



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

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## ARTICLE INFO

### Keywords:

Body size  
MODIS  
Nesting guild  
Species distribution modeling  
Texture analysis  
Tropical ecosystem  
Vegetation structure

## ABSTRACT

Global biodiversity loss is most pronounced in the tropics. Monitoring of broad-scale patterns of habitat is essential for biodiversity conservation. Image texture measures derived from satellite data are proxies for habitat heterogeneity, but have not been tested in tropical forests. Our goal was to evaluate image texture to predict tropical forest bird distributions across Thailand for different guilds. We calculated a suite of texture measures from cumulative productivity (1-km fPAR-MODIS data) for Thailand's forests, and assessed how well texture measures predicted distributions of 86 tropical forest bird species in relation to body size, and nesting guild. Finally, we compared the predictive performance of combining (a) satellite image texture measures, (b) habitat composition, and (c) habitat fragmentation. We found that texture measures predicted occurrences of tropical forest birds well ( $AUC = 0.801 \pm 0.063$ ). Second-order homogeneity was the most predictive texture measure. Our models based on texture were significantly better for birds with larger body size ( $p < 0.05$ ), but did not differ among nesting guilds ( $p > 0.05$ ). Models that combined texture with habitat composition measures ( $AUC = 0.928 \pm 0.038$ ) outperformed models that combined fragmentation with habitat composition measures ( $AUC = 0.905 \pm 0.047$ ) ( $p < 0.05$ ). The incorporation of texture, composition, and fragmentation variables significantly improved model accuracy over texture-only models ( $AUC = 0.801 \pm 0.063$  to  $AUC = 0.938 \pm 0.034$ ;  $p < 0.05$ ). We suggest that texture measures are a valuable tool to predict bird distributions at broad scales in tropical forests.

## 1. Introduction

Confronting the crisis of biodiversity loss due to human activities and climate change requires efficient and accurate measures of broad-scale patterns of biodiversity (Kissling et al., 2018; Radeloff et al., 2019; Razenkova et al., 2020). Habitat variables derived from remotely sensed data are key to predict species distributions (Estes et al., 2010; He et al., 2015; Suttidate et al., 2019). However, habitat variables derived from land cover classifications often overlook within-class heterogeneity, which is an important component of wildlife habitat. The challenge is to develop habitat variables that can capture habitat features that are associated with species' ecological needs and can be used to monitor

species distributions over large areas.

Habitat heterogeneity influences species distributions (Fischer et al., 2008; Haralick et al., 1973; Tuttle et al., 2006). Here, we consider habitat heterogeneity in forests to be both the vertical structure of vegetation layers and the horizontal structure of different vegetation forms, heights, and canopy gaps (Culbert et al., 2012). Habitat heterogeneity affects individual animals by influencing the availability of habitat components, exposure to habitat edges, degree of habitat connectivity, and interactions among individuals (Cuervo and Møller, 2019). Individual species may select habitat for nesting and foraging in association with specific levels of vertical and horizontal vegetation structure (Bellis et al., 2008; St-Louis et al., 2014).

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Species distribution models often include habitat variables derived from satellite land-cover classifications (Turner, 2014), but those ignore within-class heterogeneity, which is ecologically important for many species, especially birds (St-Louis et al., 2014). Image texture measures derived from satellite data can capture both between-habitat and within-habitat structure, providing a potential advantage over, or complement to, measures characterizing habitat composition and habitat fragmentation derived from a given land cover classification. Indeed, image texture measures improve models of species distributions (Bellis et al., 2008; St-Louis et al., 2014). The texture of a satellite image contains information about the spatial arrangement of objects, or habitat patches and is described with two classes of texture measures: first-order (occurrence) and second-order (co-occurrence). First-order texture measures are based on the frequency distribution of pixel values 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) (Culbert et al., 2012; Haralick et al., 1973; St-Louis et al., 2014). In other words, first-order measures are based on individual-pixel values, which reflect their compositional variability, whereas second-order measures are determined by the interaction or co-occurrence of pixel values, which reflect their spatial arrangement and dependence. For example, a closed-canopy, single-species forest has high second-order homogeneity if adjacent pixels have similar reflectance values. In contrast, a multi-species forest with canopy gaps has strong differences in reflectance values among adjacent pixels and hence low second-order homogeneity. Additionally, texture measures reflect heterogeneity among land cover classes, such as reflectance differences between forest and grassland (Culbert et al., 2009; Wallis et al., 2016).

Texture measures derived from remotely sensed data predict both bird species richness and individual bird species distributions well. For example, texture predicts bird species richness in North American desert shrub- and grassland (St-Louis et al., 2009; St-Louis et al., 2014), in a Wisconsin habitat complex of grassland, savanna, and woodland (Wood et al., 2013), in the US Midwest (Culbert et al., 2012), across the United States (Tuanmu and Jetz, 2015), in South American highland forests (Bellis et al., 2015), tropical forests in southeastern Ecuador (Wallis et al., 2016), and the Andes (Wallis et al., 2017). Similarly, texture predicts many individual species distributions, including mountain bongo antelope (*Tragelaphus eurycerus isaaci*) in East African montane forest (Estes et al., 2008; Estes et al., 2010), Loggerhead Shrike (*Lanius ludovicianus*) in the Chihuahuan Desert of New Mexico (St-Louis et al., 2010), or Greater Rhea (*Rhea Americana*) in Argentina grassland (Bellis et al., 2008). Image texture differences are related to differences in habitat use between phenotypes of the white-throated sparrow (*Zonotrichia albicollis*) (Tuttle et al., 2006), are useful in determining probability of occurrence of bird species in Maine (Hepinstall and Sader, 1997) and in Switzerland (Zellweger et al., 2013). These studies show the successful application of image texture derived from remotely sensed data in explaining species distributions.

When analyzing texture, one important question is the spatial resolution of the data that are analyzed. The advantage of high (< 10 m) or medium (10–30 m) resolution imagery is that it captures considerable structural detail. In contrast, the advantages of coarse (> 250 m) resolution data are that they are recorded more frequently, which is especially important in cloudy areas, that larger areas can be analyzed more efficiently, and that global products such as the MODIS product suite are available. However, the question is if texture measures derived, for example, from 1-km MODIS fPAR data can capture within-class habitat heterogeneity accurately enough to predict bird distributions. MODIS fPAR data are available at high temporal resolution and over broad scales, thus providing a potentially great opportunity to develop relevant, consistent, texture measures for biodiversity assessments in the tropics (Coops et al., 2019; Radeloff et al., 2019; Suttidate et al., 2019). Given differences in the scale of habitat selection among bird species, it

may well be that textures from coarse-resolution satellite data can predict some species' distributions well, but not others. For example, predictive power may vary according to body size, or nesting requirements so that larger-bodied birds with larger territories are predicted better. The question how well satellite image texture predicts bird species distributions is especially relevant in the tropics given both rampant biodiversity loss and frequent cloud cover there.

Our goal was to evaluate the usefulness of satellite-derived texture measures as proxies for habitat heterogeneity for avian distribution models in tropical ecosystems in Thailand. Our objectives were to:

- test the relationships between texture measures and overall tropical forest bird distributions, as well as distributions of different nesting guilds and body sizes;
- compare species distribution models based on texture measures with models based on measures of habitat composition and habitat fragmentation, and to examine whether these variables complement each other when modeling species distribution of tropical birds.

## 2. Methods

### 2.1. Study area

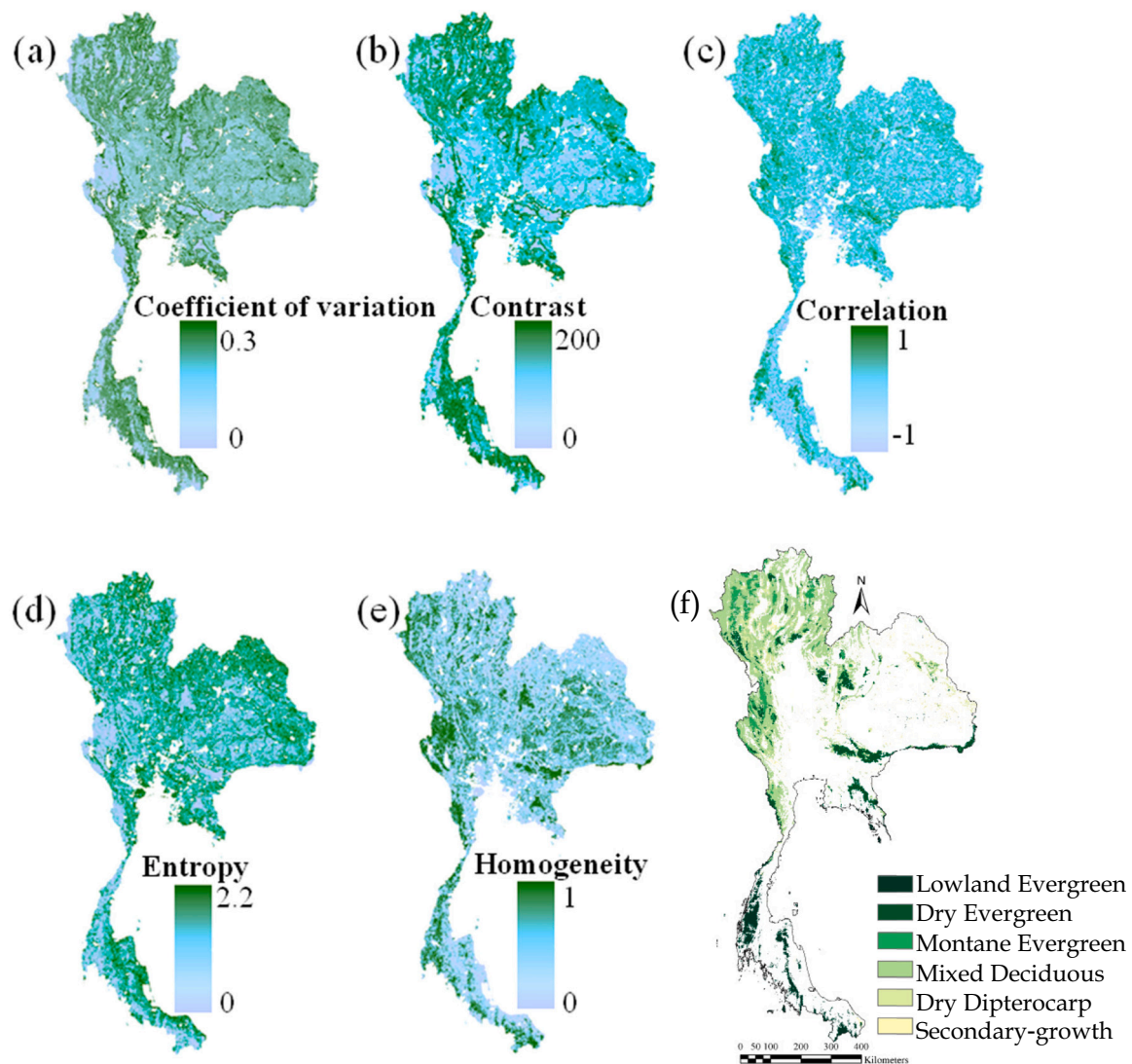
Our study area was Thailand's tropical forest area (Fig. 1). Forest covers approximately 163,765 km<sup>2</sup> (about 30 % of the country), and major forest types are (a) montane evergreen forest, (b) dry evergreen forest, (c) lowland evergreen forest, (d) mixed deciduous forest, (e) dry dipterocarp forest, and (f) secondary-growth forest. Elevation ranges from 0 to 2564 m (DNP, 2000), annual precipitation ranges from 1000 to 4000 mm, and average annual temperature from 26 to 29 °C (Thai Meteorological Department, 2010). Thailand is a global biodiversity hotspot (Myers et al., 2000), and home to >1000 bird species (Bird Conservation Society of Thailand Records Committee, 2012). However, agriculture, illegal logging, and urban growth have caused habitat loss and fragmented forests in Thailand, and many bird species are threatened (Laurance et al., 2012; Pattanavibool and Dearden, 2002; Suttidate, 2022). This is why there is an urgent need for ecologically relevant habitat metrics, consistently produced, for modeling distributions of individual bird species across broad areas.

### 2.2. Data

#### 2.2.1. Study species and occurrence data

We chose tropical forest birds in Thailand as our focal taxa for several reasons. First, there are many bird species in Thailand experiencing population decline due to habitat loss and fragmentation (Pattanavibool and Dearden, 2002; Suttidate, 2022). Second, each bird species' ecological niche is unique, so the heterogeneity of primary productivity may be closely related to various aspects habitat that birds select in association with various life history characteristics, including choice of nesting habitat, feeding habitat, mating sites, and migratory stopover sites. Heterogeneity may also be perceived differently by birds of different body size. Image texture may capture aspects of habitat heterogeneity that reveal how individual species respond to (Etard et al., 2020; Newbold et al., 2016). Finally, birds are well studied taxon in Thailand, so there is good occurrence data available.

To examine if texture performs better in modeling distributions of birds that share similar traits, we first grouped forest birds based on nesting habitat into the following guilds: (a) canopy nesting birds, (b) tree cavity nesters, (c) understory nesting birds, (d) ground nesting birds, and (e) all birds, which included all birds in the four guilds. Second, we grouped forest birds based on body size (average body mass of males and females) and classified them into four quartile groups: (1) body size >110 g (average 703 g), (2) body size from 31 g to 110 g, (average 52 g), (3) 15 g to 31 g (average 25 g), and (4) 5 g to 15 g



**Fig. 1.** 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 and habitat composition measures: (a) First-order coefficient of variation, (b) second-order homogeneity, (c) second-order contrast, (d) second-order correlation, (e) second-order entropy, and (f) proportion of six forest habitat types.

(average 9 g). We obtained all bird life history information from Birds of the World database (Billerman et al., 2020).

As our source of birds locations, we obtained data on bird species occurrences from the Global Biodiversity Information Facility (GBIF) (<http://www.gbif.org/>) (GBIF.org, 2020). The GBIF data for birds in Thailand is mainly based on opportunistic observations and some field survey data, and includes data from eBird and iNaturalist. For our investigation of the ability of texture measures to predict bird distributions, we focused on resident forest bird species that inhabit the various forest types of Thailand all year round. We analyzed all georeferenced records collected from 2000 to 2015, to temporally coincide with our image texture and landscape metric data. We included all species with >30 unique localities, the minimum sample size required for species distribution modeling (Hernandez et al., 2006; Pearson et al., 2007). Using these criteria, we assembled 12,858 georeferenced locations of 86 forest specialist bird species that were taxonomically distributed within 5 orders and 28 families. All bird occurrence records were georeferenced to the spatial resolution of the environmental data (1 km).

## 2.2.2. Texture measure data

We calculated a suite of texture measures (Fig. 1) based on cumulative annual productivity, one of the three Dynamic Habitat Indices that

captures the amount of green vegetation that is available in a given pixel (DHIs <http://silvis.forest.wisc.edu>). The cumulative DHI that we analyzed was based on the median fPAR values from 2003 to 2015 at 1-km resolution, resulting in 13 cumulative DHI metrics (one for each year). For details on the DHIs calculation see (Hobi et al., 2017; Radeloff et al., 2019).

We calculated three first-order texture measures: (a) entropy, (b) mean, and (c) coefficient of variation in a  $3 \times 3$  pixel moving window. We also calculated eight second-order texture measures: (a) angular second moment, (b) contrast, (c) correlation, (d) dissimilarity, (e) entropy, (f) homogeneity, (g) mean, and (h) coefficient of variation (Haralick et al., 1973). We selected these texture measures based on their ability to characterize vegetation structure, and hence relevant measures for modeling bird species distributions (Bellis et al., 2008; Hepinstall and Sader, 1997; Wood et al., 2012). We reduced the radiometric resolution of the imagery to 6 bits (64 values) to limit the size of the Grey Level Co-occurrence Matrix (GLCM) and avoid matrices that were too sparsely populated (Culbert et al., 2012). We calculated the texture measures on GLCMs composed of the mean of the four possible adjacent pixels ( $0^\circ$ ,  $45^\circ$ ,  $90^\circ$  and  $135^\circ$ ) (Haralick et al., 1973). All texture measures were calculated using ENVI software. Many texture measures are correlated and we therefore applied a Pearson correlation coefficient



threshold ( $|r| > 0.7$ ) to exclude collinear variables (Dormann et al., 2013) (Fig. A1). Using the threshold, we reduced the original eleven texture measures to five texture measures: (a) first-order coefficient of variation, and second-order, (b) homogeneity, (c) correlation, (d) contrast, and (e) entropy.

### 2.2.3. Habitat composition data

Habitat composition measures are commonly used to predict bird species distributions at broad scales (Jetz and Rahbek, 2002; Kerr and Packer, 1997; Kreft and Jetz, 2007). We calculated habitat composition at 1-km resolution based on categorical 30-m resolution land-cover data. Our land cover data source was the 2000 Thailand land cover map, derived from Landsat TM, ETM+ (DNP, 2000). We estimated the relative abundance of primary and second-growth forests in six forest habitat types: (a) montane-evergreen forest, (b) dry-evergreen forest, (c) lowland-evergreen forest, (d) mixed-deciduous forest, (e) dry-dipterocarp forest, and (f) secondary-growth forest.

### 2.2.4. Habitat fragmentation data

We calculated five fragmentation measures of forest habitat from the 2000 Thailand land cover map: (a) core, (b) edge, (c) perforation, (d) bridge, and (e) loop by applying Morphological Spatial Pattern Analysis (MSPA) as implemented in GUIDOS (Vogt et al., 2007), setting the edge width to 30-m. MSPA is based on morphological image segmentation and results in a per-pixel classification and description of the geometry, pattern, fragmentation, and connectivity of a landscape (Soille and Vogt, 2009; Vogt et al., 2007). Among our five fragmentation metrics, (a) core is defined as forest pixels whose distance to the non-forested areas is greater than the given edge width, and is considered focal habitat area for birds, (b) edge as those 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, (c) perforation is the edge within a forest interior where forested areas are adjacent to other land cover classes, (d) bridge is a set of contiguous non-core forest pixels connecting at least two forest patches, (e) loop is a group of pixels that connect different parts of the same forest patch (Saura et al., 2011; Soille and Vogt, 2009).

## 2.3. Species distribution models

We parameterized generalized linear models (GLM) using logistic regression to (a) evaluate how well fPAR MODIS texture measures alone can predict bird species distributions, and (b) evaluate whether combining measures of texture with habitat composition and fragmentation variables derived from a land cover classification could improve model performance. We fitted six possible combinations of the different types of measures: (a) texture, (b) composition, (c) fragmentation, (d) texture + composition, (e) fragmentation + composition, and (f) texture + fragmentation + composition.

To check for multicollinearity among the 16 variables characterizing texture, habitat composition, and fragmentation, we calculated Pearson correlation coefficients and found that  $|r| < 0.7$  among all variables (Fig. A2). To address potential nonlinearities in the relationship between species distributions and predictors, we included both linear and quadratic forms of the predictors in models. We selected the best model by ranking all models based on the Akaike Information Criterion (AIC). We conducted each model run with two sets of pseudo-absences, each chosen at random within 3 km of species presence locations, to obtain reliable distribution model predictions (Thuiller et al., 2009). We chose the 3-km buffer size based on the size of the home range of Wreathed Hornbill (*Rhyticeros undulatus*) during non-breeding season, which is 28 km<sup>2</sup> determined by a telemetry study in Khao Yai National Park, Thailand (Poonswad and Tsuji, 1994). We used Wreathed Hornbill home range because it is the largest bird we analyzed and individual home range size estimates for most of our other bird species were not available. We generated ten times as many pseudo-absences as we had

presence records for each species (Barbet-Massin et al., 2012).

To evaluate model performance, we used 10-fold cross-validation on the two pseudo-absence replicates, for a total of 20 replicates for each species (Elith et al., 2011). During model calibration, we gave equal weighting to presence data and pseudo-absence data. We used AUC values to test model performance, and considered values above 0.7 to be indicative of useful models (Elith et al., 2006; Swets, 1988). GLMs were fitted within the BIOMOD2 package (Thuiller et al., 2009).

The importance of the variables included in each species' model was derived from default setting of BIOMOD2 package. Each variable's importance was calculated in BIOMOD2 by computing one minus the Pearson correlation coefficient between a model prediction with all variables and model prediction in which the considered variable was randomly permuted. Therefore, one minus the correlation coefficient represents the probability that the variable contributes to the model. The higher the probability, the more that variable contributed in predicting the distribution (Thuiller et al., 2009). We then computed the explained variance for each texture measure as a percentage.

### 2.3.1. Species distribution model comparison

To determine if including texture measures improved species distribution models of tropical forest birds in Thailand, we compared the average AUC values for all birds in a given guild between models constructed with composition, texture, and fragmentation variables separately, between composition versus texture + composition, and between fragmentation + composition versus texture + fragmentation + composition. We used Wilcoxon signed rank tests for related samples to test for significant difference among models. Additionally, we checked if the texture + composition + fragmentation models for all bird species consistently included texture measures (Araújo and Luoto, 2007; Bate-man et al., 2012). All statistical analyses were conducted in R program (RCoreTeam, 2021).

## 3. Results

### 3.1. Texture measures versus habitat composition and fragmentation as predictors of species distributions

Texture measures alone predicted the distributions of our 86 tropical forest bird species well with an average AUC value of  $0.801 \pm 0.063$  (Table 1). However, the predictive accuracies of models varied considerably among species, body size classes, and nesting guilds. Of all species modelled, Brown Hornbill (the combined records of Tickell's Brown Hornbill (*Anorrhinus tickelli*) and Austen's Brown Hornbill (*A. austeni*) (Kemp and Boesman, 2020)) had the highest AUC values, at 0.937 (Table A1). When we compared each variable category separately, we found that the composition models ( $0.890 \pm 0.055$ ) outperformed fragmentation models ( $0.844 \pm 0.040$ ) ( $p < 0.05$ ), and texture models ( $0.801 \pm 0.063$ ) ( $p < 0.05$ ). However, we found again considerable variation in AUC values among species, and AUC values of the composition models were not the highest for all species. For example, texture measures predicted Grey Peacock-pheasant (*Polyplectron bicalcaratum*), Yellow-vented Flowerpecker (*Dicaeum chrysorrheum*), Greater Necklaced Laughingthrush (*Pterorhinus pectoralis*), Lesser Necklaced Laughingthrush (*Garrulax monileger*), and Buff-vented Bulbul (*Iole charlottae*) distributions better than measures of composition or fragmentation alone (Table A1).

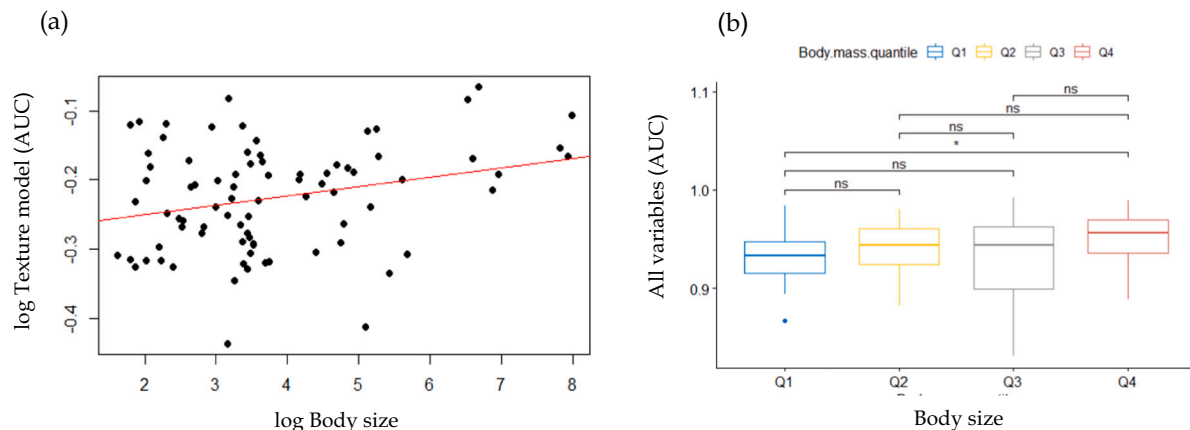
The AUC values of our models based on texture measures were significantly better for birds with larger body size ( $p < 0.05$ ) (Fig. 2). While texture measures alone predicted distributions of birds in all four body size quartiles well, they best predicted birds with large body size (AUC score  $0.823 \pm 0.068$ ) (Table 2). The composition-only models had significantly better AUC values than texture-only models and fragmentation-only models ( $p < 0.05$ ) in all body size quartiles and when summarizing across all species (Figs. 3 and 4).

Among nesting guilds, texture measures predicted each nesting guild

**Table 1**

AUC scores (average and standard deviation) for species distribution models including texture, composition, and fragmentation, separately and in combination. Results are shown for all 86 species together, and grouped by bird nesting guilds.

Nesting guild	Texture	Composition	Fragmentation	Texture + Composition	Fragmentation + Composition	All 3 variable categories
All species (86 species)	0.801 ± 0.063	0.890 ± 0.055	0.844 ± 0.040	0.928 ± 0.038	0.905 ± 0.047	0.938 ± 0.034
Canopy (11 species)	0.806 ± 0.086	0.900 ± 0.039	0.846 ± 0.043	0.934 ± 0.042	0.912 ± 0.040	0.939 ± 0.040
Cavity (17 species)	0.817 ± 0.071	0.894 ± 0.054	0.853 ± 0.036	0.927 ± 0.035	0.911 ± 0.044	0.939 ± 0.027
Understory (45 species)	0.788 ± 0.052	0.884 ± 0.055	0.834 ± 0.036	0.923 ± 0.041	0.895 ± 0.052	0.934 ± 0.036
Ground (13 species)	0.820 ± 0.057	0.895 ± 0.069	0.862 ± 0.044	0.938 ± 0.027	0.926 ± 0.034	0.950 ± 0.025



**Fig. 2.** Relationship between texture measures and bird body size: (a) relationship between AUC values for texture only-models and average body size for all individual birds, (b) comparison AUC values among different bird body size groups.

**Table 2**

AUC scores (average and standard deviation) for species distribution models including texture, composition, and fragmentation, separately and in combination. Results are shown for all 86 bird species grouped by quartile of body mass; number is average body mass (grams) within the quartile.

Body size	Texture	Composition	Fragmentation	Texture + Composition	Fragmentation + Composition	All 3 variable categories
Q1 (703.190 g)	0.823 ± 0.068	0.874 ± 0.067	0.846 ± 0.049	0.924 ± 0.030	0.896 ± 0.046	0.933 ± 0.027
Q2 (51.98 g)	0.793 ± 0.045	0.897 ± 0.048	0.854 ± 0.033	0.930 ± 0.034	0.918 ± 0.040	0.940 ± 0.027
Q3 (24.57 g)	0.789 ± 0.066	0.885 ± 0.057	0.832 ± 0.038	0.919 ± 0.048	0.893 ± 0.059	0.931 ± 0.045
Q4 (9.11 g)	0.795 ± 0.060	0.900 ± 0.046	0.840 ± 0.032	0.938 ± 0.035	0.913 ± 0.041	0.949 ± 0.029

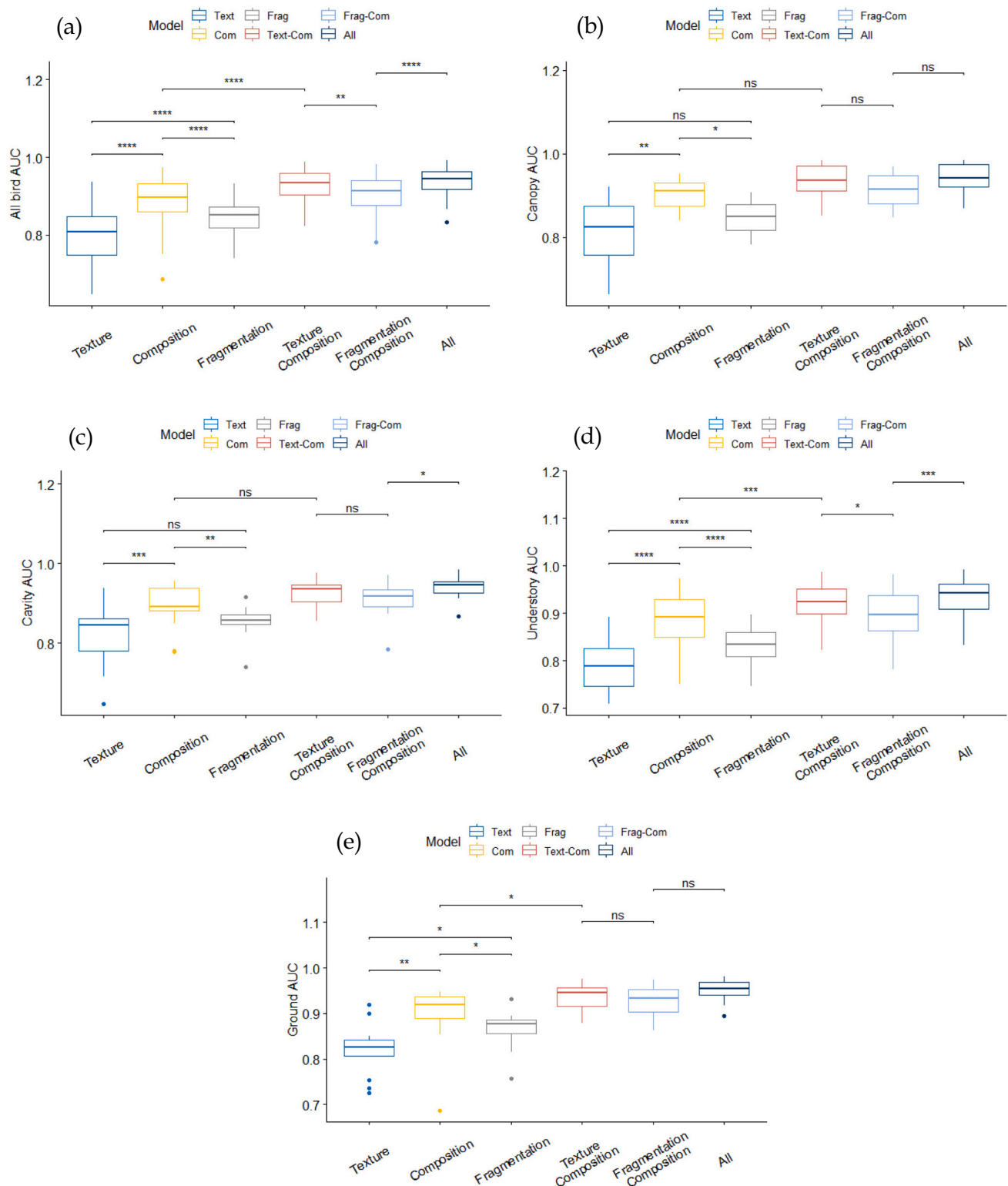
well with no significant difference among guilds ( $p > 0.05$ ). However, models composed of fragmentation variables alone performed differently among nesting guilds. We found that birds that nest in tree cavities ( $0.853 \pm 0.036$ ) and on the ground ( $0.862 \pm 0.044$ ) had significantly higher AUC values than birds that nest in understory ( $0.834 \pm 0.036$ ) ( $p < 0.05$ ). Again, composition models showed better predictive performance than fragmentation-only models and texture-only models in all nesting guilds. Whereas fragmentation models performed significantly better than texture models for ground nesting birds and understory birds, there was no significant difference for canopy and cavity birds. In addition, texture + composition models significantly outperformed fragmentation + composition models for understory birds ( $p < 0.05$ ) but not for canopy, cavity, and ground nesting birds (Fig. 3).

### 3.2. Texture measures complement other habitat variables in species distribution models

In models for all bird species, texture variables complemented the

other habitat variables well, and models that combined the three types of variables had the best performance. The incorporation of texture measures with habitat composition and fragmentation measures significantly improved species distribution models for the 86 bird species, on average  $0.938 \pm 0.034$  SD (Table 1). In addition, the models including all measures for all bird species consistently included texture measures, especially contrast and homogeneity (Fig. 6). Likewise, including texture measures significantly improved model performance compared with habitat composition-only models from an average of  $0.890 \pm 0.055$  SD to  $0.928 \pm 0.038$  SD for all species ( $p < 0.001$ ) (Table 1 and Fig. 3). Interestingly, the models that combined texture with composition ( $0.928 \pm 0.038$ ) were significantly better than those that combined fragmentation with composition ( $0.905 \pm 0.047$ ) ( $p < 0.05$ ).

Among different body size quartiles, adding texture measures to composition-only models and to fragmentation + composition models significantly improved model performance for birds with large body size ( $0.924 \pm 0.030$  versus  $0.896 \pm 0.046$ ), and for birds with small body size ( $0.938 \pm 0.035$  versus  $0.913 \pm 0.041$ ) ( $p < 0.05$ ). However,

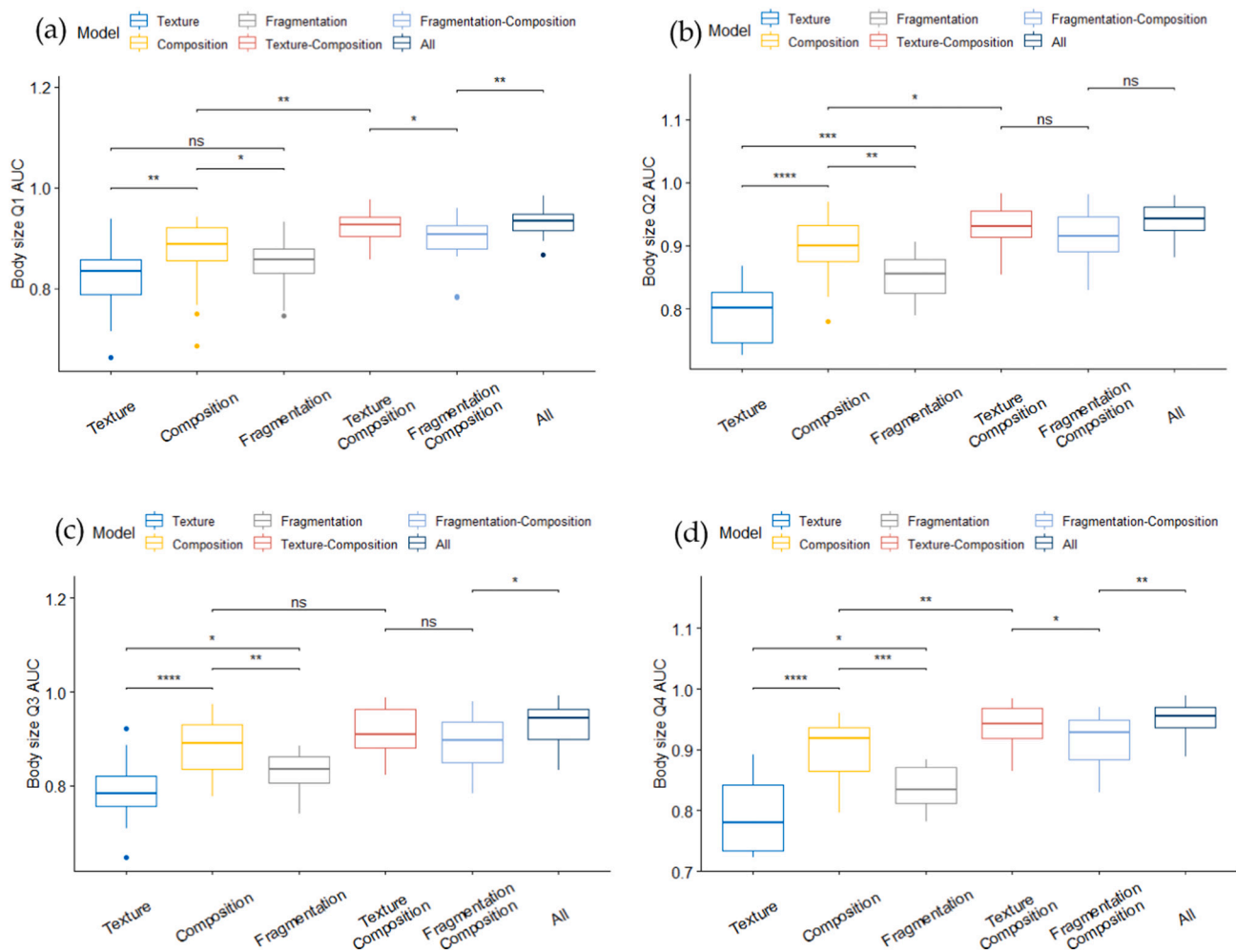


**Fig. 3.** Species distribution model comparisons for (a) all birds, (b) birds nested in tree canopy, (c) tree cavity, (d) understory, and (e) ground.

medium size birds showed no significant difference. For models including all variables, birds with small body size ( $0.949 \pm 0.029$ ) had significantly better AUC values than birds with large body size ( $0.933 \pm 0.027$ ) ( $p < 0.05$ ) (Fig. 4).

Among nesting guilds, adding texture measures to composition-only models significantly improved model performance for ground ( $p < 0.05$ )

and understory nesters ( $p < 0.001$ ). Furthermore, models included all variables significantly improved model performance for cavity ( $p < 0.05$ ) and understory nesters ( $p < 0.001$ ) (Fig. 3). We found that there was no model improvement when incorporating texture measures for canopy nesters, and there were no significant differences between texture-only models and fragmentation-only models, or between texture



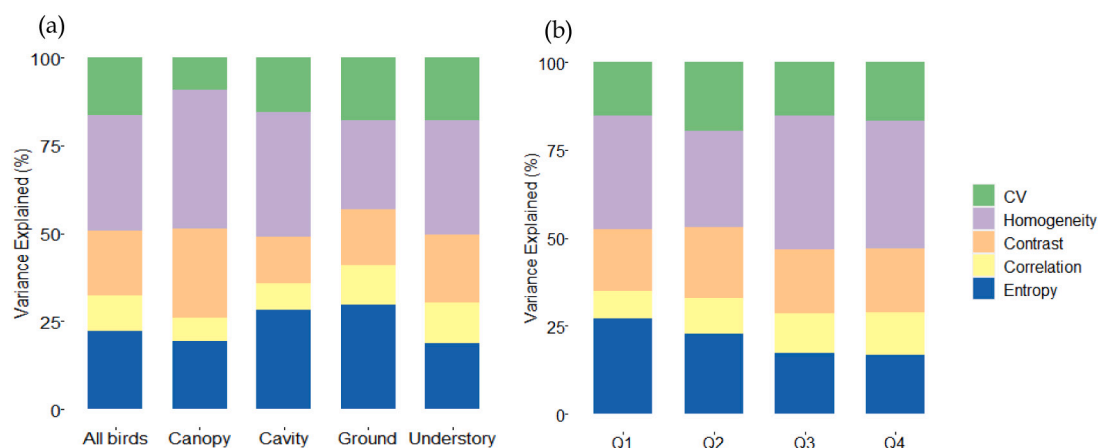
**Fig. 4.** Species distribution model comparisons for different bird body size groups: (a) large body size birds (Q1), (b) medium body size birds (Q2), (c) medium body size birds (Q3), and (d) small body size birds (Q4).

+ composition models versus fragmentation + composition models.

### 3.3. Variable importance of different texture measures

Second-order homogeneity was the best predictor of overall bird species distributions when using texture measure alone (Fig. 5). Among

nesting guilds canopy, cavity, and understory nesters were most strongly associated with second-order homogeneity, while ground nesters were most strongly associated with second-order entropy. Among different body size groups, larger birds were strongly associated with second-order homogeneity and entropy whereas smaller birds were highly associated with second-order homogeneity and contrast. Contrast was



**Fig. 5.** Variable importance of five texture measures contributed to bird distribution model. Variable importance is calculated as a percentage for (a) all birds and birds nested in tree canopy, tree cavity, understory, and on the ground, (b) for different bird body size groups.

the best complementary measure in models that included all variables (Fig. 6). The nature of the relationships between texture measures and species distributions varied, being positive, negative, or nonlinear for different species and guilds. Almost all texture measures had nonlinear relationships in the most parsimonious model for each species (lowest AIC) (results not shown). For example, for the Brown Hornbill, which had the highest model accuracy, we found that the probability of occurrence increased as homogeneity and correlation values increased but not linearly, while the probability of occurrence decreased as coefficient of variation and contrast increased. The probability of occurrence was highest at medium entropy values. These results indicate that the probability of occurrence of Brown Hornbill was highest in the most homogeneous forest cover (Fig. 7).

#### 4. Discussion

Our goal was to evaluate the utility of image texture derived from satellite data as proxies for habitat heterogeneity, and to incorporate texture measures with habitat composition and habitat fragmentation measures in avian habitat models in tropical forest, Thailand. We found that image texture measures derived from cumulative primary productivity of 1-km MODIS fPAR effectively predicted the distributions of tropical forest birds across Thailand. Texture measures performed well in bird species distribution models for a range of body sizes and nesting guilds, and large-bodied species were predicted especially well. Additionally, we found that the incorporation of image texture, habitat composition, and habitat fragmentation improved the predictions of models significantly for all birds, and for different body sizes and nesting guilds.

Our results are in line with previous findings that image texture measures contribute to predicting bird distributions (Bellis et al., 2008; St-Louis et al., 2014). We advanced understanding of the contribution of image texture to predicting species distributions through our findings that image texture derived from 1-km MODIS data (versus finer resolution data) provides considerable predictive power, and that this is true for tropical forest bird species, a group that was previously not explored.

Texture measures predicted the distributions for forest bird species with large body size best. This may be because large birds, such as hornbill, woodpecker, and pheasant species perceive and utilize forest structure at broader scales than smaller species, and thus are more affected by forest heterogeneity as captured by 1-km resolution MODIS data. We also compared the predictive power of texture measures for different nesting guilds, and found that texture measures predicted birds in all nesting guilds equally well, including ground, understory, tree cavity, and canopy nesters. While modeling bird distribution patterns

has been effective in habitats with low vertical structure, such as grassland (Bellis et al., 2008), and for habitat generalists in temperate forests (Hepinstall and Sader, 1997), our results highlight that image texture derived from MODIS fPAR can capture habitat heterogeneity and successfully predict species distribution patterns even in tropical forests with their highly complex vertical and horizontal structure.

When comparing model accuracy of the texture-based models with those based on habitat composition and fragmentation, composition measures outperformed fragmentation and texture measures across different nesting guilds and body size groups, as we expected. This supports the theory that structural heterogeneity of vegetation structure is more important in explaining species diversity at small-scales (Bellis et al., 2008; St-Louis et al., 2010; St-Louis et al., 2014), but spatial patterns of landscape elements are more important at broad-scales (Culbert et al., 2012; Hutto, 1985; Wood et al., 2016). However, we did find exceptions to this theory, in that birds nesting in tree canopy, tree cavities, and large bodied birds showed no significant difference in model accuracy when modeling with texture-only variables or fragmentation-only variables. We speculate that this may be because of large body size birds, and birds that nest in tree canopies or tree cavities may perceive within-forest areas of low structural complexity similarly to their perception for fragmented forest.

Texture measures complemented habitat composition measures significantly, and the combination of texture and composition outperformed the combination of composition and fragmentation measures in predictions of all birds, understory birds, and birds of both large and small body size. This indicates that texture measures successfully captured detailed habitat heterogeneity, 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. The combination of texture with habitat composition and fragmentation measures yielded the highest model accuracies. Interestingly, the best models included a relatively even mix of texture, fragmentation, and habitat composition suggesting that each measure is important and is complementary to the other measures, in that it contributes to different factors that shape species distributions, and each species may respond to those factors differently.

Among the texture measures, second-order homogeneity was most important in predicting tropical forest bird distributions and 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. This may be related to the fact that

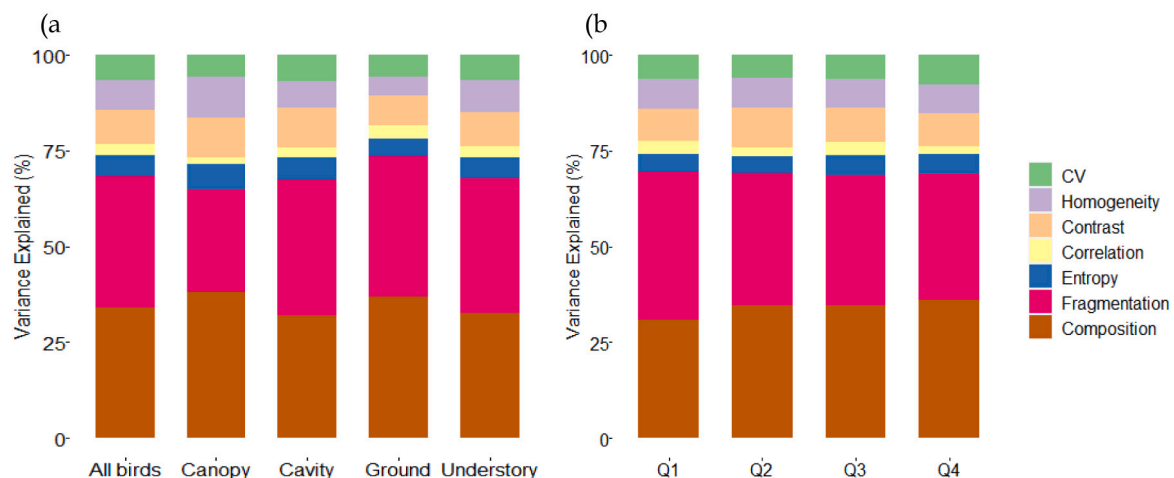
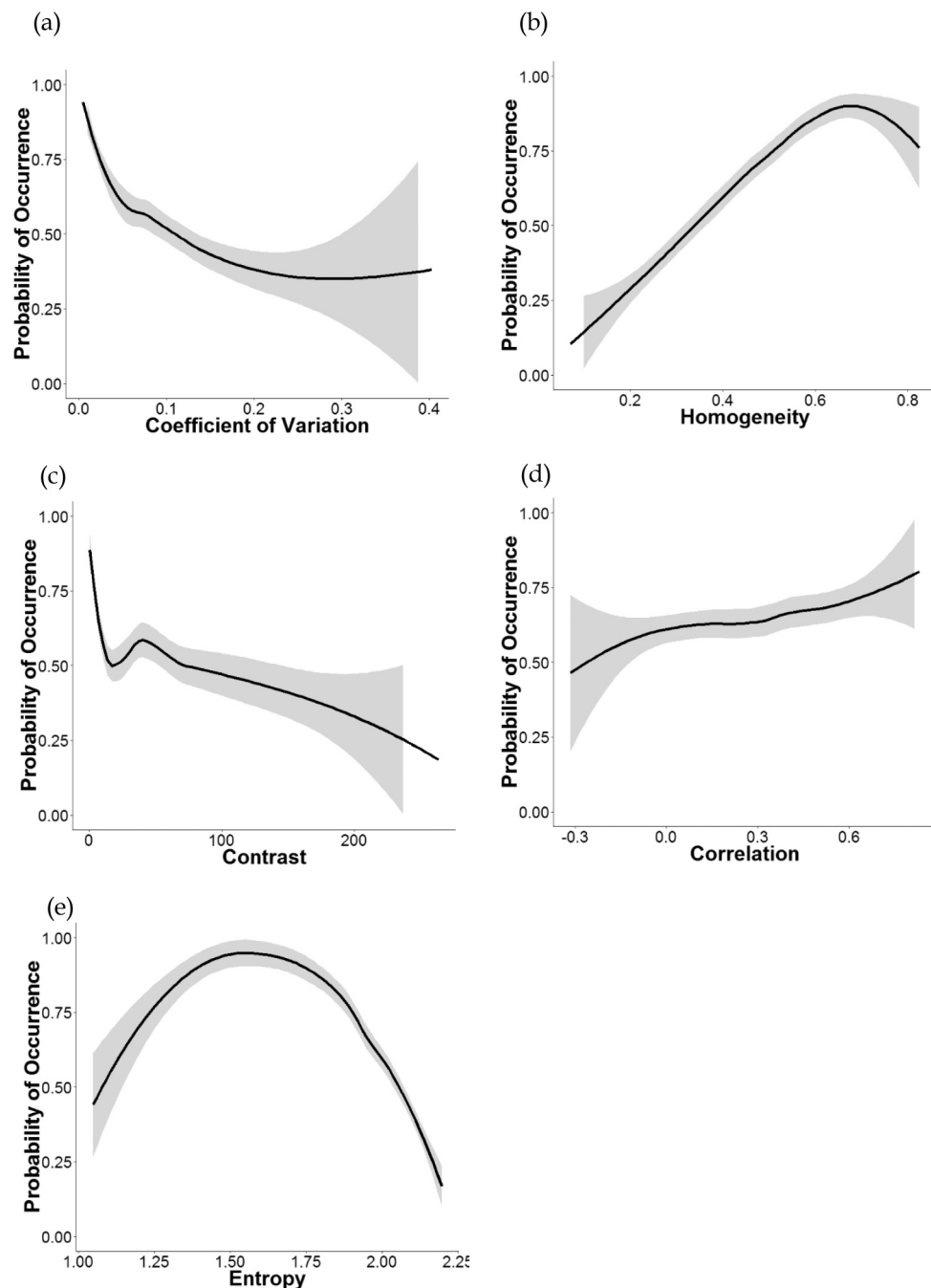


Fig. 6. Variable importance of all three categories of texture, habitat composition and fragmentation contributed to bird distribution models. Variable importance is calculated as a percentage for (a) all birds and birds nested in tree canopy, tree cavity, understory, and on the ground, (b) for different bird body size groups.





**Fig. 7.** Response curves depict the relationship between the probability of occurrences of Brown Hornbill and texture measures: (a) coefficient of variation, (b) contrast, (c) correlation, (d) entropy, and (d) homogeneity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

among different forest types, evergreen forests are generally more texturally homogenous than deciduous forests and secondary-growth forests (Fig. A3). Most of our study species inhabit evergreen forests, which may be why homogeneity of habitat was more important than other texture measures. In contrast, we found that second-order entropy was the most important factor in predicting ground nesting species, such as pheasants and partridges. Birds nesting on the ground utilizes a variety of forest habitat structure from evergreens to scrub and have a mixed diet of invertebrate, grains, buds, seeds, and fallen fruits. Ground nesters may therefore respond positively to higher heterogeneity (Tuanmu and Jetz, 2015; Wallis et al., 2016; Wood et al., 2016).

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 (Bar-Massada and Wood, 2014; Culbert et al., 2012). To improve ecological interpretability, we developed texture measures based on fPAR rather than individual spectral bands of satellite imagery (Estes et al., 2010; Tuttle et al., 2006). Texture measures from MODIS fPAR can be conceptualized as a measure of spatial variability and spatial arrangement of vegetation productivity (i.e., the available energy within a landscape). This makes texture measures based on fPAR more ecologically meaningful and thus more applicable for biodiversity modeling at broad-scales (Coops et al., 2009; Hobi et al., 2017; Radeloff et al., 2019). For example, we found that second-order homogeneity, which reflects uniformity of green biomass, was the most important texture measure in models of the distribution of large

bodied birds, especially those that utilize large tree canopies and cavities, such as hornbills. We suggest that these species require highly productive habitat and may perceive areas of homogeneous primary productivity within a large area as suitable habitat for foraging and nesting. However, the ecological meaning of texture based on 1-km MODIS fPAR differs from texture measures derived from higher resolution remote sensing images, such as 30-m Landsat data, and the two capture different aspects of vertical and horizontal complexity of vegetation structure (Wood et al., 2012). For example, 1-km texture measures can capture habitat heterogeneity aspects that are more meaningful for larger birds with large home ranges, while 30-m Landsat can capture a variety of microhabitats that are more important for smaller birds or birds that can persist in disturbed habitat or birds that require complex habitat for nesting, foraging, or predator avoidance. MODIS 1-km spatial resolution may have been one reason for the somewhat lower predictive power for some smaller body size species utilizing understory habitat. However, the lower temporal frequency of Landsat images can make it challenging to acquire cloud free imagery that characterizes the same phenological stages over broad spatial scales as MODIS does (Culbert et al., 2009; Wallis et al., 2016), and MODIS data is also more user-friendly because derived products, such as fPAR, are available across the globe.

#### 4.1. Study limitations

Limited availability of occurrence data for some bird species, particularly endangered and threatened species, make our texture measure analysis of the distributions of these species less reliable. Additionally, there were four bird species for which body mass and length estimates were unavailable, which is why we had to exclude them from our analyses of body size versus texture measures. More generally, we could only analyze occurrence points, and lacked true absence data, which would have strengthened our analysis of texture measures in species distribution models. However, our finding demonstrated that texture measures had high predictive performance with presence-only data, suggesting texture can be useful in characterizing habitat structure in species distribution models. Furthermore, while it was beyond the goals of our study, incorporating texture measures with other habitat variables, such as climate and disturbances, to predict bird distributions could improve prediction accuracy for conservation planning purposes.

#### 4.2. Conservation implications

Our results showed that texture explained tropical bird distributions well, particularly for species with large body size, and canopy and cavity nesting species. This suggests that species distribution models would benefit from inclusion of texture measures as proxies for habitat heterogeneity, because habitat heterogeneity is difficult to assess directly, but has a large influence for the distribution of many bird species.

Texture measures from MODIS can overcome the limited availability of medium-resolution (i.e. 30 m) remotely sensed data in tropical regions. While Landsat data offers the advantage of 30-m resolution, frequent cloud cover limits its availability in many tropical regions. Moreover, MODIS texture measures derived from proxies of primary productivity measure not only represent horizontal and vertical complexity of tropical forests but also reflect the amount of energy available for species.

Texture can be incorporated into species distribution models with other variables such as disturbance, land use change, and climate to predict potential suitable habitat and improve distribution maps in order to more accurately identify priority areas for conservation and potentially expand protected areas, improve connectivity, and monitor forest quality. Furthermore, texture measures could be used as indicators to assess deforestation effects on birds in tropical regions. For example, pristine evergreen forests are highlighted in texture analyses due to their high homogeneity, whereas deforested areas have values in

contrast or entropy metrics. Using this technique, species distributions and conservation status can be rapidly updated when new occurrence data or new satellite data become available.

In summary, we found that texture measures derived from coarse-resolution MODIS data are valuable when predicting tropical forest bird species distribution patterns across large areas. Texture measures derived from MODIS fPAR captured habitat heterogeneity for several taxonomic groups, and across a variety of forest habitats, ranging from secondary-growth forests to moist evergreen forests. The combination of texture measures and with composition and fragmentation metrics improved model performance highlighting the texture provided complementary information. The successful application of texture-based MODIS fPAR indicate its broader applicability for biodiversity assessments as a promising tool for assessing and predicting biodiversity patterns in response to environmental change.

#### CRedit authorship contribution statement

**Napat Suttidate:** Conceptualization, Investigation, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Anna M. Pidgeon:** Conceptualization, Writing – review & editing, Funding acquisition. **Martina L. Hobi:** Data curation, Software, Validation, Writing – review & editing. **Philip D. Round:** Resources, Validation, Writing – review & editing. **Maxim Dubinin:** Data curation, Software, Validation, Writing – review & editing. **Volker C. Radeloff:** Conceptualization, Supervision, Resources, Writing – review & editing, Funding acquisition.

#### Declaration of competing interest

All authors declare that they have no conflicts of interest.

#### Data availability

Data will be made available on request.

#### Acknowledgements

We gratefully acknowledge support by the NASA “Science of Terra and Aqua” program, the NASA program “Biodiversity and Ecological Forecasting” program, and NSF’s “Dimensions of Biodiversity” program. We thank K.E. Jenks for providing the Thailand land cover map. We thank M. Ozdogan, B. Zuckerberg, and I. Baird for insightful comments on earlier drafts of this manuscript.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2023.110002>.

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