessments. Additionally, texture measures derived from MODIS

fPAR are able to capture phenological changes in vegetation at broad-scales, and potentially be applied in monitoring spatial and temporal dynamics of habitat heterogeneity. The texture measures from MODIS fPAR are a promising tool for assessing and predicting biodiversity patterns in response to environmental changes.

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## Tables

Table 7. List of five bird taxonomic groups and guild affiliation in the study.

Order	Foraging	Nesting	Diet	Example
Bucerotiformes	Canopy	Old-growth tree cavity	Fruit	Hornbill
Cuculiformes	Arboreal	Canopy	Insect, vertebrate, fruit	Cuckoo, Malkoha
Galliformes	Ground	Ground	Invertebrate, grain, bud, seed, fallen fruit	Jungle fowl, Partridge, Pheasant
Passeriformes	Arboreal	Low vegetation to canopy	Fruit, insect, nectar, bud	Flowerpecker, Laughingthrush, Flycatcher, Bulbul, Babbler
Piciformes	Canopy	Small tree cavity	Fruit, insect	Barbet, Piculet, Yellownape

Table 8. Five texture measures derived from the cumulative productivity with description of texture characteristics, and the statistical equations.

	Description	Equation <sup>1</sup>
<b>First-order texture</b>		
Coefficient of Variation	Dispersion of fPAR	$\frac{SD_{fPAR}}{\overline{fPAR}}$
<b>Second-order texture</b>		
Contrast	A measure of the local fPAR intensity variation in values among neighboring pixels	$\sum_{n=0}^{N-1} n^2 \left\{ \sum_{i=1}^N \sum_{j=1}^N p(i, j) \right\}$
Correlation	Linear dependency of fPAR on neighboring pixels	$\sum_{i,j=0}^{N-1} P_{i,j} \left[ \frac{(i - \mu_i)(j - \mu_j)}{(\sigma_i^2 \cdot \sigma_j^2)^{1/2}} \right]$
Entropy	Disorderliness of fPAR (i.e., Shannon diversity)	$-\sum_i \sum_j p(i, j) \log(p(i, j))$
Homogeneity	A measure of sum in values of fPAR among neighboring pixels	$\sum_i \sum_j \frac{1}{1 + (i - j)^2} p(i, j)$

<sup>1</sup> From Haralick et al. (1973)

Table 9. AUC scores for texture, texture + composition, and all three sets of variable models of the bird distribution for all species and five taxonomic orders. The number are the average and standard deviation of AUC values for bird species in the groups. All three model scenarios for each taxonomic group were significantly different at  $P < 0.001$ .

	Texture	Texture + Composition	Texture + Composition + Fragmentation
All species	0.801 ± 0.077	0.927 ± 0.056	0.938 ± 0.062
Bucerotiformes	0.871 ± 0.049	0.945 ± 0.043	0.946 ± 0.043
Cuculiformes	0.807 ± 0.087	0.921 ± 0.063	0.924 ± 0.073
Galliformes	0.834 ± 0.091	0.928 ± 0.099	0.938 ± 0.096
Passeriformes	0.794 ± 0.077	0.928 ± 0.051	0.939 ± 0.059
Piciformes	0.794 ± 0.071	0.92 ± 0.064	0.931 ± 0.064

## Figures

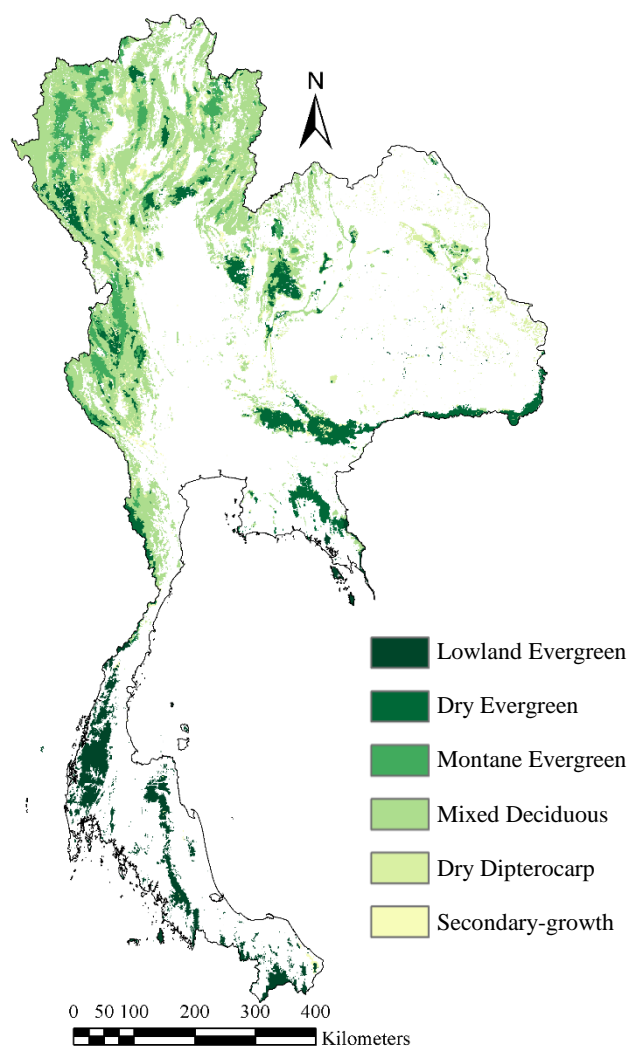


Figure 6. Study area, including six main forest habitat for birds in Thailand

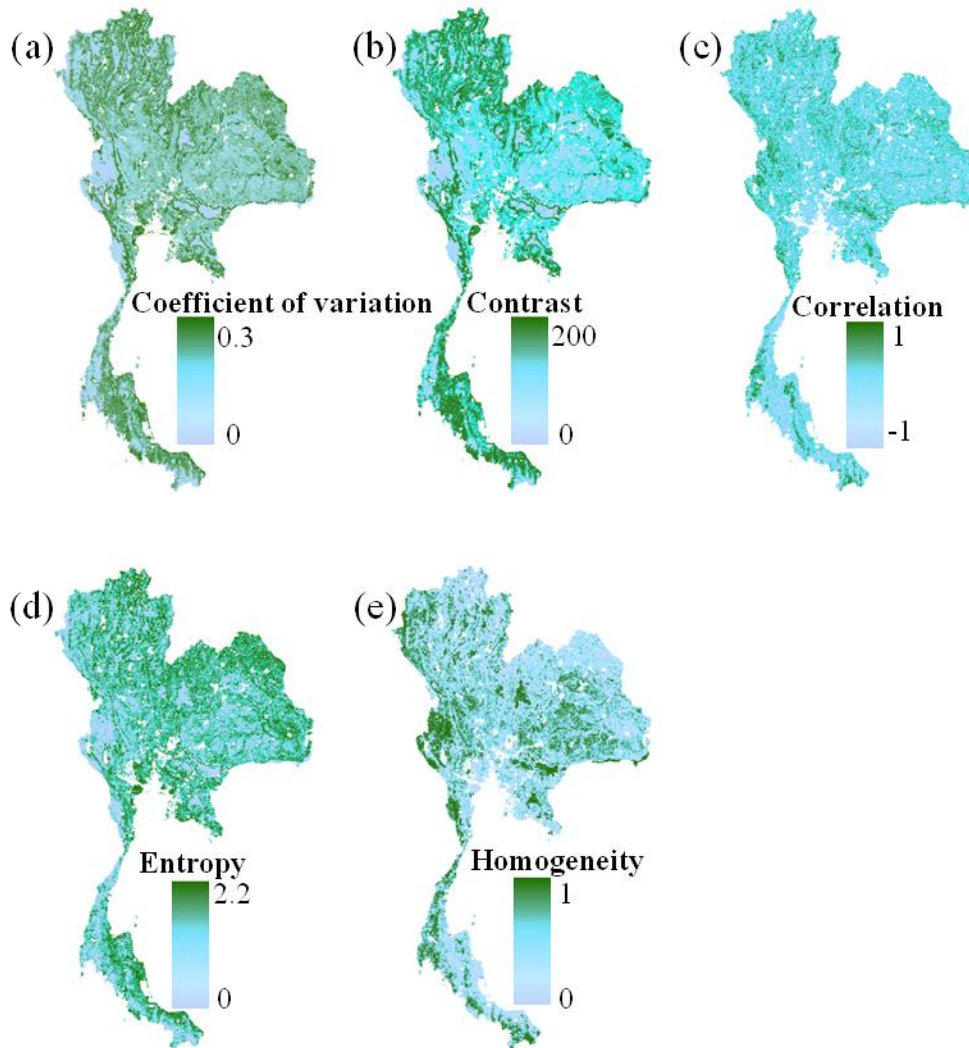


Figure 7. Spatial patterns of habitat heterogeneity captured by the five texture measures of cumulative productivity (i.e., the cumulative Dynamic Habitat Index) derived from 1-km resolution MODIS FPAR. First-order coefficient of variation (a) quantify composition of habitat heterogeneity. Second-order contrast (b), correlation (c), entropy (d), and homogeneity (e) quantify spatial arrangement of cumulative fPAR values.



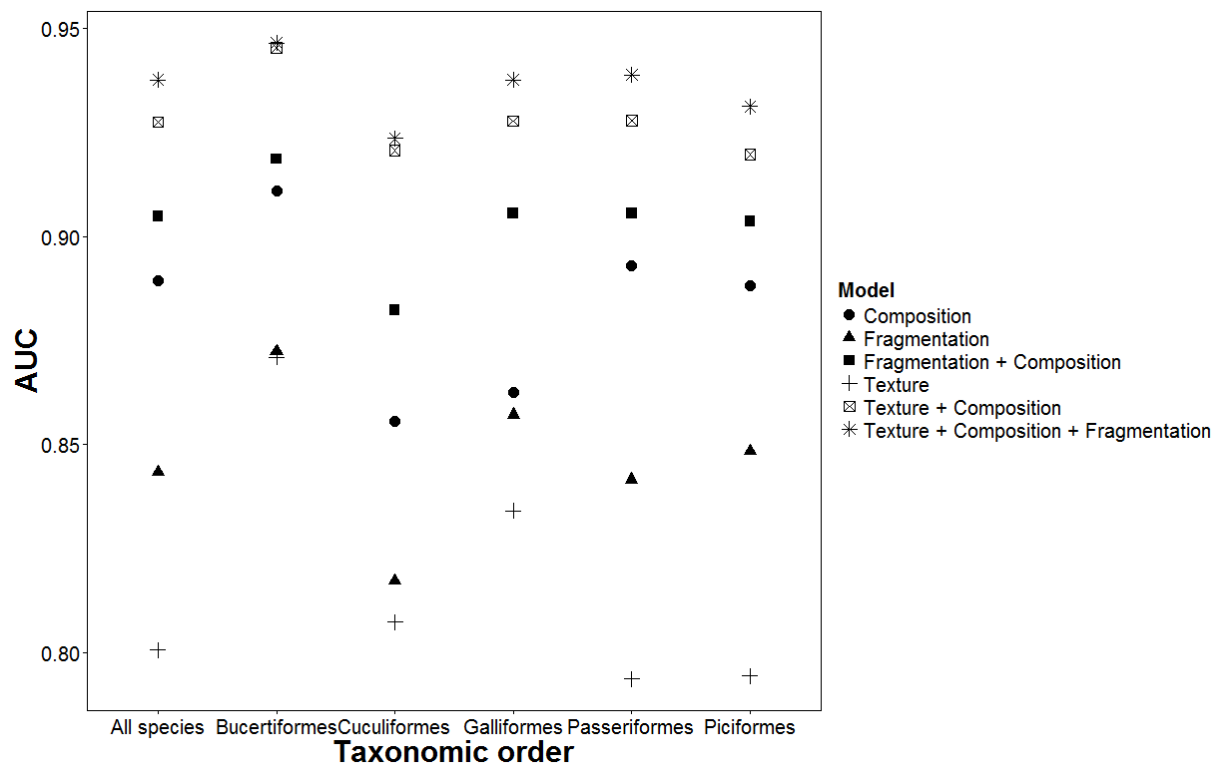


Figure 8. Plot summarizes AUC values of six distribution model scenarios for five bird taxonomic orders. The AUC values are the average of AUC for individual bird species in Bucerotiformes, Cuculiformes, Galliformes, Passeriformes, and Piciformes taxonomic orders. Six models scenarios for the model comparison are texture models, composition models, fragmentation models, texture + fragmentation models, fragmentation + composition models, and texture + composition + fragmentation models.

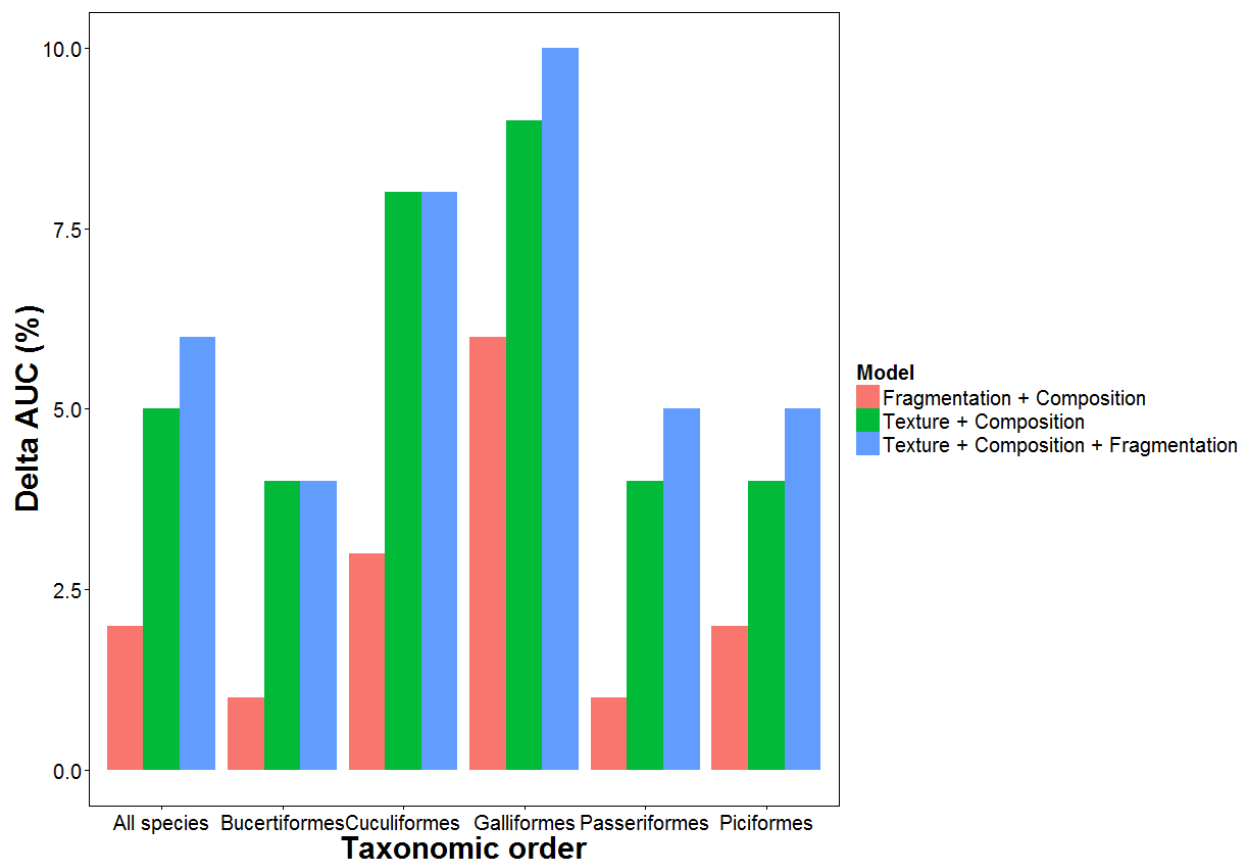


Figure 9. The relative gain of AUC values (%) of bird species distribution models for five taxonomic orders calculated from the differences between composition models and models integrating fragmentation, texture, and both fragmentation and texture.

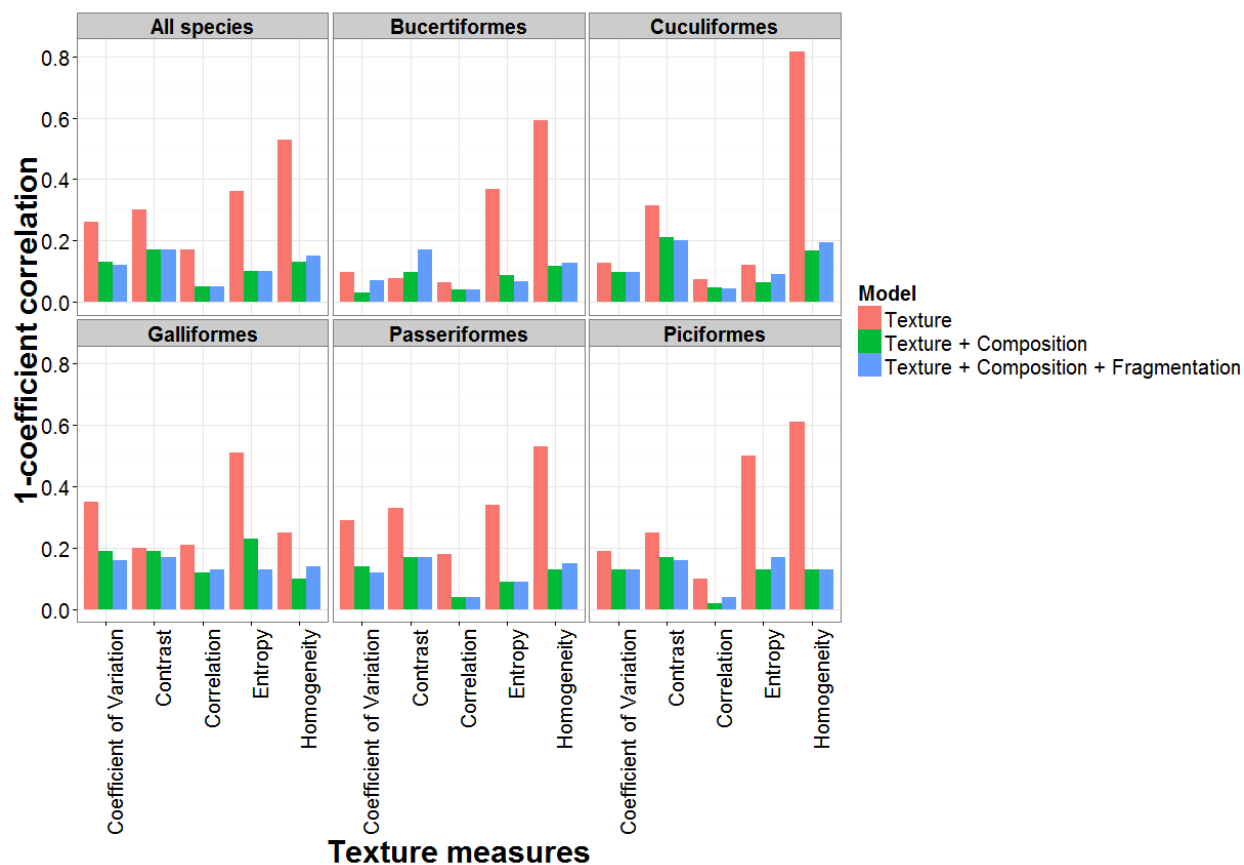


Figure 10. Variable importance of five texture measures used to predict the patterns of distributions for tropical forest birds. variable importance is obtained from 1- Pearson's coefficient correlation for three model scenarios of texture, texture + habitat, and texture + composition + fragmentation. The amplitude of the bar represents the relative contribution of each variable for predicting the response.

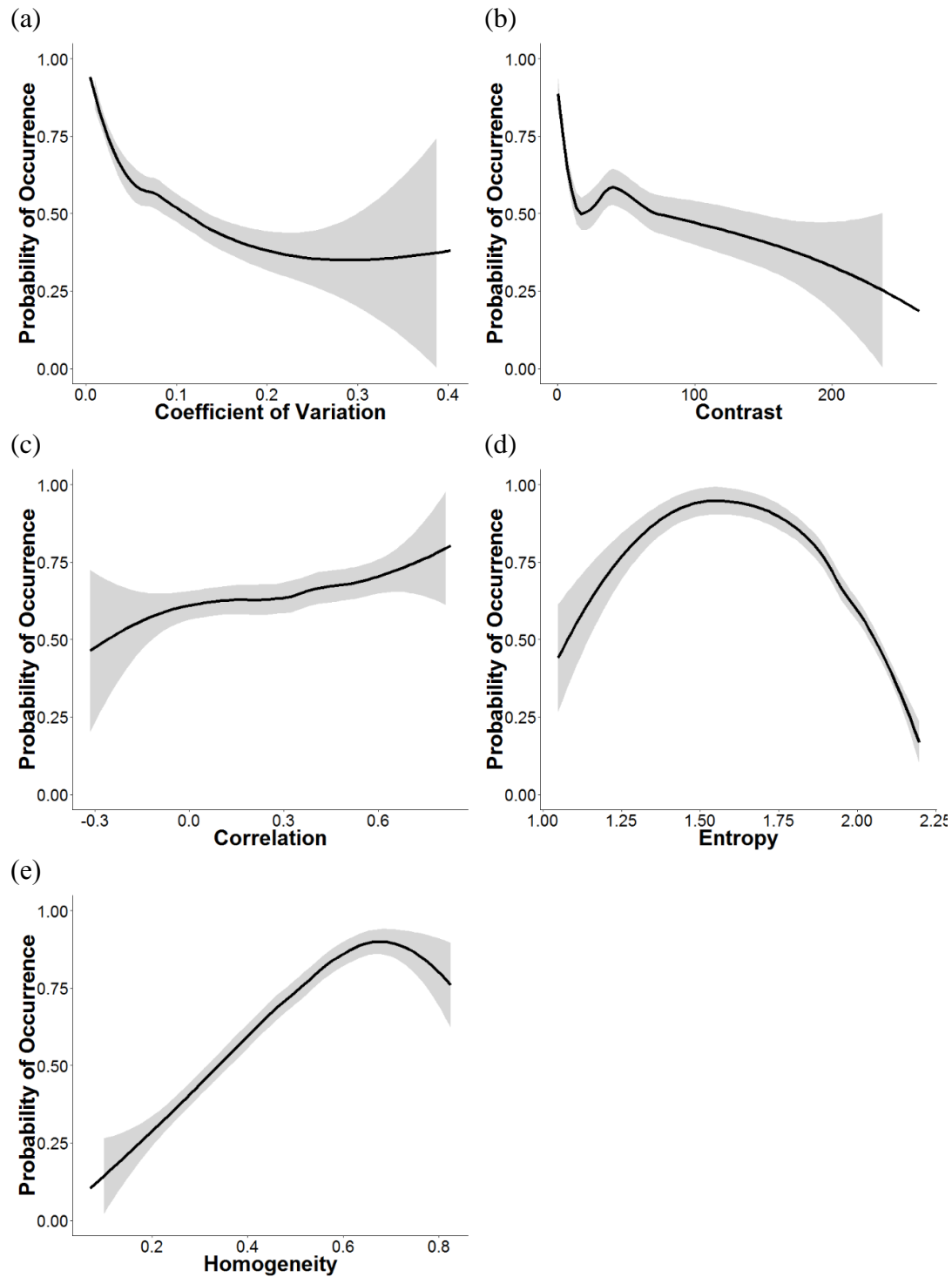


Figure 11. Response curves depict the relationship between the probability of occurrences of Tickell's brown hornbill and texture measures: (a) coefficient of variation, (b) contrast, (c) correlation, (d) entropy, and (e) homogeneity.

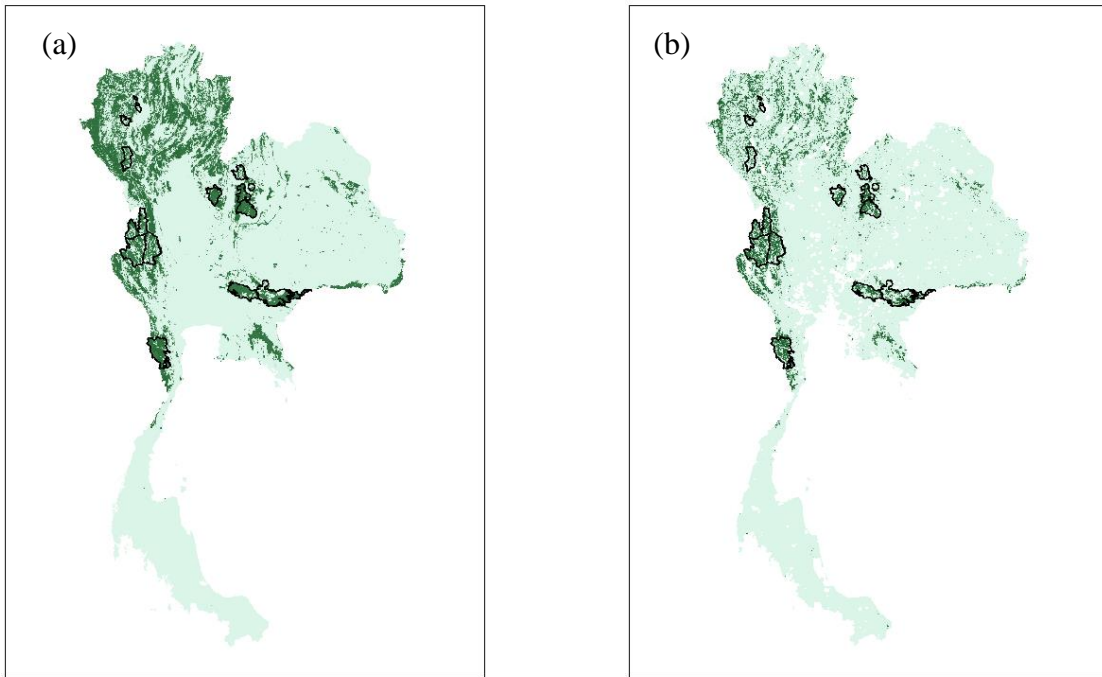


Figure 12. Predicted habitat suitability maps for Tickell's brown hornbill overlays with their known distributions in 15 protected areas in Thailand; (a) modeled with habitat composition variables, (b) modeled with texture, habitat composition, and fragmentation.

## Appendices

Appendix 8. AUC scores for texture, habitat composition, fragmentation, texture + composition, fragmentation + composition, and texture + composition + fragmentation models of the distribution of 86 tropical forest bird species. The AUC are the average of the 20 individual runs (2 replicates each of 10-fold cross validations) for each model scenarios. IUCN represents IUCN Red List categories of bird species: LC= least concern, NT = Near Threatened. Species are classified by taxonomic orders in bold.

Common name	<i>Scientific name</i>	IUCN	Texture	Composition	Fragmentation	Texture Composition	Fragmentation Composition	All Variables
<b>BUCEROTIFORMES</b>								
Tickell's Brown Hornbill	<i>Anorrhinus tickelli</i>	NT	0.937	0.942	0.885	0.969	0.932	0.962
Oriental Pied Hornbill	<i>Anthracoceros albirostris</i>	LC	0.845	0.848	0.861	0.941	0.876	0.947
Great Hornbill	<i>Buceros bicornis</i>	NT	0.847	0.924	0.857	0.936	0.934	0.946
Wreathed Hornbill	<i>Rhyticeros undulatus</i>	LC	0.857	0.937	0.860	0.935	0.933	0.931
<b>CUCULIFORMES</b>								
Banded Bay Cuckoo	<i>Cacomantis sonneratii</i>	LC	0.777	0.839	0.808	0.888	0.884	0.883
Asian Emerald Cuckoo	<i>Chrysococcyx maculatus</i>	LC	0.826	0.892	0.837	0.961	0.911	0.961
Chestnut-breasted Malkoha	<i>Phaenicophaeus curvirostris</i>	LC	0.879	0.942	0.872	0.977	0.953	0.984
Green-billed Malkoha	<i>Phaenicophaeus tristis</i>	LC	0.748	0.750	0.754	0.857	0.781	0.867
<b>GALLIFORMES</b>								
Bar-backed Partridge	<i>Arborophila brunneopectus</i>	LC	0.735	0.686	0.757	0.944	0.883	0.954
Scaly-breasted Partridge	<i>Arborophila chloropus</i>	LC	0.819	0.878	0.866	0.913	0.890	0.918
Red Junglefowl	<i>Gallus gallus</i>	LC	0.807	0.854	0.816	0.879	0.862	0.894

Siamese Fireback	<i>Lophura diardi</i>	LC	0.826	0.940	0.895	0.956	0.923	0.951
Silver Pheasant	<i>Lophura nycthemera</i>	LC	0.899	0.920	0.932	0.959	0.959	0.981
Grey Peacock Pheasant	<i>Polyplectron bicalcaratum</i>	LC	0.920	0.898	0.879	0.916	0.918	0.929
<b>PASSERIFORMES</b>								
Yellow-bellied Warbler	<i>Abroscopus superciliosus</i>	LC	0.722	0.838	0.812	0.864	0.842	0.893
Spectacled Barwing	<i>Actinodura ramsayi</i>	LC	0.841	0.947	0.876	0.975	0.973	0.980
Great Iora	<i>Aegithina lafresnayei</i>	LC	0.870	0.889	0.823	0.935	0.895	0.934
Green Iora	<i>Aegithina viridissima</i>	NT	0.842	0.916	0.781	0.976	0.915	0.980
Black-throated Sunbird	<i>Aethopyga saturata</i>	LC	0.730	0.932	0.874	0.937	0.944	0.956
Brown-cheeked Fulvetta	<i>Alcippe poioicephala</i>	LC	0.788	0.838	0.808	0.898	0.850	0.906
Little Spiderhunter	<i>Arachnothera longirostra</i>	LC	0.772	0.862	0.799	0.906	0.864	0.923
Streaked Spiderhunter	<i>Arachnothera magna</i>	LC	0.749	0.909	0.831	0.909	0.915	0.926
Yellow-bellied Fairy-flycatcher	<i>Chelidorhynchus hypoxantha</i>	LC	0.887	0.961	0.860	0.974	0.955	0.964
Golden-fronted Leafbird	<i>Chloropsis aurifrons</i>	LC	0.684	0.845	0.825	0.852	0.848	0.868
Blue-winged Leafbird	<i>Chloropsis cochinchinensis</i>	LC	0.778	0.871	0.850	0.896	0.875	0.907
Orange-bellied Leafbird	<i>Chloropsis hardwickii</i>	LC	0.736	0.943	0.898	0.954	0.949	0.943
Chestnut-tailed Minla	<i>Chrysominla strigula</i>	LC	0.884	0.973	0.881	0.986	0.979	0.988
Common Green Magpie	<i>Cissa chinensis</i>	LC	0.833	0.898	0.853	0.913	0.907	0.933
White-rumped Shama	<i>Copsychus malabaricus</i>	LC	0.725	0.810	0.790	0.823	0.785	0.832
Tickell's Blue Flycatcher	<i>Cyornis tickelliae</i>	LC	0.813	0.814	0.842	0.909	0.870	0.942
Grey Treepie	<i>Dendrocitta formosae</i>	LC	0.804	0.908	0.825	0.941	0.916	0.959

Thick-billed Flowerpecker	<i>Dicaeum agile</i>	LC	0.728	0.858	0.803	0.935	0.879	0.948
Yellow-vented Flowerpecker	<i>Dicaeum chrysorrheum</i>	LC	0.871	0.864	0.859	0.931	0.893	0.943
Plain Flowerpecker	<i>Dicaeum minullum</i>	LC	0.734	0.864	0.834	0.924	0.884	0.936
Orange-bellied Flowerpecker	<i>Dicaeum trigonostigma</i>	LC	0.891	0.929	0.883	0.980	0.950	0.989
Bronzed Drongo	<i>Dicrurus aeneus</i>	LC	0.708	0.867	0.796	0.863	0.840	0.879
Lesser Racket-tailed Drongo	<i>Dicrurus remifer</i>	LC	0.727	0.856	0.814	0.920	0.888	0.928
Black-throated Laughingthrush	<i>Dryonastes chinensis</i>	LC	0.814	0.905	0.897	0.918	0.913	0.919
Slaty-backed Forktail	<i>Enicurus schistaceus</i>	LC	0.753	0.926	0.885	0.945	0.957	0.964
White-bellied Erpornis	<i>Erpornis zantholeuca</i>	LC	0.765	0.929	0.871	0.942	0.937	0.944
Little Pied Flycatcher	<i>Ficedula westermanni</i>	LC	0.729	0.945	0.881	0.979	0.952	0.976
White-crested Laughingthrush	<i>Garrulax leucolophus</i>	LC	0.769	0.854	0.844	0.908	0.881	0.909
Lesser Necklaced Laughingthrush	<i>Garrulax monileger</i>	LC	0.827	0.818	0.789	0.873	0.829	0.882
Greater Necklaced Laughingthrush	<i>Garrulax pectoralis</i>	LC	0.828	0.767	0.745	0.897	0.784	0.911
Eurasian Jay	<i>Garrulus glandarius</i>	LC	0.662	0.876	0.793	0.926	0.873	0.933
Common Hill Myna	<i>Gracula religiosa</i>	LC	0.847	0.867	0.847	0.899	0.878	0.915
Bar-winged Flycatcher-shrike	<i>Hemipus picatus</i>	LC	0.743	0.886	0.834	0.904	0.895	0.931
Ashy Bulbul	<i>Hemixos flava</i>	LC	0.758	0.891	0.851	0.951	0.898	0.964
Buff-vented Bulbul	<i>Iole olivacea</i>	NT	0.921	0.910	0.879	0.965	0.928	0.970
Asian Fairy-bluebird	<i>Irena puella</i>	LC	0.819	0.894	0.860	0.960	0.915	0.965
Mountain Bulbul	<i>Ixos mcclllandii</i>	LC	0.745	0.942	0.823	0.951	0.938	0.960
Silver-eared Mesia	<i>Leiothrix argenteauris</i>	LC	0.810	0.934	0.872	0.944	0.957	0.959
Pin-striped Tit Babbler	<i>Macronus gularis</i>	LC	0.774	0.829	0.812	0.874	0.863	0.889



Dark-backed Sibia	<i>Malacias melanoleucus</i>	LC	0.853	0.959	0.862	0.987	0.968	0.992
Abbott's Babbler	<i>Malacocincla abbotti</i>	LC	0.886	0.928	0.884	0.941	0.929	0.958
Sultan Tit	<i>Melanochlora sultanea</i>	LC	0.824	0.780	0.870	0.854	0.872	0.926
Large Niltava	<i>Niltava grandis</i>	LC	0.838	0.969	0.896	0.969	0.966	0.973
Dark-necked Tailorbird	<i>Orthotomus atrogularis</i>	LC	0.818	0.796	0.802	0.892	0.829	0.893
Yellow-cheeked Tit	<i>Parus sponotus</i>	LC	0.818	0.951	0.861	0.972	0.959	0.962
Short-billed Minivet	<i>Pericrocotus brevirostris</i>	LC	0.758	0.912	0.829	0.908	0.897	0.946
Mountain Tailorbird	<i>Phyllergates cuculatus</i>	LC	0.794	0.938	0.821	0.968	0.931	0.970
Blyth's Leaf Warbler	<i>Phylloscopus reguloides</i>	LC	0.851	0.945	0.863	0.957	0.949	0.968
Blue Pitta	<i>Pitta cyanea</i>	LC	0.837	0.901	0.890	0.929	0.903	0.940
White-browed Scimitar Babbler	<i>Pomatorhinus schisticeps</i>	LC	0.726	0.890	0.855	0.908	0.936	0.944
Long-tailed Broadbill	<i>Psarisomus dalhousiae</i>	LC	0.825	0.919	0.906	0.926	0.945	0.941
Rufous-winged Fulvetta	<i>Pseudominla castaneiceps</i>	LC	0.888	0.951	0.876	0.984	0.969	0.981
Blyth's Shrike-babbler	<i>Pteruthius aeralatus</i>	LC	0.795	0.930	0.851	0.963	0.940	0.974
Black-headed Bulbul	<i>Pycnonotus atriceps</i>	LC	0.797	0.849	0.808	0.884	0.858	0.903
Stripe-throated Bulbul	<i>Pycnonotus finlaysoni</i>	LC	0.767	0.827	0.784	0.870	0.843	0.889
Black-crested Bulbul	<i>Pycnonotus flaviventris</i>	LC	0.720	0.828	0.799	0.863	0.837	0.881
White-throated Fantail	<i>Rhipidura albicollis</i>	LC	0.722	0.921	0.834	0.950	0.928	0.964
Silver-breasted Broadbill	<i>Serilophus lunatus</i>	LC	0.747	0.863	0.855	0.899	0.863	0.917
Chestnut-vented Nuthatch	<i>Sitta nagaensis</i>	LC	0.765	0.956	0.826	0.976	0.969	0.984
Golden Babbler	<i>Stachyridopsis chrysaea</i>	LC	0.834	0.936	0.882	0.962	0.952	0.970

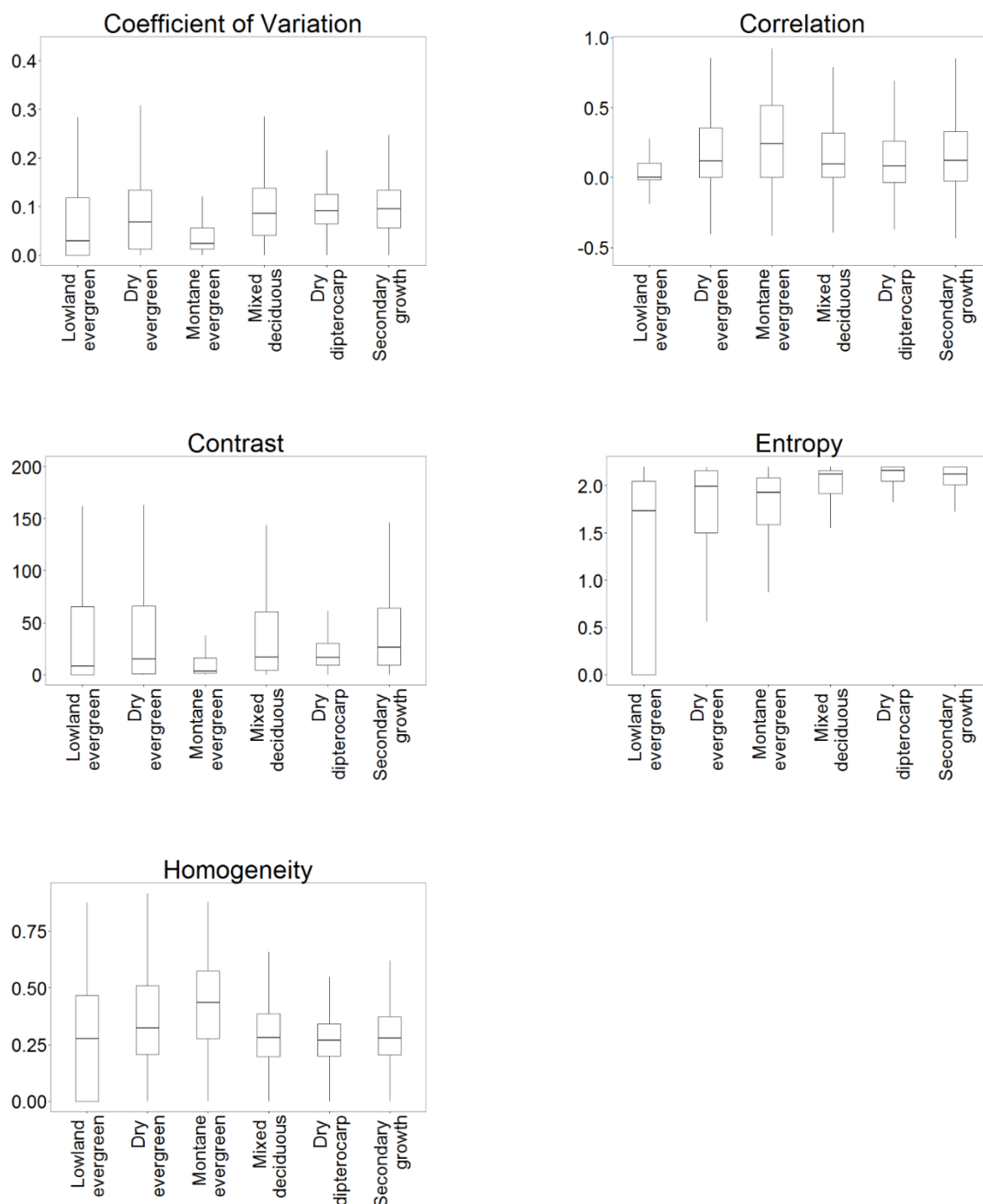
Grey-throated Babbler	<i>Stachyris nigriceps</i>	LC	0.811	0.919	0.816	0.948	0.934	0.957
Large Woodshrike	<i>Tephrodornis virgatus</i>	LC	0.849	0.880	0.840	0.933	0.891	0.932
Silver-eared Laughingthrush	<i>Trochalopteron melanostigma</i>	LC	0.800	0.951	0.825	0.983	0.981	0.945
<b>PICIFORMES</b>								
Greater Flameback	<i>Chrysocolaptes guttacristatus</i>	LC	0.881	0.907	0.888	0.939	0.925	0.944
Greater Yellownape	<i>Chrysophlegma flavinucha</i>	LC	0.788	0.884	0.852	0.899	0.907	0.911
Grey-capped Pygmy Woodpecker	<i>Dendrocopos canicapillus</i>	LC	0.646	0.777	0.740	0.869	0.784	0.866
Blue-throated Barbet	<i>Megalaima asiatica</i>	LC	0.738	0.891	0.846	0.927	0.891	0.947
Blue-eared Barbet	<i>Megalaima australis</i>	LC	0.867	0.884	0.855	0.915	0.914	0.919
Green-eared Barbet	<i>Megalaima faiostricta</i>	LC	0.860	0.932	0.871	0.946	0.940	0.950
Moustached Barbet	<i>Megalaima incognita</i>	LC	0.877	0.954	0.915	0.963	0.955	0.964
Great Barbet	<i>Megalaima virens</i>	LC	0.715	0.887	0.829	0.903	0.918	0.928
White-browed Piculet	<i>Sasia ochracea</i>	LC	0.780	0.880	0.842	0.918	0.899	0.953





Appendix 11. Habitat heterogeneity captured by five texture measures for different forest types.

The boxplots indicate 95th, 75th, 50th, 25th and 5th percentiles of measure values. The values were calculated from 1,000 randomly selected pixels within each forest type at the 1-km resolution based on Landsat land cover map of Thailand.



### **Chapter 3: Habitat connectivity for endangered Indochinese tigers in Thailand**

#### **Abstract**

Habitat connectivity is crucial for the conservation of species restricted to small, fragmented, and isolated populations within human-dominated landscapes. However, identifying habitat connectivity, especially for top predators, is challenging due to trophic interactions between primary productivity and prey species influencing the distribution of predator's habitats and their capacity to move and disperse. Our goal was to assess current and potential habitat connectivity for Indochinese tigers (*Panthera tigris*) in Thailand. We quantified currently occupied and potentially suitable habitat and dispersal corridors across Thailand based on habitat suitability for the Indochinese tiger. We estimated habitat suitability with an ensemble species distribution model based on camera-trap data from 15 protected areas with trophic interactions and abiotic variables. We employed graph theory to evaluate the relative importance of habitat patches and dispersal corridors to the overall connectivity network. Our analyses showed that habitat suitability models both with and without trophic interactions performed well. However, including trophic interactions between plant productivity, prey (wild boar, sambar, muntjac, and gaur) and predator (tiger) significantly improved model performance ( $P < 0.001$ ). Currently-occupied habitat patches were highly fragmented and isolated with high resistance to movement within the dispersal corridors. Potential habitat patches were mostly isolated. However, we identified potential habitat patches that could serve as target sites for reintroduction and restore connectivity, especially in the Western Forest complex. The Western Forest Complex habitat patch and the Kaeng Krachan dispersal corridor were the most important habitat patch and corridor for maintaining the overall habitat connectivity network. More broadly, our results highlight the value of integrating trophic interactions into assessments of connectivity to predict

habitat suitability and delineate dispersal corridors, and thus offer an effective tool for conservation planning of tigers and other large carnivores.

## Introduction

Human activities are changing the Earth's ecosystems with profound consequences for biodiversity (Chapin et al. 2000; Sala et al. 2000). The loss and fragmentation of habitat poses an imminent threat to the viability of many species, especially those with large home ranges (Brook et al. 2008; Pimm et al. 2014). Survival of these species depends upon maintaining connectivity between isolated populations (Fahrig and Merriam 1985; Noss et al. 1996; Taylor et al. 1993). Landscape connectivity is defined as the degree to which a landscape facilitates or impedes individual dispersal between habitat patches (Taylor et al. 1993). Connectivity can mitigate impacts of climate change by allowing species to track their fundamental niches (Noss 2001). In addition, connectivity plays a crucial role in conservation planning where the goal is often to preserve resilient habitat networks, and design linkages of high quality habitat (i.e., dispersal corridors) between remnant patches or protected areas (Soule and Terborgh 1999). The assessment of functional connectivity, defined as ecological response of organisms to landscape elements (e.g., patches), and the ability of individuals to disperse across non-habitat areas (Moilanen and Hanski 2001; Moilanen and Nieminen 2002; Tischendorf and Fahrig 2000; Uezu et al. 2005), requires understanding of the requirements of dispersing species, the spatial distribution of habitat suitability, and the potential connections between them (Goodwin and Fahrig 2002; Urban et al. 2009). However, models identifying habitat connectivity networks typically focus on a single species, and disregard the influence of species interactions due to incomplete assessments of competition, or trophic interactions (Beier et al. 2011).

Trophic interactions shape the realized niche that ultimately determines movement or dispersal success, and therefore functional habitat connectivity. Trophic interactions in conjunction with abiotic factors determine the distributions and abundance of species



(Hutchinson and MacArthur 1959). Specifically, trophic interactions play a crucial role in controlling distributions of large mammal communities through the interrelationships of plants, herbivores, omnivores, and carnivores at different trophic levels (Finke and Snyder 2010; Power 1992). This role of trophic interactions on species distributions has relevance for the assessment of habitat connectivity of large carnivores because trophic interactions influence the spatial structure of habitat suitability, and the movement behavior of both predator and prey in acquiring food resources in different habitat patches.

Trophic interactions can provide ecological insights into how species respond to landscape heterogeneity, and consequently define habitat suitability and dispersal corridors. However, studies of habitat connectivity for large carnivores typically define habitat suitability based on abiotic factors only due to a paucity of data on prey species. Such models assume that trophic interactions are implicit in models, for example, of jaguar (*Panthera onca*) (Rabinowitz and Zeller 2010), grizzly bears (*Ursus arctor*), and cougar (*Puma concolor*) (Chetkiewicz and Boyce 2009). Yet, if trophic interactions are not explicitly accounted for when modeling habitat suitability, it is possible that habitat patches and dispersal corridors will not be ecologically relevant (Kanagaraj et al. 2013). Previous studies have demonstrated that the incorporation of trophic interactions into habitat suitability for large carnivores improves predictions of habitat suitability and is essential to assess habitat connectivity (Hebblewhite et al. 2014; Kanagaraj et al. 2011; Kanagaraj et al. 2013). A study of the Bengal tigers in the Terai Arc Landscape of India and Nepal demonstrates that including trophic interactions with Chital and Sambar results in the best habitat suitability model for connectivity assessment (Kanagaraj et al. 2011; Kanagaraj et al. 2013). However, while some studies of large carnivore connectivity have included food resources into habitat suitability models, habitat connectivity studies assessing interactions

among different trophic levels between predator, prey, and primary productivity are few and far between.

Different methods have been proposed to estimate habitat connectivity, depending on the landscape structure, the scientific questions, and the species of interest (Kindlmann and Burel 2008). 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 Fahring 2000). Commonly used modeling approaches to quantify habitat connectivity are: least-cost path analysis (Adriaensen et al. 2003; Rabinowitz and Zeller 2010; Tischendorf and Fahring 2000), circuit analysis (McRae et al. 2008), graph theory (Bunn et al. 2000; Urban and Keitt 2001), and metapopulation modeling (Hanski 1999; Moilanen and Nieminen 2002).

The combination of least cost modeling, circuit analysis, and graph theory has been successfully applied to restore or preserve habitat connectivity for species-level conservation (Brodie et al. 2015; Ziolkowska et al. 2012). Least-cost path analysis integrates the matrix between patches using an individual's movement routes within a landscape (Adriaensen et al. 2003). However, the limitation of least-cost path analysis for landscape connectivity is that only a single path is identified, even though alternative paths with just slightly higher cost may exist (Driezen et al. 2007). Furthermore, connectivity measures focusing on optimum routes only fail to incorporate variation in the behavior among individuals, and for the same individual over time (Belisle 2005). Circuit analysis, on the other hand, identifies multiple pathways for connectivity, thus providing a better assessment how individuals would move across landscape, and can complement least-cost modeling. Furthermore, graph theory evaluates the relative importance of individual landscape elements in maintaining overall habitat connectivity throughout the network

of patches and corridors (Calabrese and Fagan 2004; Urban and Keitt 2001; Urban et al. 2009). Graph-based metrics can quantify landscape elements as a source or a stepping stone based on habitat availability and species traits (e.g., dispersal distance), and evaluate functional connectivity (Saura and Pascual-Hortal 2007; Saura and Rubio 2010). Although while a combination of methods is a promising approach, corridor locations derived from least-cost modelling and circuit analysis are sensitive to the relative cost values assigned (i.e., the ecological costs associated with individuals dispersing through different land cover classes), and to the spatial configuration of habitat patches (McRae et al. 2008). Therefore, conducting least-cost modeling and circuit analysis using a habitat suitability map can yield ecological connectivity network. A number of studies have applied a combined approach to the analysis of landscape connectivity in order to guide conservation and restoration efforts, such as European bison (*Bison bonasus*) (Ziolkowska et al. 2012).

One species for which habitat connectivity is very important is tigers (*Panthera tigris*). 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 (Lynam 2010; Seidensticker et al. 2010; Wikramanayake et al. 2004), and decreased prey availability (Barber-Meyer et al. 2013; Karanth et al. 2004a; Steinmetz et al. 2013). Long-term persistence of tigers depends on large, well-connected habitat patches. Thus, it is important to assess connectivity of suitable habitat for tigers in order to provide essential information for conservation planning such as habitat restoration projects, translocations, and reintroductions (Karanth et al. 2014; Lynam et al. 2001; Sunquist et al. 1999). Tiger populations in Thailand are at risk of extinction, even though Thailand occupies the historical center of tiger's range (Lynam 2010; Lynam et al. 2001). However, due to socio-economic developments

and poaching, only 250-350 tigers remain in Thailand according to recent estimates, and they are splintered into small, isolated subpopulations (Rabinowitz 1993; Smith et al. 1999; Ngoprasert et al. 2012). Furthermore, these subpopulations are vulnerable to extinction due to deforestation, illegal trade, and insufficient prey due to poaching (Simcharoen et al. 2014b; Steinmetz et al. 2006; Steinmetz et al. 2013). In 2010, the Global Tiger Initiative identified priority areas for tiger conservation (Sanderson et al. 2010). However, incomplete assessments of tiger distributions and habitat connectivity in many regions still continue to hamper conservation efforts. Thailand is one of the regions that still needs better understanding of the patterns of tiger distributions and habitat connectivity (Lynam 2010).

Habitat availability for tigers depends ultimately on the full range of resources and environmental conditions that allow the species to survive and reproduce, including shelter, availability of prey species, absence of human disturbances, and connectivity to other occupied patches for breeding and to maintain genetic diversity (Dinerstein et al. 2007; Kanagaraj et al. 2013; Wikramanayake et al. 2004). Tigers prefer a mosaic of forest and grassland habitats with disturbed and undisturbed tracts of forest that maximize the density of prey abundance, and offer cover for hunting, breeding, and raising cubs (Karanth et al. 2003; Smith et al. 2010; Karanth and Stith 1999). This is why tigers are restricted to forest and grassland habitats within the suite of protected areas in Thailand (Rabinowitz 1993; Smith et al. 1999). In terms of species interactions, tiger distribution is primarily driven by prey availability, while intra-guild predation (i.e., leopard, cloud leopard, and dhole) appears to have little effect on tiger occurrences (Jenks et al. 2012; Ngoprasert et al. 2012; Steinmetz et al. 2013). The most common ungulate prey species are wild boar, red muntjac, sambar deer, gaur, and banteng (Ngoprasert et al. 2012). Although

tigers' biology is well-studied, it remains unclear how trophic interactions predict habitat suitability, and influence habitat connectivity patterns.

Here, we combined species distribution modeling at different trophic levels and connectivity metrics in a novel way to understand the mechanism underlying patterns of habitat connectivity for the Indochinese tiger in Thailand. We tested the hypothesis that trophic interactions between primary productivity (i.e., cumulative productivity, and seasonality in productivity), prey, and predator play a significant role in predicting habitat suitability for tigers. We also employed an integrative approach of least-cost modeling, circuit analysis, and graph theory to assess connectivity pattern across Thailand. Conducting the cost-path analyses (i.e., least-cost modeling and circuit analysis) based on habitat suitability together with spatial data on dispersal barriers provided more ecological resistance surface to yield potential dispersal corridors. Via graph theory, we then evaluate the relative importance of habitat patches and dispersal corridors in maintaining overall connectivity networks.

Our goal was to assess currently occupied and potential habitat connectivity for the Indochinese tigers in Thailand. Our specific objectives were to:

- (i) test the trophic interaction hypothesis based on food resources and environmental variables that provide the best prediction of habitat suitability.
- (ii) identify currently occupied and potential habitat patches and dispersal corridors
- (iii) evaluate the relative importance of habitat patches and dispersal corridors in maintaining an overall habitat connectivity network in order to identify priority sites for tiger and prey reintroduction.

## Methods

### *Study area*

Thailand covers 513 115 km<sup>2</sup> of land area between latitudes 5°45′ and 20° 27′ N and longitudes 97° 22′ and 105° 37′ E. Elevation ranges from 0 to 2565 m. The climate is influenced by seasonal monsoons and varies among regions. Most forested areas have been converted for commercial forestry. The recent estimate shows only 32% of natural forest remains cover, mostly within protected areas with the dominant coverage at higher elevations (RFD 2013). Thailand is a global biodiversity hotspot (Myers et al. 2000), and home to more than 300 mammal species, including endangered tigers (IUCN 2014). However, Thailand's native mammal community is collapsing, with up to 12 species threatened by rapid habitat loss and fragmentation due to increasing human populations, economic development, and land use change (Gibson et al. 2013; Trisurat et al. 2010a; Woodruff 2013), rates of which will likely rise due to emerging international free market policies in 2015 (i.e., ASEAN Economic Community) (Fox and Vogler 2005).

### *Camera trap survey data*

We collected camera trap data during 1997-2013 from 15 protected areas (Figure 13). We selected camera locations to maximize chances of capturing animals where animal signs were found (i.e., prints and scats) close to wildlife trails, stream beds, and ridges, and to span gradients in elevation (ranging from 0-1351 m) and multiple mammal habitat conditions (e.g., hill evergreen forests, mixed deciduous forest, dry dipterocarp forest, and grassland). We attached the cameras to the base of trees about 50 cm aboveground with approximately 0.5 km spacing between cameras. We operated cameras 24 hours per day, and cameras recorded time and date for each exposure. We did not use baits or lures. We selected tiger and the four most common

ungulate prey species of tigers: Eurasian wild boar (*Sus scrofa*), Gaur (*Bos gaurus*), Red muntjac (*Muntiacus muntjac*), and Sambar deer (*Rusa unicolor*) (Ngoprasert et al. 2012) to conduct habitat suitability, connectivity, and corridor analyses.

### *Habitat variables*

We predicted potential habitat suitability for tigers using trophic and abiotic variables considered critical to tiger reproduction and survival. We included (1) the probability of occurrence of four prey ungulate species; (2) primary productivity; (3) proportion of habitat types; (4) mean elevation; (5) slope; (6) terrain ruggedness; (7) distance to nearest rivers and streams; (8) mean annual precipitation; (9) distance to nearest forest edge; (10) distance to nearest human settlement and roads. We calculated continuous values of each habitat variable within 1-km resolution. This grain scale has been previously applied in the calculation of habitat variables in studies of mammal carnivores and ungulate prey species in Thailand (Jenks et al. 2012; Ngoprasert et al. 2012; Steinmetz et al. 2013).

Trophic variable included the probability of occurrence of four prey ungulate species, and primary productivity. The direct effects of consumption and productivity, i.e., the bottom of food webs of herbivores and their predators, throughout food webs play important role for distributions of prey and predator species in the community (Power 1992). We extracted the cumulative annual productivity and seasonal variation in productivity from the Dynamic Habitat Indices, derived from fPAR-MODIS primary productivity product. Details about the way the fPAR composite image was derived can be found in Radeloff et al (in preparation). We employed the probability of occurrence of four prey ungulate species as a surrogate for prey availability or abundance.

Abiotic variables included habitat types, elevation, slope, terrain ruggedness, distance to nearest rivers or streams, mean annual precipitation, and human disturbance variables (Ngoprasert et al. 2012; Simcharoen et al. 2014a). We computed the proportion of eight habitat types: grassland, secondary forest, bamboo forest, mixed deciduous forest, dry dipterocarp forest, hill evergreen forest, moist evergreen forest, and dry evergreen forest using the Thailand land cover map of 2000 provided by the Thailand Department of National Parks, Wildlife, and Plant Conservation. The land cover map is derived from Landsat TM and ETM+ using supervised classification approach at the scale of 1:50,000. We calculated mean elevation, slope (0-90°), and terrain ruggedness from the Shuttle Radar Topography Mission (SRTM). We extracted mean annual precipitation derived from averages for the period of 1961-1990 from the WorldClim data (Hijmans et al. 2005). We also calculated distance to nearest rivers or streams, forest edge, and human settlement or road, using the Thailand land cover map of 2000. We chose distance to the nearest forest edge and human settlement or road as a surrogate for hunting pressure because hunting intensity is inversely related to the distance that poachers have access to wildlife habitat (Ngoprasert et al. 2012).

### *Tiger habitat suitability*

To estimate habitat suitability for tigers, we employed an ensemble modeling approach relating the camera trap data to the environmental variables. An ensemble method combines multiple types of Species Distribution Models (SDMs) to reach a consensus outcome for probability of species occurrence to account for variability among SDM algorithms (Araujo and New 2007; Thuiller 2003; Thuiller et al. 2009). We included ten different species distribution modelling algorithms implemented within the BIOMOD2 package version 3.1-64 in R (Thuiller



et al. 2009; R Development Core Team 2015): three regression methods (generalized linear model, GLM; generalized additive model, GAM; and Multiple Adaptive Regression Splines, MARS), two classification methods (flexible discriminant analysis, FDA and classification tree analysis, CTA), and four machine-learning methods (artificial neural networks, ANN; generalized boosted model, GBM; random forests, RF; and maximum entropy, MAXENT), and a climate envelope method (surface range envelope, SRE) (Phillips et al. 2006; Thuiller et al. 2009). We set model algorithms with default parameters. The SDM algorithms require background data, and we combined true absences and generated pseudo-absences from within a 50-km buffer of each presence location based on average home range size for tigers (Simcharoen et al. 2014b). We generated ten times the number of occurrence records for all species (Barbet-Massin et al. 2012).

In order to evaluate the predictive performance of the SDMs for prey species and tigers, we calculated AUC (Fielding and Bell 1997) with 10-fold cross-validation by splitting a random subset of 90% of the observed data for the model calibration, and the remaining 10% of the data for model evaluation (Bateman et al. 2012; Elith et al. 2011). To provide an unbiased measure of model performance and obtain standard deviations for evaluation metrics (Pearce and Ferrier 2000), we repeated data splitting ten times with the two pseudoabsence replicates (a total of 20 replicates for each model algorithm). To ensure all replicates were comparable, we rescaled each replicate within Biomod2 using a binomial GLM. We considered AUC values above 0.7 to be indicative of useful models (Swets 1988). To obtain the consensus distribution for ungulate prey and tigers, we selected the top five performing models; GLM, GAM, GBM, RF, and MAXENT with  $AUC > 0.7$  (Elith et al. 2006), and used an ensemble forecast technique by calculating the weighted mean distributions across selected SDMs. In order to transform the probabilistic

consensus distribution from the ensemble technique to a binary suitable/non-suitable habitat for each prey species and tigers, we considered suitability values above the sensitivity-specificity sum maximization threshold (Liu et al. 2005).

To compare the effects of trophic interactions in habitat suitability models for tigers, we modeled tigers with three different sets of variables: abiotic variables, prey, or abiotic and trophic interactions (i.e., primary productivity, and prey availability). For the tiger model obtained with trophic interactions, we first computed species distributions for the four prey ungulate species (i.e., wild boar, gaur, muntjac, and sambar) with primary productivity (i.e., cumulative productivity, and seasonality in productivity) as a measure of forage availability for ungulate prey, and abiotic variables described above. The predicted distributions of ungulate species were a surrogate for trophic interactions between plants and herbivores (Ngoprasert et al. 2012; Jenks et al. 2012), and we included them as predictor variables for the tiger model.

To determine whether trophic interactions (selection of abiotic variables versus trophic interaction variables) significantly improve the prediction of current distributions of Indochinese tigers, we tested the differences in model outputs produced with abiotic variables, prey, and abiotic + prey with Wilcoxon signed-rank tests for related samples (Araujo and Luoto 2007). The importance of the variable for each species was calculated using a randomization procedure as one minus the Pearson's correlation coefficients between the standard prediction and the prediction where the considered variables was randomly permuted. If the correlation is high (i.e., there is a small difference between the two predictions), the variable permuted is considered not important for the model. Therefore, one minus the correlation coefficient represents, for a given variable, the probability that the coefficient can contribute to the model.

The higher the probability, the higher a variable contributes in predicting the pattern (Thuiller et al. 2009).

#### *Identify habitat patches and dispersal corridors*

To assess habitat connectivity for tigers in Thailand (Figure 14), we integrated three connectivity models: least cost modelling, circuit analysis, and graph theory. To identify potential habitat patches, we considered suitable patches that were greater than 70 km<sup>2</sup> based on average home range size for female tigers from Huai Kha Khaeng Wildlife Sanctuary (Simcharoen et al., 2014b). Previous studies in Thailand have shown that tiger home ranges vary depending on location, season, year, and prey availability in the region (Simcharoen et al. 2014a; Simcharoen et al. 2014b).

To identify locations of dispersal corridors, we employed least-cost path modeling (Adriaensen et al. 2003). We used a probabilistic habitat suitability map for tigers derived from the model including trophic interactions to generate least-cost path corridors for tigers. Least-cost paths can be identified by accumulating cost surface values along possible routes for two or more source patches. A cost surface is derived by quantifying the resistance of different land cover classes and summing the travel cost over the route of least resistance when individuals move between two patches (Adriaensen et al. 2003). We inverted the habitat suitability map for tigers with a linear function as a measure of resistance surfaces, rescaled from 1 (lowest resistance) to 100 (highest resistance). Dispersing tigers avoid agricultural areas and human disturbance, but may travel through a mosaic of forest and grassland with disturbed and undisturbed tracts of forest offering cover for movement (Smith 1993; Wikramanayake et al. 2004). We therefore included potential dispersal barriers for tigers: agriculture area, settlement,

highways, major roads, and rivers into the resistance surface map. We assigned grid cells that included the potential dispersal barriers to the maximum cost value to ensure that constructed least-cost paths will not cross them unless no other possibility of movement exists (Adriaensen et al. 2003; Ziolkowska et al. 2012). To determine the position of least-cost path locations, we used the cost distance tools in ArcGIS 10.1 (ESRI 2011) with scripts written in Python 2.7 (Python Software Foundation 2013). We constructed the least-cost path between a given habitat patch and its nearest neighbors with Euclidean distances, assuming that corridors to further patches will pass through habitat patches between them. To synthesize the movement of individuals across landscape matrices, we calculated the effective distance (i.e., the accumulative cost along the least cost paths), taking into account the landscape structure and movement behavior of tigers.

To complement the least-cost path analyses, we conducted a connectivity analysis based on electrical circuit theory (McRae et al. 2008). Least-cost path can identify a corridor location, but a least-cost path corridor is an optimal, linear route only, and it is likely that broader areas are used as corridors than just the optimal path. There are no clear methods to determine optimum width for corridors, and quantify the quality of corridors in facilitating organism movements (Beier et al. 2008; Sawyer et al. 2011). Therefore, we employed Circuitscape software version 3.5 (McRae and Shah, 2009) to identify other potential movement routes around the least-cost path corridor and quantify how tigers would move across the landscape within a given corridor width. We buffered the least-cost paths by 10 km and identified define dispersal corridors within that range that are wide enough to support the tiger movement, based on average home range size for tigers. We then assessed the flow of current between each pairwise combination of suitable habitat patches within 10-km buffer of least-cost paths.

*Assess the importance of habitat patches and dispersal corridors*

To evaluate the relative importance of individual patches and dispersal corridors for the overall connectivity network, we used the Probability of Connectivity index (*PC*) based on graph theory (Saura and Pascual-Hortal 2007; Urban and Keitt 2001; Saura and Rubio 2010). *PC* indicates the probability that two tigers randomly placed in the study area are in habitat patches that are reachable from each other (Saura and Pascual-Hortal 2007; Saura and Rubio 2010). The probability of individual tigers moving between habitat patches depends on both the amount of suitable habitat (nodes of the graph), and the distance and resistance to movement across the matrix (links of the graph). We defined a graph component composed as a set of nodes corresponding to the suitable habitat patches with  $> 70 \text{ km}^2$  (the average female tiger home range in Thailand). Each pair of nodes was connected through links (least cost paths) depicting potential movement paths of tigers.

To assess the probability of connectivity, we used effective distances to calculate inter-patch-cost-dispersal probabilities ( $p_{ij}$ ) as a decreasing exponential function of the effective distance between nodes ( $d_{ij}$ ) and dispersal abilities of tigers ( $k$ ) (Urban and Keitt 2001), as follows:

$$p_{ij} = e^{-kd_{ij}} \quad (1)$$

We set  $k = 0.028, 0.012,$  and  $0.011$  to obtain a dispersal probability of 0.5 based on dispersal distance of tigers in Thailand of 25, 58, and 64 km, corresponding to values obtained from field observations (Robert Steinmetz, personal communication). We then computed *PC* for landscape elements (i.e., habitat patches, and dispersal corridors) and for each dispersal distance.

$PC$  summarizes the contribution of all habitat patches to tiger movements across the whole study area, as follows:

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

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 Torne 2009).

To assess the relative importance of each habitat patches and dispersal corridors to overall connectivity, we calculated  $d(PC)_k$ , which prioritizes and ranks removal operations (Bodin and Saura 2010). The  $d(PC)_k$  can be partitioned into three fractions which quantify the role of each habitat patch and dispersal corridor in maintaining or enhancing the movements of tigers with respect to habitat availability, connectivity, and stepping stone (Saura et al. 2014; Saura and Rubio 2010), as follows:

$$dPC_k = dPC_{intra_k} + dPC_{flux_k} + dPC_{connector_k} \quad (3)$$

The intra fraction ( $dPC_{intra_k}$ ) is the contribution of habitat patch  $k$  given by the suitable habitat that it contains. The flux fraction ( $dPC_{flux_k}$ ) measures the degree of connection of a habitat patch  $k$  with the other habitat patches. The connector fraction ( $dPC_{connector_k}$ ) corresponds to the contribution of a habitat patch and dispersal corridor  $k$  to the connectivity between other habitat patches as a stepping stone or connectivity facilitating dispersal between

them. We used Conefor 2.6 software software to calculate all graph theoretical measures (Saura and Torne 2009).

## Results

### *Tiger habitat suitability*

Habitat suitability models for the Indochinese tiger in Thailand performed well with abiotic variables, trophic interactions, and the combination of abiotic and trophic interactions (Figure 15 and Table 10). However, the incorporation of trophic interactions significantly improved model performance. Of all three tiger habitat models, accuracy of model performance was highest with tiger + abiotic + prey (AUC = 0.954, SD = 0.06), followed by tiger + abiotic (AUC = 0.939, SD = 0.06), and tiger + prey (AUC = 0.932, SD = 0.05). Model performance was significantly different (Wilcoxon signed-rank test,  $P < 0.001$ ) between tiger + abiotic and tiger + abiotic + prey, and between tiger + abiotic and tiger + prey. The predictive power of the habitat suitability models was greater with tiger + abiotic than with prey models. However, models were significantly improved when trophic interactions (i.e., primary productivity and ungulate prey) were included into tiger + abiotic model. These results supported the importance of trophic interactions and that incorporating trophic interactions between primary productivity, herbivores, and carnivores can provide better predictions of habitat suitability for apex predators.

Prey habitat suitability was the most important variable in predicting habitat suitability for tigers (Figure 16 and Table 10). In the trophic interaction model (tiger + abiotic + prey), the occurrence of tigers was more likely where occurrences of wild boar, gaur, mixed deciduous, distance to human settlement, and distance to forest edge increased. For the prey-only model, tiger occurrence was best predicted by high occurrences of wild boar and gaur. For the abiotic-

only model, tiger occurrences were more likely at higher proportion of mixed deciduous forest and dry evergreen forest, further distance to human settlement, and forest edge. The occurrence of wild boar was the best predictor of tiger habitat suitability in both models of tiger + prey and tiger + abiotic + prey.

The effect of variables on predictions of habitat suitability for ungulate prey varied among species. Habitat suitability of wild boar, gaur, muntjac, and sambar were all highly correlated with cumulative productivity, seasonality in productivity, annual precipitation, and forest edge. Occurrences of all four species increased as cumulative productivity increased. Occurrences of wild boar and gaur were highest at a moderate level of seasonality in productivity, while seasonality in productivity had little effect on muntjac and sambar. Occurrences of all four species were highest at annual precipitation range of 1000-1500 mm, but decreased with higher annual precipitation. Distance to forest edge affected species differently. Increased distance to forest edge was associated with increased probabilities of occurrence for gaur and muntjac, but wild boar and sambar were higher at medium distances to forest edge (~ 15 – 20 km) than in either low and high distance to forest edge.

#### *Habitat patches and dispersal corridors*

The Indochinese tiger populations currently occupy only eight habitat patches, and they are highly isolated (Figure 17a). Currently occupied habitat patches covered 8,675 km<sup>2</sup> ranging from 85 – 3,665 km<sup>2</sup> with a mean area of 528 km<sup>2</sup>. Total area was 8,675 km<sup>2</sup> with 94.8% of currently occupied patches inside protected areas. The largest habitat patch is located in the Western Forest Complex (Huai Kha Khaeng, Thungyai, and Mae Wong Wildlife Sanctuaries). We identified seven potential connections occurring between currently occupied patches (Figure



17a). However, there were only two dispersal corridors of 25-km dispersal distance (between Kaeng Krachan and Kuiburi, and between Banglang and Hala-Bala); and three connections of 58-km and three of 64-km dispersal distances, respectively (between Kaeng Krachan and Kuiburi, between Banglang and Hala-Bala, and Khao Yai and Thap Lan). All other connections among occupied habitat patches were either blocked by dispersal barriers (e.g., ACE highways, agriculture, and urban) or were too far for tigers to disperse (Table 11).

The potential habitat of the Indochinese tiger in Thailand was also highly fragmented, and habitat fragments were largely unconnected with long dispersal corridors (Figure 17b). We identified 26 potential tiger habitat patches ranging from 74 – 1,513 km<sup>2</sup> with a mean area of 305 km<sup>2</sup>. Total area was 7,929 km<sup>2</sup> with 88.8% located in protected areas. The largest patch was located in Salawin Wildlife Sanctuary. We identified 13 connections (i.e., least-cost paths among suitable habitat patches) with a dispersal distance of 25 km; 20 connections with a dispersal distance of 58 km; and 22 connections with a dispersal distance of 64 km (Figure 17b).

The pattern of resistance to movement for tigers (i.e., current) was heterogeneously distributed among the least-cost path corridors for both currently occupied and potential patches (Figure 17c and d). For currently occupied patches, the least-cost path corridor between the Kaeng Krachan and Kuiburi habitat patches had the lowest resistance for tiger movement, meaning that there was no barrier separating them, and dispersal between them is possible. Conversely, the resistance of movement between Huai Kha Khaeng located in the Western Forest Complex (WFC) patch and Kaeng Krachan patch, and between Khao Yai and Thap Lan patches were high and tiger dispersal is not likely (Figure 17c, Table 11). For the resistance of movement among potential dispersal corridors, we found that there was low resistance of

movement among the least-cost path corridors in the northern Thailand, which can potentially serve as dispersal corridors connecting currently occupied patches to unoccupied suitable patches (Figure 17d).

#### *Importance of patches and dispersal corridors*

The spatial patterns of currently occupied and potential connectivity networks were locally connected, but not regionally and nationally. The relative importance of currently occupied habitat patches and dispersal corridors in maintaining the overall connectivity for Indochinese tigers in Thailand were similar at all dispersal distances (Figure 18). For existing tiger populations (Figure 18a, b and c), the Western Forest Complex habitat patch covered Huai Kha Khaeng, Thung Yai, and Mae Wong Wildlife Sauntuaries was most important in maintaining tiger habitat connectivity in Thailand (as quantified by the percentage of contribution to overall connectivity;  $dPC = 61 - 63 \%$ ). This habitat patch is highly valuable to maintaining a connectivity network because it covers a large area of quality habitat (highest  $dPC_{intra}$ ). However, the Kaeng Kracha habitat patch was well connected to the other habitat patches which tiger populations could potentially disperse (highest  $dPC_{flux}$ ). The Keng Kracha habitat patch could also serve as a stepping stone because it has a topological position that can sustain connectivity among other habitat patches (highest  $dPC_{connector}$ ) (Table 12). In terms of the relative importance of dispersal corridors between currently occupied patches, the Kaeng Krachan – Kuiburi dispersal corridor showed the highest contribution to the connectivity network ( $dPC_{connector} = 9 - 11\%$ ) (Table 13). This corridor also had the highest dispersal probability and lowest resistance to movement.

For the relative importance of potential habitat patches and dispersal corridors, Western Forest Complex habitat patch had the highest contribution to overall connectivity ( $dPC = 47 - 52\%$ ). The Kaeng Krachan – Kuiburi dispersal corridor was the most important linkage ( $dPC_{connector} = 6\%$ ). Several potential habitat patches and dispersal corridors located in the Western Forest Complex and northern Thailand were important in maintaining the overall potential connectivity network, but there are currently unoccupied by tiger populations based on the recent surveys (Figure 18e, d, and f).

## **Discussion**

Our goal was to assess the connectivity of currently-occupied and potential habitat for the endangered Indochinese tiger in Thailand. Our results reveal that the incorporation of trophic interactions between primary productivity, herbivores, and carnivores significantly improved predictions of habitat suitability for apex predators, such as the Indochinese tiger. However, current tiger populations in Thailand are limited to small, unconnected areas of high-quality habitat. Potential dispersal corridors between existing tiger populations were long with high resistance to movement. The habitat patches and corridors within the Forest Western Complex and Kaeng Krachan forest complex were the most importance for maintaining overall functional connectivity for Indochinese tigers in Thailand. Potential habitat patches that could serve as priority sites for reintroduction and dispersal corridors in terms of their likelihood facilitating movement were also highly fragmented and isolated, suggesting that it will be difficult to regain functional connectivity across all of Thailand.

### *Tiger Habitat suitability*

Our results suggest that the incorporation of trophic interactions can significantly improve predictive power of habitat suitability models, and hence provide more realistic habitat predictions for connectivity assessments. Our finding was consistent with prior findings that tiger presence is highly correlated with prey availability (Hebblewhite et al. 2014; Karanth et al. 2004b; Ngoprasert et al. 2012). Habitat models of tigers in other regions that included prey occurrence also had enhanced predictive performance (Hebblewhite et al. 2014; Kanagaraj et al. 2011), that revealed important ecological patterns of habitat connectivity (Kanagaraj et al. 2013).

Our ensemble modeling approach for predicting habitat suitability indicated that the distribution of habitat suitable for tigers was mainly driven by the distributions of their main ungulate prey species, and avoidance of areas with high human disturbance. Although, this finding is not new, it confirms our hypothesis of habitat suitability for tigers' dispersal based on previous studies of tigers in Thailand (Ngoprasert et al. 2012). For tiger connectivity in other regions, tigers' habitat suitability associate with prey availability (Kanagaraj et al. 2013; Wikramanayake et al. 2004). Additionally, our results are similar to habitat suitability of other studies for other large carnivores, where suitable habitat depends on both food resources (e.g., prey availability, primary productivity, and land cover types) and the absence of human disturbances (Brodie et al., 2014). For example, studies grizzly bears in North America are positively correlated with forage variables (i.e., greenness, soil wetness, and nearest rivers), while cougars are well predicted by terrain ruggedness, greenness, and avoidance of roads (Chetkiewicz and Boyce 2009). Similarly, European brown bears occurrence is associated with forest cover, higher elevations, and avoidance of roads and human activity in the east-central

Alps (Boitani et al., 1999; Guthlin et al., 2011), and the Italian Alps (Peters et al., 2015). In Borneo indicated that local abundance of sun bears (*Helarctos malayanus*) and Sunda clouded leopards (*Neofelis diardi*) is related to elevation, logging, and road density (Brodie et al., 2014). And last but not least, connectivity models for Jaguars included land cover type, percent tree and shrub cover, elevation, and human disturbance (Rabinowitz and Zeller 2010). In addition to including prey availability, we integrated the cumulative annual productivity and seasonal variation in productivity derived from the DHIs, which has been successfully used for the occurrence of moose in Canada (Michaud et al. 2014), but not yet in the tropics. Our results demonstrated that primary productivity variables were important factors in predicting the occurrence of ungulate prey species, and ultimately those for tigers in Thailand.

#### *Connectivity assessment*

The remaining large, intact habitats for Indochinese tigers in Thailand are mostly located within protected areas. However, the suitable habitat patches were highly fragmented with high resistance values in the dispersal corridors. Our results demonstrated that the habitat patch located in the Western Forest Complex was the largest area of suitable habitat, but it had low dispersal probability and high resistance to movement due to its isolation. Based on available information for Indochinese tigers in Thailand, individual tigers may not be able to travel to the nearest currently occupied patches due to patch isolation and high resistance in urban and agricultural areas. Moreover, the East-West economic corridor, a highway connecting Myanmar to Vietnam through Thailand, is a dispersal barrier that may block tiger movement within the dispersal corridor between the Western Forest Complex and Kaeng Krachan Forest Complex. Our results indicate that tiger populations in Kaeng Krachan and Kuiburi occur in large, well-

connected patches and that potential dispersal corridors for tigers exist or can be restored among these patches.

Currently occupied and potential connectivity networks were isolated and unconnected, and regaining connectivity across the country may prove to be difficult. Habitat connectivity remains intact only in protected areas within the Western Forest Complex and Kaeng Krachan Forest Complex. By ranking the relative importance of each habitat patch and dispersal corridor in maintaining the connectivity among existing tiger populations and potential suitable habitat for tigers' dispersal, we identified the areas where future reintroduction efforts should focus. We found that the habitat patch located in the Western Forest Complex was the most important refuge for tigers because it covers a large extent of suitable habitat with abundant prey (Simcharoen et al. 2014a; Simcharoen et al. 2014b; Trisurat et al. 2010b). However, we also found that this habitat patch is becoming isolated, which could eventually lead to inbreeding depression, as is the case for the isolated Bengal tiger (*Panthera tigris*) populations in India and Nepal (Smith and McDougal, 1991). Whereas, Kaeng Krachan patch has smaller habitat area, it is well connected to Kuiburi habitat patch. Therefore, the Kaeng Krachan patch is an important stepping stone, and dispersal corridor between both patches, and is the most important in maintaining a connectivity network in the region. Indeed, habitat loss and fragmentation of these habitats would likely decrease the probability of tiger survival in the region. Other currently occupied patches had low contribution to an overall connectivity network because they were isolated and far from the largest patch. However, the dispersal corridor between Taplan and Khao Yai connected relatively large suitable habitat areas and had low resistance to movement that could also play an important role in the conservation of tiger populations.

### *Management implications*

In terms of improving the connectivity of tiger populations in Thailand, our study suggests several conservation strategies. First, it is important to enhance the quality of currently-occupied patches by decreasing conflicts with land use policy, and enact effective anti-poaching law. Second, it is necessary to protect both currently occupied and potential habitat patches and dispersal corridors identified by this study. Third, it is crucial to maintain high value habitat patches and dispersal corridors to ensure persistence of a connectivity network. Fourth, we suggest restoring degraded habitat through strategic land-use planning because tigers are habitat generalists and can disperse through a mosaic of degraded forests. Fifth, we identified several priority patches and dispersal corridors for connectivity, where future introductions would contribute to facilitate existing tiger populations. The important, unoccupied potential habitat patches and corridors occurred in protected areas located in the north of Thailand. We recommend the investigation of these potential habitat patches and corridors as candidate sites for reintroduction of tigers and their prey.

### **Conclusion**

The ultimate goal for tiger conservation is to create large and well-connected populations that can persist long-term. Our analysis demonstrated that habitat connectivity for Indochinese tigers in Thailand is currently very low, because habitat patches are highly isolated patches and exist only within protected areas. However, we identified priority areas for conserving existing tiger population, and candidate habitat patches and dispersal corridors for future reintroductions. For the long-term persistence of tigers, it is crucial to protect both currently-occupied and potential habitat patches and corridors. Enhancing the quality of currently occupied habitat and

reintroducing tiger populations and their prey would substantially increase the overall connectivity among the Indochinese tiger populations. Our connectivity analyses also highlight the importance of incorporating trophic interactions when quantifying habitat suitability, and combining least-cost modeling, circuit analysis, and graph theory approaches with species' dispersal ability to improve assessments of habitat quality and its connectivity. Our results stemming from this approach are novel and important for the understanding of current patterns of habitat connectivity and for developing management strategies to ensure long term survival of tigers in the region as well as other carnivores.

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## Tables

Table 10. Mean model performance and ensemble measures (AUC scores) of top performing habitat suitability models for tiger + abiotic, tiger + prey, tiger + prey + abiotic, wild boar, gaur, muntjac, and sambar. The hypothesis on the role of trophic interactions in habitat suitability performance assessing the differences between: abiotic versus prey model; and abiotic versus abiotic + prey models based on Wilcoxon signed-rank tests.

Model	GLM	GAM	GBM	RF	MAXENT	Ensemble
Tiger + Abiotic	0.763 ± 0.055	0.693 ± 0.068	0.784 ± 0.054	0.707 ± 0.070	0.774 ± 0.060	0.939 ± 0.06***
Tiger + Prey	0.735 ± 0.061	0.757 ± 0.061	0.761 ± 0.058	0.726 ± 0.071	0.772 ± 0.067	0.932 ± 0.052***
Tiger + Prey + Abiotic	0.784 ± 0.055	0.692 ± 0.059	0.805 ± 0.043	0.734 ± 0.053	0.782 ± 0.058	0.954 ± 0.060***
Wild boar	0.855 ± 0.017	0.858 ± 0.015	0.880 ± 0.016	0.854 ± 0.020	0.876 ± 0.016	0.962 ± 0.028
Gaur	0.790 ± 0.027	0.806 ± 0.038	0.844 ± 0.025	0.812 ± 0.030	0.825 ± 0.029	0.962 ± 0.047
Muntjac	0.896 ± 0.010	0.917 ± 0.011	0.932 ± 0.010	0.936 ± 0.011	0.930 ± 0.010	0.976 ± 0.018
Sambar	0.913 ± 0.013	0.929 ± 0.018	0.941 ± 0.009	0.904 ± 0.029	0.934 ± 0.013	0.981 ± 0.019

\*\*\*  $P < 0.001$

Table 11. Cost dispersal probabilities ( $p_{ij}$ ) and sum of cost of resistance movement (Resistance) calculated for each dispersal distance delineated dispersal corridors between currently occupied habitat patches for Indochinese tigers in Thailand. Higher values of cost dispersal probability indicate the high probability of movement between suitable patches. Higher values of cost of resistance movement indicate the low probability of movement between suitable patches.

Corridor <sup>1</sup>	Distance (km)	$p_{ij}$ 25 km	$p_{ij}$ 58 km	$p_{ij}$ 64 km	Resistance
KK-KB	13	0.69	0.85	0.86	59.98041
BL-HB	20	0.58	0.79	0.81	disconnected
KY-THP	36	0.37	0.65	0.68	223.1436
HKK-KK	195	0.00	0.10	0.12	1551.59
PK-KY	258	0.00	0.05	0.06	disconnected
PK-HKK	605	0.00	0.00	0.00	disconnected
KB-BL	950	0.00	0.00	0.00	disconnected

<sup>1</sup> KK-KB = Kaeng Krachan and Kuiburi, BL-HB = Banglang and Hala-Bala, KY-THP = Khao Yai and Thaplan, Huai Kha Khaeng and Kaeng Krachan, PK-KY = Phu Khieo and Khao Yai, Phu Khieo and Huai Kha Khaeng, and Kuiburi and Banglang.

Table 12. Contribution of each currently occupied habitat patches to the maintenance of an overall landscape connectivity as measured by the relative importance of the probability of connectivity index  $dPC$  (%) and its fractions for tigers' movement at 64 km.

Node	$dPC$	$dPC_{intra}$	$dPC_{flux}$	$dPC_{connector}$
Phu Khieo	0.77	0.61	0.16	0.00
Western Forest Complex	62.85	53.15	9.69	0.00
Khao Yai	1.06	0.16	0.88	0.03
ThaplanP	3.30	2.36	0.94	0.00
Kaeng Krachan	38.02	19.10	17.56	1.36
Kuiburi	13.57	1.71	11.86	0.00
Bang Lang	2.34	1.96	0.38	0.00
Hala-Bala	0.41	0.03	0.38	0.00

Table 13. Contribution of each dispersal corridor to the maintenance of the overall landscape connectivity as measured by *dPCconnector* (%) for all tiger dispersal distances.

Corridor <sup>1</sup>	<i>dPCconnector</i> 25	<i>dPCconnector</i> 58	<i>dPCconnector</i> 64
KK-KB	9.0	11.1	11.2
BL-HB	0.3	0.4	0.4
KY-THP	0.5	0.8	0.9
HKK-KK	0.4	6.2	7.2
PK-KY	0.0	0.0	0.1
PK-HKK	0.0	0.0	0.0
KB-BL	0.0	0.0	0.0

<sup>1</sup> KK-KB = Kaeng Krachan and Kuiburi, BL-HB = Banglang and Hala-Bala, KY-THP = Khao Yai and Thaplan, Huai Kha Khaeng and Kaeng Krachan, PK-KY = Phu Khieo and Khao Yai, Phu Khieo and Huai Kha Khaeng, and Kuiburi and Banglang.



## Figures

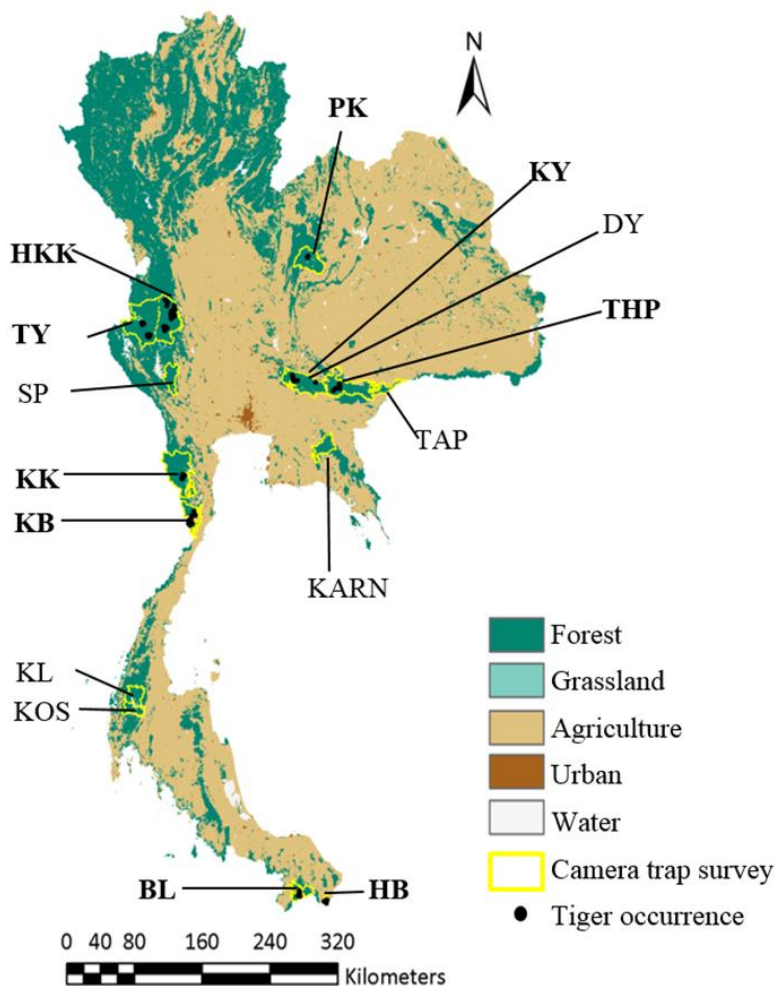


Figure 13. Study area, filed surveys in 15 protected areas across Thailand: Bang Lang National Park (BL), Don Yai Wildlife Sanctuary (DY), Hala-Bala Wildlife Sanctuary (HB), Huai Kha Khaeng Wildlife Sanctuary (HKK), Kaeng Krachan National Park (KK), Khao Ang Rua Nai Wildlife Sanctuary (KARN), Khao Sok National Park (KOS), Klong Saeng Wildlife Sanctuary (KLS), Khao Yai National Park (KY), Kuiburi National Park (KB), Phu Khieo Wildlife Sanctuary (PK), Ta Phraya National Park (TAP), Thap Lan National Park (THP), Thung Yai Naresuan-West Wildlife Sanctuary (TYW), Salak Pra Wildlife Sanctuary (SP). Tiger occurrences were in black dots within protected areas with bold names.

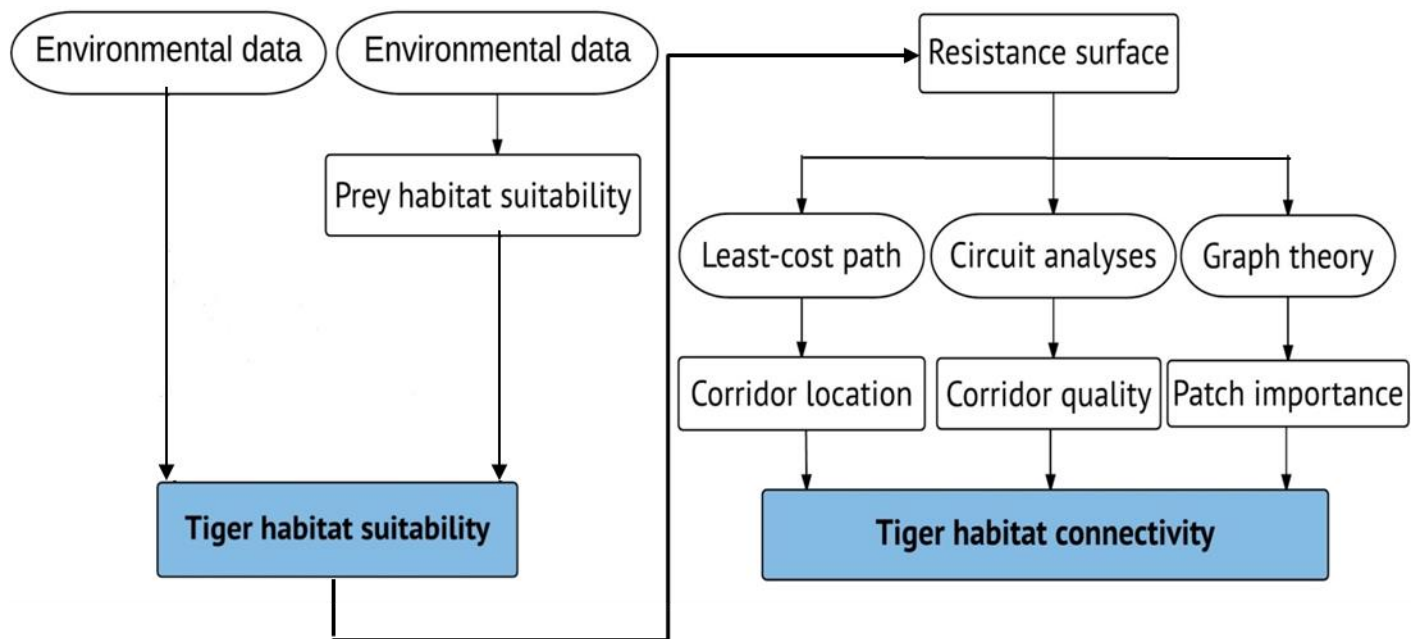


Figure 14. Flowchart synthesizing the procedure used for assessing habitat connectivity for the Indochinese tigers in Thailand.

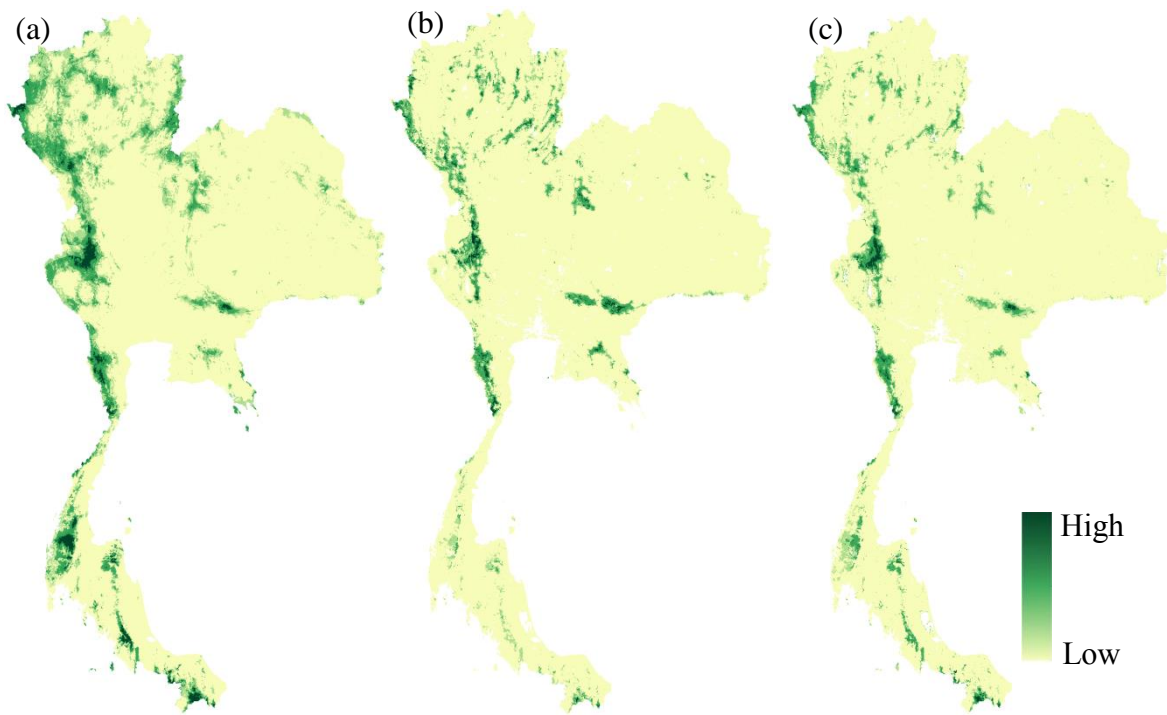


Figure 15. Habitat suitability models for the Indochinese tigers in Thailand derived from an ensemble of species distribution models showing the probability of occurrence, (a) habitat suitability models based on tiger + abiotic variables, (b) tiger + prey, (c) tiger + prey + abiotic variables.

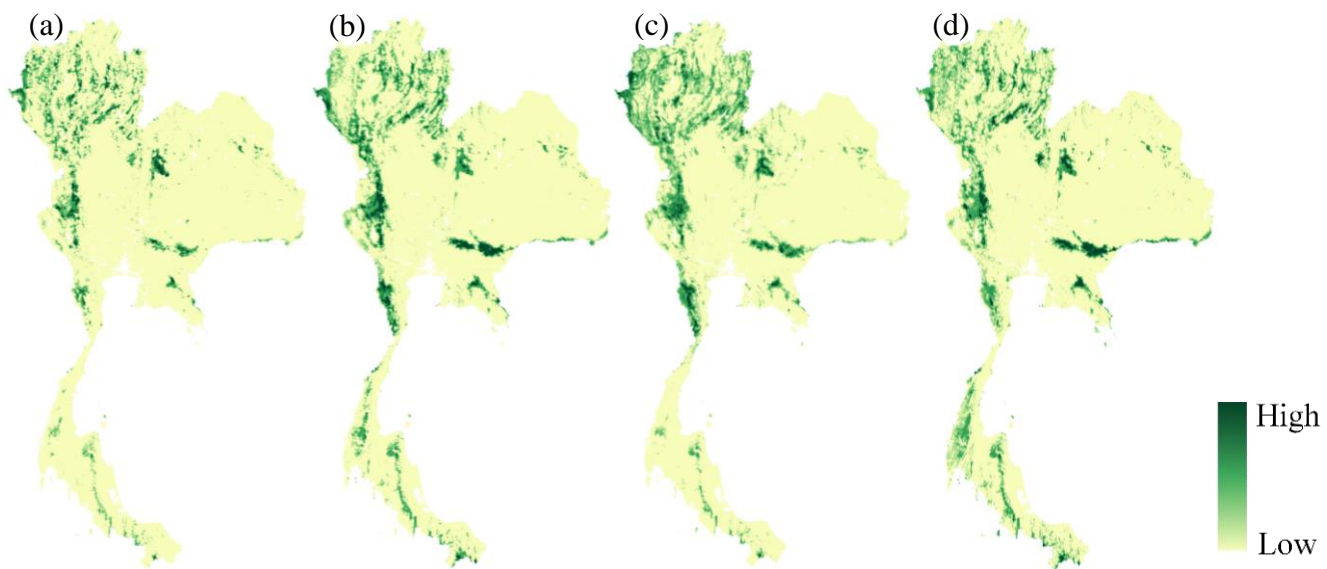


Figure 16. Habitat suitability models for ungulate prey: (a) wild boar, (b) gaur, (c) muntjac, (d) sambar derived from an ensemble of species distribution models showing the probability of occurrence.

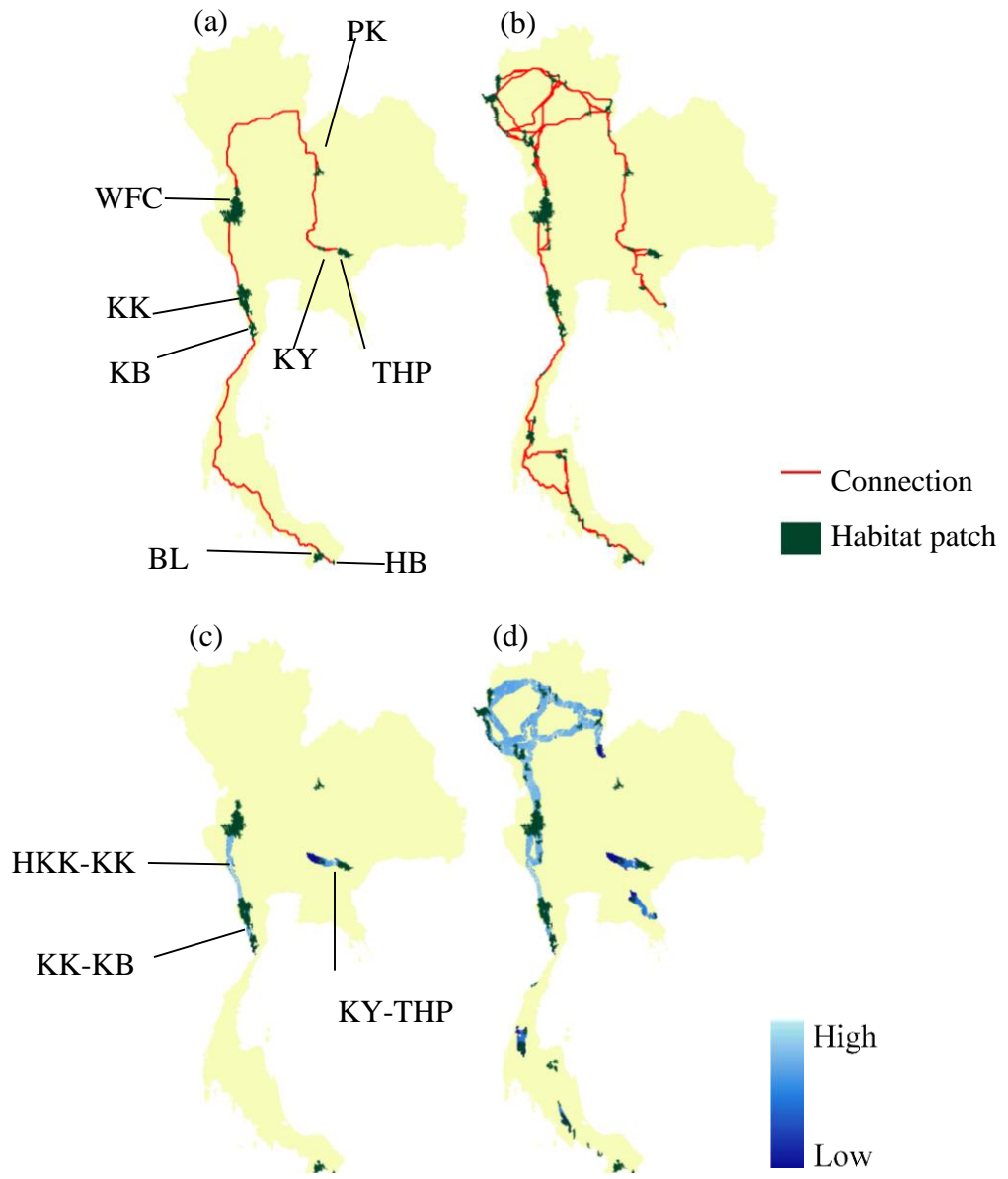


Figure 17. Connectivity across Thailand, (a) currently occupied habitat patches (dark green) and least-cost path corridors (red line), (b) potential habitat patches and least-cost path corridors, (c) currently occupied habitat patches and circuit analysis corridors with 10 km buffers, (d) potential habitat patches and circuit analysis corridors with 10 km buffers, showing high probability of tigers' movements (light cyan) and low probability of tigers' movements (dark blue).

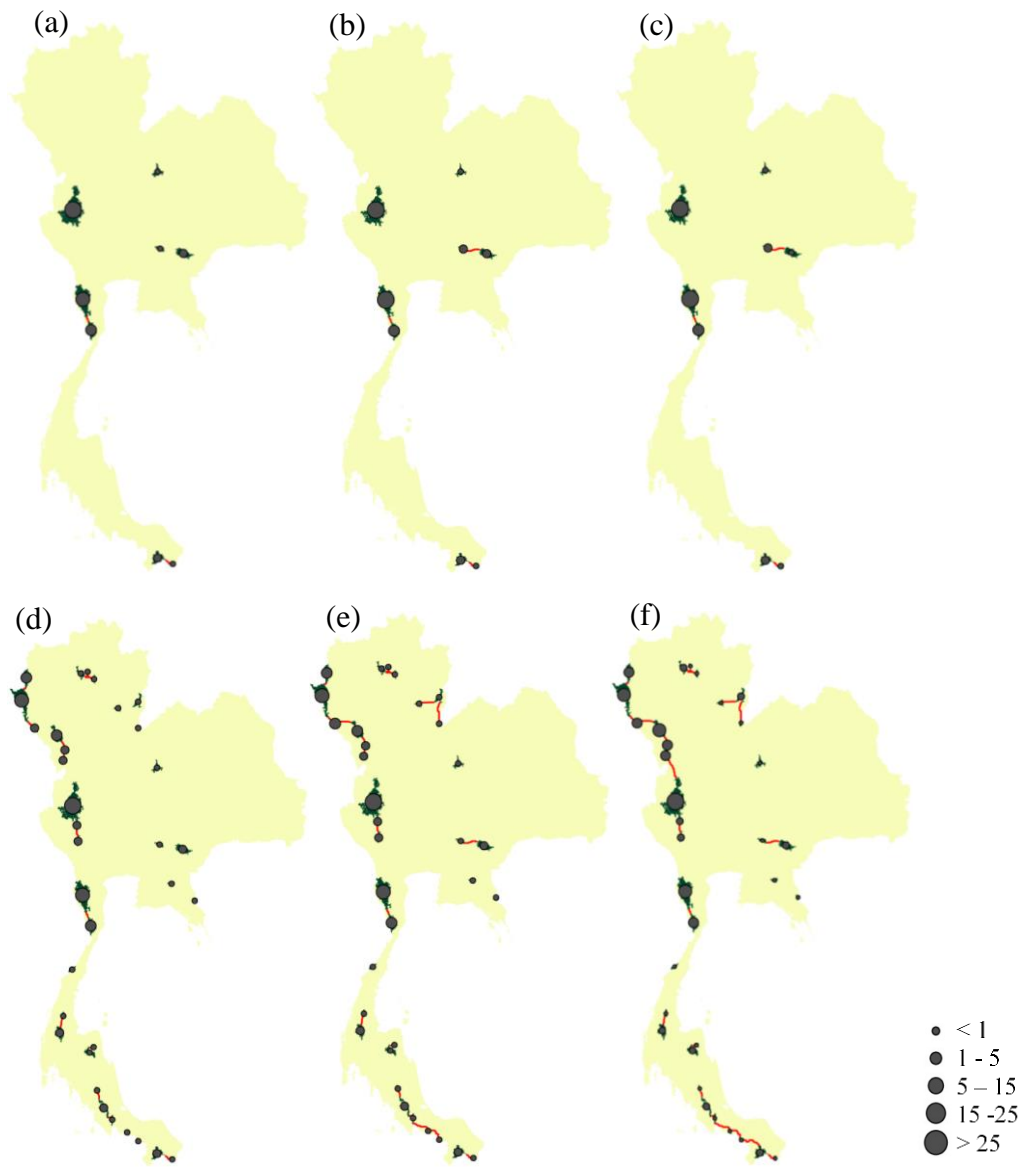


Figure 18. The relative importance of habitat patches and dispersal corridors for Indochinese tigers in Thailand. The importance of each habitat patch is shown in term of its contribution to maintain an overall landscape connectivity as measured by the probability of connectivity index for both currently occupied: (a), (b), and (c), and potential habitat patches: (d), (e), and (f) for the dispersal distance of 25 km, 58 km, and 64 km, respectively.

## Appendices

Appendix 12. AUC scores for individual models of the distribution of tiger habitat, as indicated by abiotic variables, including proportions of habitat type, elevation, slope, distance to nearest river, distance to nearest forest edge, distance to nearest village or road, and annual precipitation. Avg and Run SD are the average and standard deviation of the 20 individual runs (2 replicates each of 10-fold cross validations) for each model algorithm. Full AVG and Full SD are the average and standard deviation of each model run without setting aside testing data. Ensemble AUC scores for top performing models was 0.939, with standard deviation 0.06.

Model	Run Avg	Run SD	Full Avg	Full SD
GLM	0.763	0.055	0.81	0.00
GBM	0.784	0.054	0.89	0.00
CTA	0.716	0.067	0.79	0.03
FDA	0.761	0.050	0.81	0.00
MARS	0.751	0.055	0.84	0.00
RF	0.707	0.070	0.97	0.00
MAXENT	0.774	0.060	0.88	0.00
ANN	0.734	0.055	0.75	0.06
SRE	0.659	0.067	0.66	0.00
GAM	0.693	0.068	0.89	0.00

Appendix 13. AUC scores for individual models of the distribution of tiger habitat, as indicated by trophic interactions, including cumulative annual productivity, seasonal variation in productivity, Eurasian wild boar, gaur, muntjact, and sambar deer. Avg and Run SD are the average and standard deviation of the 20 individual runs (2 replicates each of 10-fold cross validations) for each model algorithm. Full AVG and Full SD are the average and standard deviation of each model run without setting aside testing data. Ensemble AUC scores for top performing models was 0.932, with standard deviation 0.052.

Model	Run Avg	Run SD	Full Avg	Full SD
GLM	0.735	0.061	0.763	0.002
GBM	0.761	0.058	0.882	0.003
CTA	0.725	0.067	0.815	0.008
FDA	0.717	0.073	0.795	0.003
MARS	0.734	0.062	0.817	0.001
RF	0.726	0.071	0.973	0.000
MAXENT	0.772	0.067	0.844	0.002
ANN	0.740	0.090	0.824	0.001
SRE	0.625	0.046	0.625	0.009
GAM	0.757	0.061	0.822	0.003



Appendix 14. AUC scores for individual models of the distribution of tiger habitat, as indicated by the combination of trophic interactions and abiotic variables, including species distributions of Eurasian wild boar, gaur, muntjact, sambar deer, proportions of habitat type, elevation, slope, distance to nearest river, distance to nearest forest edge, distance to nearest village or road, and annual precipitation. Avg and Run SD are the average and standard deviation of the 20 individual runs (2 replicates each of 10-fold cross validations) for each model algorithm. Full AVG and Full SD are the average and standard deviation of each model run without setting aside testing data. Ensemble AUC scores for top performing models was 0.954, with standard deviation 0.060.

Model	Run Avg	Run SD	Full Avg	Full SD
GLM	0.784	0.055	0.819	0.004
GBM	0.805	0.043	0.915	0.004
CTA	0.753	0.035	0.797	0.028
FDA	0.726	0.075	0.829	0.011
MARS	0.769	0.067	0.851	0.000
RF	0.734	0.053	0.972	0.000
MAXENT	0.782	0.058	0.903	0.001
ANN	0.729	0.050	0.733	0.031
SRE	0.614	0.069	0.659	0.003
GAM	0.692	0.059	0.920	0.001

Appendix 15. Resistance surface for tigers across Thailand. Resistance ranges from 1 (green) to 100 (blue). Note that resistance everywhere within a suitable habitat patch has been set to 1.

