Measuring the effects of road proximity on the distribution of commercially valuable bird species in an Indonesian protected area

# Abstract

Deforestation is the most critical threat to biodiversity in Indonesia. However, roads that accompany and facilitate deforestation also increase access to interior forest. Hunters use this increased access to supply Indonesia’s thriving wildlife trade with live and dead animals, which may further reduce the habitat available to especially persecuted species. We used occupancy modeling to quantify the effect of proximity to roads on the distribution of songbird communities in primary tropical forest within Cagar Alam Gunung Niyut, a protected area in West Kalimantan, Indonesia, on the island of Borneo. We found that commercially valuable species were more likely to be detected further from roads than other species in the community (*µ* = 5.34, BCI 0.23 – 12.00) but were not more sensitive to deforestation than other species (*µ* = 3.06, BCI -1.64 – 10.03). These findings suggest that relatively low occupancy near roads by commercially valuable species is likely driven by trapping pressure and not edge effects. Trapping pressure measurably decreased habitability of otherwise suitable forest near roads for commercially valuable species, even though the study was conducted inside a Cagar Alam (Nature Preserve), which is the highest level of protection designated by the Indonesian national government. Community-based conservation that engages local communities in designing and implementing conservation strategies could provide an alternative to increased enforcement.

# Introduction

Indonesia’s tropical forests are global biodiversity hotspots (Myers et al. 2000, Brooks et al. 2002). Across the archipelago, agricultural expansion, logging, mining and fires drive ongoing deforestation (Achard 2002, Sodhi et al. 2004, Hansen et al. 2013, Margono et al. 2014, Abood et al. 2015), making land use change the leading cause of species endangerment and extinction (Nijman 2010, Nijman et al. 2012, Newbold et al. 2015, Symes et al. 2018). Roads facilitate land use change by increasing access to nearby forest (Laporte et al. 2007). In addition, they provide access points to previously inaccessible interior forest for hunting and trapping and transportation networks for distribution (Suárez et al. 2009, Harris et al. 2017, Symes et al. 2018). Commercial hunting and trapping feed the international wildlife trade in which Indonesia supplies Europe and East Asia with wildlife for pets, consumption, and medical applications (Collar and Juniper 1992, Bennett et al. 2002, Alves et al. 2010, Alves and Alves 2011, Drury 2011, Fernandes-Ferreira et al. 2012, Nóbrega Alves et al. 2013, Bush et al. 2014, McNamara et al. 2016). For example, research has documented the export of Javan and Sunda slow loris (*Nycticebus javanicus* and *N. coucang*) to Europe and Sunda pangolin (*Manis javanica*) and helmeted hornbill (*Rhinoplax vigil*) to East Asia, primarily China. Commercially valuable species are thus doubly threatened by habitat loss and hunting or trapping, both of which increase with proximity to roads (Laporte et al. 2007, Suárez et al. 2009, Harris et al. 2017, Symes et al. 2018).

The same access points and transportation networks that supply the international wildlife trade also supply a lesser known but thriving domestic bird trade (Nijman 2010, Harris et al. 2017) encompassing thousands of species and millions of individuals (Jepson and Ladle 2005, Chng et al. 2015, 2016, 2018, Chng and Eaton 2016, Rentschlar et al. 2018). The caged bird trade and Indonesia’s rapid rate of deforestation have driven avian species declines, extirpations, and extinctions (e.g. Javan pied starling (*Gracupica jalla*), Bali starling (*Leucopsar rothschildi*), straw-headed bulbul (*Pycnonotus zeylanicus*); Collar and Juniper 1992, Collar et al. 1994, Wright et al. 2001, Jepson and Ladle 2005, Harris et al. 2017, Bergin et al. 2017). Most of these declines have been documented on Java, which has the most dense human population of any island in the world, retains a small fraction of its historical forest, and is the cultural and demand center of the bird trade (Burivalova et al. 2017).

Conservationists suspect that commercially valuable bird species in Kalimantan (Indonesian Borneo) are also declining (Lee et al. 2016) because recent and accelerating land use change (Miettinen et al. 2011, 2012) may have increased access to forested areas for trapping. However, Borneo’s remoteness and image as a bastion of pristine forest have shielded its bird trade from investigation prior to 2018, when Rentschlar *et al.* found that it is widespread and lucrative (Rentschlar et al. 2018). Contrary to its pristine reputation, Kalimantan lost an estimated 15.4% of its forested land area between 2000-2010 alone (Miettinen et al. 2011, 2012) to massive commercial expansion of oil palm plantations and logging combined with associated forest fires (Curran 2004). Sumatra has experienced similar changes to Kalimantan over a similar period, and Sumatran forest bird species that are sold for more money have declined more steeply, implicating the trade in their decline. Furthermore, commercially valuable birds are absent from Sumatran forest less than 5 km from a road (Harris et al. 2017). This information along with suspected declines of Bornean forest species (Harris et al. 2015) suggests that commercially valuable birds in Kalimantan are likely disappearing even from intact and protected forests.

If these declines are occurring, and especially if they are occurring in protected areas species under extreme demand in the Indonesian bird trade such as grey-cheeked bulbul (*Alophoixus tephrogenys*) and white-rumped shama (*Copsychus malabaricus*) may quickly and quietly vanish in the manner of straw-headed bulbul (Lee et al. 2016, Bergin et al. 2017, Chiok et al. 2019). While forest birds are trapped and sold in Kalimantan (Rentschlar et al. 2018), no study has yet documented the effects of trapping on wild bird communities in Kalimantan. If trapping pressure on commercially valuable species is intense enough to exclude them from occupying near-road habitat in this remote location in Kalimantan, no corner of the archipelago is immune to trapping pressure. Because proximity to roads increases access to intact forest and thereby increases trapping pressure in nearby forest (Harris et al. 2017), we quantified effects of trapping by comparing habitat use of commercially valuable species to that of non-valuable species over a gradient of distance to roads. We hypothesized that commercially valuable birds would be less likely to be found near roads than non-valuable birds in Gunung Niyut Nature Reserve in West Kalimantan, Indonesia. We used a hierarchical community occupancy model to account for variation in detection and habitat effects.

# Methods

## Study area

Cagar Alam Gunung Niyut is an isolated preserve in the northwest corner of West Kalimantan, Indonesia. Its 124,500 hectares protect an island of primary mixed dipterocarp wet forest surrounded by agricultural land. Average annual rainfall is about 2 m; the elevation of the study area is 150-400 masl. Of particular interest are its ~2000 hectares of intact lowland forest in Kabupaten Landak to the southeast. Little remains of West Kalimantan’s lowland primary forest, and this section has the potential to support threatened primary forest species, and in particular, songbird species valuable in the wild bird trade. We accessed this section through the border village Tauk (Fig. 1).

## Point counts

We defined 14 transects, spread in an approximately radial pattern around two base camps, which were approximately 5 km apart. On average, each transect contained 8 survey locations, set 300 m apart, for a total of 115 points. We visited each survey location and conducted a point count once a month from October 2017 to February 2018, for a total of five point counts per survey location, except for 12 survey locations where one point count was missed for weather or logistical reasons. Our survey team was split into two teams of three people, consisting of two trained observers and one local guide. Each team conducted point counts for half of the transects each month. At each survey location, we recorded the time, date, weather, and observer, then sat silently for 5 minutes before beginning to record detections. Then, each trained observer independently recorded detections of birds up to 100 m away. All individuals were recorded along with the detection method (visual or auditory) including individuals that could not be identified. For each unknown individual, time relative to the start of the point count was recorded. After data collection in the field, the primary recordist for each point count listened to the recording a second time to verify species identification and to identify calls that could not be identified in the field.

## Development of habitat covariates

In May 2018, a team of three observers visually estimated percent water cover, rounded to the nearest 10%, at each of the 115 point count locations. In addition, we utilized remotely sensed data and GIS to characterize forest structure and condition, topography, and measures of anthropogenic disturbance hypothesized to influence avian occupancy dynamics (Table 1). Landsat 8 Surface Reflectance NDVI images were composited and cloud masked in Google Earth Engine for the study period (October 2017- February 2018) to produce mean NDVI values across the study area (Vermote et al. 2016, Gorelick et al. 2017). We calculated forest canopy disturbance metrics utilizing LandTrendr implemented in Google Earth Engine (Kennedy et al. 2018). LandTrendr is an algorithm that uses time series analysis of Landsat imagery to fit pixel-wise change trajectories of vegetation indices to identify and map forest canopy disturbance events (Lorenz et al. 2015, Cohen et al. 2018, Kennedy et al. 2018). We considered disturbances that occurred within the last ten years to be recent for primary tropical forest in Asia and so we calculated LandTrendr disturbance metrics for 2007-2017 (Canterbury et al. 2000, Cole et al. 2014). We calculated the average value of NDVI, forest height, proportion of disturbed canopy, and proportion of intact forest across buffers with radii of 500 m from each point count location (Glisson et al. 2017).

We extracted road data from OpenStreetMap and calculated Euclidean distance to roads and other anthropogenic features in the study area including agricultural clearings, illegal logging areas, and structures located during surveys (OpenStreetMap contributors, 2018).

All spatial covariate data were processed and extracted for point count locations using ArcMap v10.6 (*ArcGIS* 2004). We assessed collinearity of habitat covariates by calculating a Variance Inflation Factor for each covariate and using a threshold of 5 to determine if variables were collinear (Sarkar 2008). We included: estimated percent water coverage within 100 m, mean canopy height within 500 m, and percent intact forest within 500 m. All continuous covariates were scaled to 0-1 as recommended by (MacKenzie and Hines 2018).

## Occupancy model

We used a multispecies single-season occupancy model to estimate the effects of habitat covariates, disturbed canopy, distance from roads, and a binary indicator of whether a species was commercially valuable on the occupancy probability of 115 sites for a community of 206 bird species. We accounted for imperfect detection using a nested detection process (Kery and Schaub 2011). We considered a species commercially valuable if it was identified as vulnerable to the pet trade by the 2015 Asian Songbird Trade Crisis Summit (Lee et al. 2016). Four of the six species we considered commercially valuable based on these criteria were also identified as both the most expensive and the most frequently sold in the Kalimantan pet market (Rentschlar et al. 2018).

We assumed that the true state of occupancy (*zi,j*) for species *i* and site *j* was a Bernoulli random variable with probability of occupancy (*ψi,j*) such that

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We assumed that the detection or non-detection (*yi,j,k*) for each species *i* at each point count location *j* and occasion *k* was a Bernoulli random variable with detection probability (*pi,j,k*) conditional on the true state of occupancy (*zi,j*)such that

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We modeled detection (*pi,j,k*) as

We modeled occupancy probability (*ψi,j*) as

Parameters in the *α* family were simple fixed effects. Parameters in the *β* family were estimated for each species, with species terms drawn from a normal distribution of mean and variance estimated from the data. Parameters in the *δ* family correspond to variance around a mean of 0 to incorporate additional variation for each species or site that could not be explained by other fixed or random effects.

While we detected 206 species in total, we excluded those species with fewer than 10 detections from our analysis (111 species). In addition, we excluded *Rhinoplax vigil, a highly-mobile species with a* far-reaching call that would likely have violated the assumption of independent detections. Furthermore, mobile species such as birds can travel among points, which would violate the assumption of independence of occurrence. To prevent this assumption from being violated, we set our points 300 m apart. To account for spatial autocorrelation, we estimated the random effect of transect (8-15 points that were spatially grouped; *δ*1). We fit the model to our point count data in a Bayesian framework using Markov Chain Monte Carlo simulation to obtain the posterior distribution for each parameter. Our models were implemented in JAGS (Plummer 2017) and run using the R package R2jags (Su and Yajima 2020). Non-informative priors were used throughout. Specifically, means and fixed effects were drawn from a normal(0, 100) distribution and sigma terms were drawn from a uniform(0, 10) distribution. We ran four chains for 50,000 iterations with a thinning interval of 20 to reduce autocorrelation and 20,000 iterations of burn-in, resulting in 1,500 samples of the posterior. We checked convergence by visually inspecting trace plots and with the Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992), ensuring that all values were less than 1.1. For full code, see supplemental information.

We report posterior means for all parameter estimates detailing how each species responded to each habitat covariates and interactions with commercial value (i.e., *β*1-7). Habitat covariates and interactions were considered to significantly affect species when the 95% Bayesian credible interval (BCI) for the mean (l) of the random effect distribution governing species’ responses did not overlap 0.

# Results

We detected a total of 206 species, 95 of which were detected at least ten times and therefore analyzed using the occupancy model. The five most frequently detected species were yellow-eared barbet (*Psilopogon australis*),golden-whiskered barbet (*Psilopogon chrysopogon*), red-throated barbet(*Psilopogon mystacophanos*),little spiderhunter(*Arachnothera longirostra*),spectacled bulbul(*Pycnonotus erythropthalmos*),and brown fulvetta (*Alcippe brunneicauda*). We detected nine species that are either sold at high prices as pets (Lee et al. 2016, Rentschlar et al. 2018) or sale of its casque (helmeted hornbill): grey-cheeked bulbul (10 detections), greater green leafbird (*Chloropsis sonnerati*; 11 detections), white-rumped shama (39 detections), Bornean banded pitta (*Hydrornis schwaneri*; 1 detection), Asian fairy-bluebird (*Irena puella*; 64 detections), blue-crowned hanging-parrot (*Loriculus galgulus*; 83 detections), crested jay (*Platylophus galericulatus*; 2 detections), helmeted hornbill(74 detections), and crested serpent-eagle (*Spilornis cheela*; 20 detections). We had insufficient detection data for crested jay and Bornean banded pitta to produce informative results using occupancy modeling, and so excluded these species from occupancy models.

## Detection probability

Detection varied between observers (*µ* = 0.92, BCI 0.80 – 1.06). Birds were more likely to be detected earlier in the day (*µ* = -0.72, BCI -0.90 – -0.53), and detection varied significantly among both sites and species, though much more among species (*σ* = 0.16 and 4.55, respectively; see Table 2). Species were more likely to occupy sites that were further from roads (*µ* = 2.35, BCI 0.75 – 4.22), and this effect was stronger for commercially valuable species compared to commercially non-valuable species (*µ* = 5.34, BCI 0.23 – 12.00; Table 1, Fig. 2). Occupancy of commercially valuable species increased faster over the distance to roads gradient than occupancy of commercially non-valuable species (Fig. 2). While all species were more likely to occupy sites with higher percent intact forest (*µ* = 1.59, BCI 0.53 – 2.76), commercially valuable species were not more likely to occupy sites with higher percentages of intact forest than commercially non-valuable species (*µ* = 3.06, BCI -1.64 – 10; Fig. 3).

# Discussion

To our knowledge, this is the first study demonstrating the community-level impact of distance to road as a proxy for forest access, which we argue indicates trapping intensity, on commercially valuable songbird species in Indonesian Borneo. Our results highlight the sensitivity of primary rainforest species to habitat disturbance, with the average species likely to occupy sites further from roads and with more intact forest. Encouragingly, our results do not suggest that commercially valuable birds in this protected area are especially sensitive to forest degradation. In addition, the average commercially valuable species occupies sites further from roads than commercially non-valuable species. This trend suggests that extreme trapping pressure near roads could be preventing commercially valuable species from inhabiting otherwise suitable forest. However, because we did not directly quantify trapping pressure, we cannot establish causation.

The IUCN Asian Songbird Trade Specialist Group identified five of the commercially valuable species detected in this study (greater green leafbird, white-rumped shama, grey-cheeked bulbul, Asian fairy-bluebird, and crested jay) as threatened by trade based on their ubiquitous presence at markets and severe population declines on Java and Sumatra (Lee et al. 2016). Our results may indicate a similar decline on Indonesian Borneo. While it is conceivable that only trapped species would learn to avoid humans, the presence of humans increases perceived predation risk for most birds (Bötsch et al. 2018). Therefore, if the primary cause of declines in occupancy near to roads was avoidance instead of the removal of individuals, the observed difference in occupancy near roads between commercially valuable and not valuable birds would be unlikely. If commercially valuable species are disappearing from primary forest in Borneo as suggested by our results, domestic demand for these species has motivated efforts to reach even very remote and rural areas. However, our study was conducted in one remnant forest, and therefore we are unable to demonstrate that our results are representative of wild bird populations across Indonesian Borneo. To gain a more complete understanding of the scale of exploitation, this study could be replicated in protected areas across Indonesia, especially in Indonesian Borneo and eastern Indonesia.

Data regarding wild populations of these birds, especially on the island of Borneo, is scarce. While greater green leafbird is classified as endangered and grey-cheeked bulbul is classified as vulnerable, white-rumped shama, Asian fairy-bluebird, crested jay, and blue-crowned hanging-parrot are classified as least concern (IUCN 2021). However, for these species, the IUCN also reports that the total number of mature individuals is unknown. This lack of data impedes our ability to eliminate the possibility that natural rareness caused these species’ low occupancy in our survey, but our personal experiences in the region have led us to suspect that it did not. During 2013-2014 Ivy Expeditions to Malaysian Borneo in which author XXX participated, both grey-cheeked bulbul and white-rumped shama (white-crowned) were detected regularly. Furthermore, two of Indonesia’s most persecuted species, straw-headed bulbul and Sunda laughingthrush (*Garrulax palliatus*), were common up until the 1990s (Chiok et al. 2019, Leupen et al. 2020).

Currently rare and valuable species may be subject to an anthropogenic Allee effect in which their increasing rareness increases their desirability which balances the increasing costs of finding and trapping ever more rare species (Courchamp et al. 2006). Indeed, supply of frequently traded species in Sumatran markets does not increase with price increases, suggesting that those species’ wild source populations are being depleted (Krishna et al. 2019). In addition, Harris et al. (2015) identified several Sumatran species whose supply was decreasing or holding steady as their market price increased, suggesting that trappers are currently engaged in trapping the few remaining individuals of these highly prized species. Long-term studies of Kalimantan markets may reveal this same signature of decline for the commercially valuable species we detected.

Data clarifying the status of songbirds in Kalimantan could help urge governments into action. Neither the regional West Kalimantan government nor the national Indonesian government has a plan to reduce trapping or promote in-situ conservation of its threatened songbirds. Globally, efforts to reduce poaching have primarily focused on increased enforcement, but this approach may instead disincentivize biodiversity conservation (Cooney et al. 2017). Community-based conservation (CBC) offers a complement to increased enforcement that engages rural residents living near wildlife in designing and implementing conservation actions. If CBC efforts invest in local governance (Berkes 2007), embrace a multi-dimensional view of human well-bring (Woodhouse et al. 2015), and are based on local context and values (Waylen et al. 2010), they are more likely to successfully reduce the negative impacts of overexploitation on wildlife and society.

Our study was not designed to measure the reach of trappers into the forest, but estimated occupancy of commercially valuable species did increase over the studied gradient of distance to roads (~2-10 km). In Sumatra, bird trappers stated that their usual maximum distance traveled from a road was about 5 km (Harris et al. 2017). If the reach of trappers in our study area was similar, we successfully studied a large portion of the trapping pressure gradient. A survey of trappers’ habits, whether conducted via interviews or field cameras, would clarify the details of their reach into the forest. In addition, understanding the role of social and economic factors in the cost-benefit analysis that governs how far trappers choose to search for birds would provide guidance for conservationists working to decrease take. Only 44% of Kalimantan primary forest is located more than 5 km from a road. However, if this hypothetical reach of trappers is reduced by 500m by changing the cost-benefit balance of searching farther into the forest, 3% additional forest would potentially be habitable for commercially valuable species (Gaveau 2017). On the other hand, road construction (e.g. planned roads; Alamgir et al. 2019) would allow trappers to penetrate deeper into the last refuges available for commercially valuable birds.

If Indonesia fails to protect the species of concern recommended by the Asian Songbird Crisis Summit (Lee et al. 2016) based upon the negative impacts of the trade on wild populations, these species are likely to quickly vanish from remaining forest across the archipelago. The Conservation Act No. 5 of 1990 prohibited the use, keeping, or destruction of protected animals and plants (UU Pemerintah Republik Indonesia No. 5 1990). In 1999 the list of protected animals and plants included a few songbirds such as Bali starling and rufous-fronted laughingthrush (*Garrulax rufifrons*; Peraturan Pemerintah Republik Indonesia No. 7 1999). Both songbirds have been traded to the very threshold of extinction: IUCN reports that fewer than 50 Bali starling remain, and fewer than 250 rufous-fronted laughingthrush remain (IUCN 2021). In 2018, the national government of Indonesia updated its protected species list to include 242 additional species, including those popular in the songbird trade such as white-rumped shama, greater green leafbird, and straw-headed bulbul (Peraturan Menteri Lingkungan Hidup dan Kehutanan 2018a). Indonesians whose cultural identities are strongly linked to keeping songbirds (a group that includes Indonesian President Joko Widodo) pressured the national government into removing of some of the most valuable and overexploited species from the list of protected species (e.g. straw-headed bulbul, which is classified by the IUCN as Critically Endangered; Peraturan Menteri Lingkungan Hidup dan Kehutanan 2018b). This unfortunate about-face highlights the massive domestic demand for them.

This demand in turn highlights that songbird species provide valuable cultural services. In Indonesia, the domestic bird trade developed from Javanese cultural practices of keeping birds in homes. Jepson (2010) and Marshall et al. (2020) describe how bird keepers practice intensive husbandry of kept birds, enter them in song contests, teach them new song variants, and pay enormous prices for the most prized individuals. Furthermore, many forest bird species, especially colorful, large, and charismatic ones, play roles in mythology, forest stewardship, and forest understanding for the Dayak and Ibon ethnic groups of Borneo (author KSL personal experience living with Dayak people). This anecdote echoes findings from Costa Rica, where forest birds have been found to provide more cultural services than their agriculture-associated counterparts (Echeverri et al. 2020). Lastly, ecotourism could potentially provide an alternative to extractive uses of forest and increase the well-being of local people under the right conditions (Chung et al. 2018), but the loss of charismatic and rare bird species reduces the value of forests for bird-watchers, an increasingly important group of ecotourists (Puhakka et al. 2011). If charismatic singers disappear from forests, the domestic caged bird industry will suffer, the cultural identity of Indonesians may be diminished, and the tourism value of forests will decline.

This study documents the effects of illegal trapping activity on wild populations of threatened songbirds. Despite residing within a Nature Preserve (*Cagar Alam*) whose regulations prohibit harvesting of any kind, valuable songbird populations are showing signs of trapping pressure in this isolated park. Our results also highlight that most species that we detected depend on primary forest for their survival, and therefore, ongoing deforestation of Gunung Niyut Nature Preserve will further decrease suitable habitat for all but a few birds in our study community. CAGN is an island of forest in an area that was mainly deforested in the 1980s and 1990s (Global Forest Watch 2018) and is one of West Kalimantan’s last large plots of intact forest. This remnant habitat is vital to the continued persistence of these primary forest species. Furthermore, we detected no individuals of straw-headed bulbul during this study, which indicates that past trapping pressure reached deep into the park. If indeed straw-headed bulbul was trapped out of CAGN in the past, currently valuable species could be trapped out in the future. However, the presence of threatened songbirds documented here underscores how vital it is to protect Gunung Niyut Nature Preserve. Road construction near or in primary forest will likely further reduce the viable habitat available for commercially valuable birds.

# Supporting Information

*Biases and possible weaknesses of this study*

Team 1 frequently observed some species that were not expected to be common and were very rarely observed by Team 2 (e.g. spectacled spiderhunter (*Arachnothera flavigaster*) observed 26 times by Team 1 and 1 time by Team 2, and expected to be “uncommon” based on Birds of the Indonesian Archipelago). In addition, Team 2 observed many common species many more times than Team 1 (e.g. blue-crowned hanging-parrot observed 0 times by Team 1 and 83 times by Team 2, and expected to be “fairly common” based on Birds of the Indonesian Archipelago). Team 2 was led by a team member with 2+ years of experience identifying Bornean bird calls, and Team 1 had only been provided a month-long training before the start of the project, so this bias is expected to relate to misidentification and detection that is biased towards loud and complex song types. Indeed, species underreported by Team 1 tended to have quieter, simpler, and/or higher-pitched calls, or were extremely common (e.g. flowerpeckers (*Prionochilus*), blue-crowned hanging-parrot, orange-bellied flowerpecker (*Dicaeum trigonostigma*), rufous-fronted babbler (*Cyanoderma rufifrons*), little spiderhunter, green iora (*Aegithina viridissima*)).

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# Tables

Table 1. Habitat covariates developed for occupancy models.

| Habitat  Covariate | Hypothesized  Effect | Data Product  Satellite and Sensor | Spatial Resolution | Data Sources |
| --- | --- | --- | --- | --- |
| Normalized Difference Vegetation Index (NDVI) |  | Landsat 8 Surface Reflectance OLI/TIRS | 30m | Vermote et al. 2016, Gorelick et al. 2017 |
| Elevation, slope,  and aspect |  | ASTER Global Digital Elevation Model V002 | 30m | NASA LP DAAC 2011 |
| Forest canopy height  ( canopy cover > 5m) |  | Forest Canopy Height Map; derived from Geoscience Laser Altimeter System (GLAS) LiDAR | 1000m | Simard et al. 2011 |
| Proportion of canopy recently disturbed (2007-2017) | Species specific response to disturbance levels | LandTrendr disturbance metrics: Landsat 7 TM & Landsat 8 OLI/TIRS TOA b | 30m | Kennedy et al. 2018 |
| Proportion of intact forest in 2016 |  | REG Borneo Forest Cover 2016; derived from Landsat 5,7, & 8 | 30m | Gaveau 2017 |
| Distance to roads |  | Open Street Map Kalimantan roads layer | 30m | OpenStreetMap contributors (2015) |

Table 2. Posterior distributions, Rhat, and effective sample size of model parameters. For occupancy parameters, only hyperparameters (mean and standard deviation of per-species random effects) are included here. A table of all parameters may be found in the Appendix.

Table

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# Figure legends

Figure 1. Study sites in Cagar Alam Gunung Niyut, Kabupaten Landak. Blue circles correspond to point count locations, pink triangles correspond to our base camps, and red circles correspond to illegal activity detected (hunting, logging, or clear-cutting for agriculture). The pink line delineates the border of Gunung Niyut Nature Preserve, red fill indicates forest loss 2011-2015 (Hansen et al. 2013), green indicates primary forest, and white indicates non-forest.

Figure 2. Most species are more likely to occupy areas further from roads, but this effect is significantly stronger for commercially valuable species. a) Each thin line traces the relationship between distance to nearest road and a species’ occupancy. The green lines indicate commercially valuable species, and purple lines indicate non-valuable species. Thick lines trace the means for each group. b) Posterior distribution of the effect of distance to road, split between commercially valuable (green) and non-valuable (purple) species. The dot indicates the mean for each group, and the horizontal error bars represent the 95% confidence interval for the mean of each group.

Figure 3. Most species are more likely to occupy areas with more intact forest, and we found similar rates of occupancy for commercially valuable and non-valuable species. a) Each thin line traces the relationship between percent intact forest within 500m and a species’ occupancy. The green lines indicate commercially valuable species, and purple lines indicate non-valuable species. Thick lines trace the means for each group. b) Posterior distribution of the effect of percent intact forest within 500m, split between commercially valuable (green) and non-valuable (purple) species. The dashed line indicates the mean for each group, and the horizontal error bars represent the 95% confidence interval for the mean of each group.

# Figures

Map

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Figure 1. Study sites in Cagar Alam Gunung Niyut, Kabupaten Landak. Blue circles correspond to point count locations, pink triangles correspond to our base camps, and red circles correspond to illegal activity detected (hunting, logging, or clear-cutting for agriculture). The pink line delineates the border of Gunung Niyut Nature Preserve, red fill indicates forest loss 2011-2015 (Hansen et al. 2013), green indicates primary forest, and white indicates non-forest.

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