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Impacts of tropical selective logging on local-scale movements of understory birds

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ABSTRACT

Widespread selective logging in tropical forest causes structural damage and associated shifts in species composition, but we lack understanding of how selective logging impacts mechanistic processes that drive these biodiversity changes. Movement is a vital mechanistic process underpinning demographic, ecological, and evolutionary processes that likely determine species responses to logging. We assessed how tropical selective logging impacts local movements of 71 understory avian species in Sabah, Malaysian Borneo, and determined whether movement patterns relate to species' conservation status, functional traits, sensitivity to logging and trophic position. We used a capture-mark-recapture methodology and a hierarchical Bayesian framework to model maximum observed local movement distances, accounting for spatial sampling heterogeneity. Across the avian community, we found a higher probability of moving shorter distances (up to 200 m) in logged forests, and higher movement probability at longer distances (above 200 m) in unlogged forests. Altered movement patterns after logging may reflect increased understory density, changed resource distribution and/or predation risks, and suggest smaller home-range sizes. Species' conservation status, body mass, foraging guild, logging sensitivity and trophic position were unrelated to the magnitude of movement change. The continued persistence of understory species in our sample after selective logging may depend on flexibility in movement behaviour, conferring resilience to habitat degradation and the retention of high conservation values. This lends further support for the protection of these logged forests for biodiversity conservation.

1. Introduction

Tropical forests are increasingly degraded by selective logging worldwide, altering forest characteristics, contributing to carbon emissions and threatening many species in biodiversity hotspots (Edwards et al., 2014b). Despite changes in its structure, a substantial amount of animal and plant species and functional diversity is retained after selective logging (Edwards et al., 2014b), although community composition of birds and dung beetles is altered as forest-interior species decline and edge-tolerant species increase (Edwards et al., 2011). This retention of biological value has led to proposals for the protection of selectively logged forests for biodiversity conservation as the next best alternative

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to protecting primary forests (Gibson et al., 2011; Meijaard and Sheil, 2007).

Our understanding of how selective logging impacts the mechanistic processes underpinning these biodiversity changes is scant, limiting our capacity to predict long-term impacts of logging on species (Cosset et al., 2019). Movement is a vital mechanistic process, influencing survival, growth, and breeding rates (Faccio et al., 2018), underpinning demographic changes and many fundamental ecological and evolutionary mechanisms (Postma and van Noordwijk, 2005). Within an animal's home range—the area where an animal tracks resources to meet its needs (Burt, 1943)—movement variation can be driven by the abundance and distribution of resources, habitat structure, and predator or mate encounters (Politi et al., 2010; Doherty et al., 2019; Schaaf et al., 2020). Considering movement can improve predictions of long-term population persistence, species conservation status, and the efficiency of conservation action (Lieury et al., 2015; Robertson et al., 2018).

Previous work used spool-and-line or telemetry techniques to assess how logging impacts movement patterns of single mammal (Colon, 2002; Wong et al., 2004; Wells et al., 2008; but see Wells et al., 2006) or bird (Dale and Slembe, 2005) species. All mammal studies showed no impact of selective logging on home-range size, movement rates or patterns, but instead found that movement strategies were affected by the heterogeneous structure of logged forest microhabitats and associated food distribution. Conversely, the understory passerine red-tailed bristlebill (*Bleda syndactyla*) in Uganda had higher movement rates and larger home-ranges in unlogged forests as their preferred dense understory habitat was scattered, compared to logged forests (Dale and Slembe, 2005). Understanding the community-wide impacts of logging on species' movement, including on habitat-sensitive rare species, thus remains a major knowledge gap.

The impact of logging on local movements might vary depending on how logging affects the distribution of food resources, and in turn the degree of species' dietary flexibility, as measured by a species' trophic position (Edwards et al., 2013; Hamer et al., 2015). Many Bornean birds feed from higher trophic positions in logged than unlogged forests, indicating more protein-rich diets (i.e. more invertebrate and less fruit, consumption of more predatory arthropods, and/or elevated trophic positions of invertebrate prey) in logged forests (Edwards et al., 2013). Because a greater proportion of fruits are produced by lianas during the non-masting years in logged forests, these denser patches of tangles would likely require movement between patches whereas a more permanent source of invertebrate prey might require less movement (Doherty et al., 2019; Marshall et al., 2020). Changes in movement, resources, and consequently trophic position, could have repercussions on species' survival and thus abundance, potentially leading to long-term declines in populations of species otherwise thought to persist after logging (Hamer et al., 2015; Messina et al., 2020).

One reason for the relative paucity of community-level research on animal movement is the difficulty of obtaining suitable data across species. Previous statistical approaches to examining community-wide movement patterns have involved using linear models with species as random effects (e.g. Tucker et al., 2018) or separately estimating responses for each species (e.g. Wells et al., 2006). These methods suffer from sparse data for the large number of rare species detected in the community, but recent advances in joint species modelling have helped overcome this by allowing species- and community-level responses to be estimated simultaneously in a hierarchical framework (Ovaskainen et al., 2019). This allows more accurate estimations for rarer species, by allowing species-level effects to be partially informed by community-level patterns (Warton et al., 2015; Ovaskainen et al., 2019).

Here, we (1) assess how tropical selective logging impacts the local movements of understory avian species, (2) determine whether species' conservation status or functional traits (i.e., body mass and foraging guild; foraging guild is its diet) are important determinants of movement patterns, (3) determine if differences in movement patterns are related to species' sensitivity to selective logging, and (4) determine whether movement patterns relate to logging-mediated changes in species' trophic positions, i.e., their position in a food web. We focus on birds as they are important drivers of ecosystem processes (Sekercioglu, 2006), and are indicators of patterns in other taxa and of forest health (Edwards et al., 2014a). Understory birds are vulnerable to anthropogenic impacts as they prefer interior forest habitats (Sekercioglu and Sodhi, 2007), often have specialized diets (i.e., certain insect or fruit sources; Marra and Remsen, 1997; Fagan et al., 2016), and tend to be small-bodied and consequently have high metabolic rates, meaning they require frequent foraging (Visco et al., 2015). This study includes 71 species spanning 19 families, representing the first empirical community assessment of the impacts of tropical selective logging on the movement patterns of whole ecological communities.

2. Materials & methods

2.1. Study site

The study was conducted in the global biodiversity hotspot of Sabah, Malaysian Borneo (Myers et al., 2000). Two habitat types (unlogged old-growth forest and twice-logged forest) were sampled in the Yayasan Sabah (YS) concession, a ~1 million ha contiguous forest block comprised of mostly lowland evergreen forest dominated by valuable timber tree species (Dipterocarpaceae) (Newbery et al., 1992; Fisher et al., 2011). Within the twice-logged forests, the first logging cycle was carried out from 1976 to 1991, with trees >0.6 m DBH extracted, yielding 73 to 166 m^3 of timber per hectare (Edwards et al., 2011). The second logging cycle was then conducted between 2001 and 2007, with trees >0.4 m DBH extracted, yielding 15 to 72 m^3 per hectare (Edwards et al., 2011). The YS concession also contains unlogged old-growth forests adjacent to these twice-logged forests, which we used as our controls.

2.2. Avifaunal sampling

We sampled the understory avian community using mist-netting techniques in a capture-mark-recapture methodology. In each habitat type (i.e. logged and unlogged forests), three sampling plots were established and each plot separated at least 1.83 km apart (Mean distances between each plot: 4.95 km ± 1.26 km; in unlogged = 6.23 km ± 2.28 km; in logged = 3.67 km ± 1.04 km). Each plot contained three 250 m transects, placed 250 m apart in parallel.

Fifteen 12 m mist-nets were placed end-to-end on each transect, allowing 70 m in total of extra space to avoid placing mist-nets over very steep gullies and fallen tree trunks. Mist-netting was conducted from 06:00 to 12:00 for two consecutive days per sampling event. Each plot was sampled three times (approximately monthly) from early June to early September in each year from 2014 to 2018. Mist-netting was not conducted in heavy rain, high winds or when elephants where in the vicinity.

To determine the movement patterns of birds, each transect was divided into five zones, each containing three mist-nets and with 50 m ± 1.2 m distance between the centre of each zone. This design allows us to detect cross-transect movements within plots, ranging up to 538 m (Fig. A1). Birds captured were identified to species, tagged with a uniquely numbered leg ring, sexed, aged, and released at the mist-net of capture within the zone. Birds that are not sexually dimorphic were not sexed. All mist-netting and bird ringing procedures conformed to set guidelines by the British Trust for Ornithology.

2.3. Movement kernel models

We develop a novel hierarchical modelling framework to estimate movement rates at both species- and community-levels, adapting recent developments in joint species occupancy modelling to allow more efficient statistical use of multispecies movement data (Ovaskainen et al., 2019). To determine how selective logging impacts the local movements of understory avian species within home ranges, we excluded long-distance movements that are likely to arise from other processes (natal or breeding dispersal). We restricted our dataset to only include within-plot movements (i.e. movements ranging up to 538 m), leaving 1210 individuals of 71 species. We calculated the maximum distance moved, *r*, between any two capture locations for each individual bird to model movements with respect to habitat type (logged or unlogged forest). Individual birds that were only recaptured within their original transect zone were assigned a maximum distance *r* of 12.5 m, which is half the buffer radius of the area sampled (see Fig. A2), as it is impossible for an individual to not move at all.

The hierarchical modelling framework developed here consists of two components: (1) the ‘state’ component, and (2) the ‘observation’ component. The ‘state’ component used movement kernels to model the probability density of movement across different distances, and how this varies across species and habitats (Nathan et al., 2012). We fitted four different movement kernel probability density functions (Rayleigh, Gamma, Log-normal and Cauchy) separately, representing different hypotheses about the distribution of underlying movement distances (Nathan et al., 2012) (see Supplementary material Appendix C). Movement kernels can be biased by spatial sampling effort, as only a subset of possible movements distances is observable for each marked individual (Nathan et al., 2012). The ‘observation’ component of the hierarchical model accounts for this, by modelling the observation process alongside the true movement process in a state-space formulation (Patterson et al., 2008). For each individual, we model the likelihood that the true maximum distance was greater than the observed maximum r_i, within the range of observable distances under our sampling design. We define the probability of observing a given maximum movement distance *r* as the proportion of space within an annulus of radius *r* that intersects our sampled area. Using ArcMap 10.6 (ESRI, 2018), we apply buffers of radius 25 m around each transect to represent this sampled space (reflecting an assumption that individuals within 25 m of a mist-net have high probability of recapture) and an annulus ring width of 1 m centred around the centre of the capture zone where the given individual was captured (Fig. A2). The radius size of the annulus ring reflects the maximum distance observed *r* for that given individual. We then calculated *Wr*, the probability of observing a movement at distance *r* for a given individual:

$$Wr = \frac{Area\ sampled\ within\ annulus\ at\ distance\ r}{Total\ area\ in\ annulus\ at\ distance\ r}$$

The intersection of the annulus ring with the sampled space represents the likelihood that an individual, moving distance *r* from its former capture location, comes within the sampled space. An annulus ring width of 1 m was used because we wanted to reduce the error of intersected space by producing as close as possible the maximum distance moved *r* (n.b. other annulus ring widths were tested, up to 12.5 m which is half the buffer radius, and there were little differences in the resulting *Wr* values).

For each individual, *i*, we then model whether each observable movement distance *r* (ranging from the observed maximum r_i up to the observable limit *max*(*r*), 538 m) is the true maximum distance moved by that individual (1) or not (0) as a Bernoulli trial:

$$p_{r_i:max(r)} \sim Bernoulli\left(X_{s,h,r_i:max(r)}\right)$$

where $X_{s,\ h,\ ri:\max(r)}$ are movement probabilities for species *s* in habitat *h* for the range of observable distances $r_{i:\max(r)}$, given by the probability density function for a given movement kernel.

We then model our observed data as Bernoulli trials:

$$d_{r_i:max(r)} \sim Bernoulli\left(w_{r_i:max(r)} \times p_{r_i:max(r)}\right)$$

where $d_{ri:\max(r)}$ is the matrix containing the observed data indicating whether an individual was observed moving a certain distance *r* (1) or not (0), $w_{ri:\max(r)}$ is the matrix containing the probabilities of observing movements to distances greater than r_i up to the observable limit (538 m), and $p_{ri:\max(r)}$ is the corresponding binary value 0 or 1 indicating whether individual *i* moved these distances (1) or not (0), as given by the movement kernel above.

Models were fitted using the software JAGS (Plummer, 2003) through the R version 3.6.2 (R Core Team, 2019) packages *rjags* (Plummer, 2019) and *R2jags* (Su and Yajima, 2015). We used non-informative (vague) priors and hyperpriors for all parameters. Under the hierarchical formulation, priors represent species-level movement parameters, which are drawn from community-level hyper-priors, allowing maximum use of information across the dataset (Ovaskainen et al., 2019). Models were run using Markov chain Monte Carlo (MCMC) methods with three parallel chains, 30,000 iterations, a burn-in of 20,000 iterations and thinned by 10. Model convergence was assessed using the Gelman-Rubin potential scale reduction parameter, Rhat, where values close to 1 indicate that the model converged (Gelman and Rubin, 1992). Rhat values between 1.0 and 1.05 were accepted. We conducted posterior predictive checks for each model (Figs. A11, A12, A13) by first computing the observed mean probability densities for each observed maximum distance. The same was then done for a simulated dataset using parameters sampled from the posterior distribution. Bayesian *p*-values were then computed, where values above 0.9 or below 0.1 indicated a doubtful fit and values close to 0.5 indicated a perfect fit (Gelman et al., 1996).

We used best-fitting models, with the lowest deviance information criterion (DIC) value (Spiegelhalter et al., 2002), for subsequent inference (Tables 1, A2). The probability of each species moving distances from 1 m to 538 m (the maximum observable distance) was predicted from each model. Differences in movement probabilities between habitats for each species were considered to be statistically significant if the 95% credible interval of the posterior distribution for habitat differences in parameter estimates did not overlap zero. The model R scripts can be found in the supplementary material (Appendix B).

We also re-ran the above models only including the more common species occurring in both habitat types to test model sensitivity to the inclusion of data-poor species. We then assessed whether a species' conservation status, functional traits (i.e., body mass and foraging guild), sensitivity to selective logging, or trophic position determine the magnitude of their change in movement between habitat types (See supplementary material Appendix C for full materials and methods). To determine if recapture rate was biased by habitat type, we examined whether habitat type (logged or unlogged forests) affected the number of recaptures per transect for all species combined, as well as testing for effects of understory habitat structure (see Appendix D for more information).

Table 1

Bayesian model performance for the movement kernel model of 71 species using probability density function (pdf) for the Cauchy distribution, Rayleigh distribution, Gamma distribution and Log-normal distribution. Models with the lowest DIC values are the most parsimonious and models with less than 2 ΔDIC are considered equally parsimonious. DIC = Deviance Information Criterion, ΔDIC = the DIC difference between the best model and that stated model, pD = the effective number of parameters, Rhat = Rhat statistic close to 1 indicates that the model converged. Rhat values up to 1.05 were accepted. All parameters in each model had Rhat values less than the maximum presented below.

Distribution	DIC	ΔDIC	pD	Rhat
Cauchy	3976.1	0.00	0.2	<1.03
Log-normal	3977.3	1.20	0.4	<1.008
Gamma	3977.5	1.40	0.4	<1.05
Rayleigh	3978.1	2.00	0.4	<1.27

3. Results

A total of 4922 individual birds comprising 119 species were captured between 2014 and 2018, of which 1210 individuals of 71 species spanning 19 families were recaptured at least once and used in this study. Total mist-netting hours equated to 38,835 mist-net hours (unlogged: 20,300 mist-net hours, logged: 18,535 mist-net hours). We found no impact of habitat type or understory habitat metrics on species recapture rates per transect (Appendix D).

3.1. Movement patterns

Across the full dataset (71 species), the three heavier-tailed movement kernel models had relatively small differences with ΔDIC values within 2.00 (Table 1) and showed similar patterns of community-level movement with respect to habitat (Figs. 1, 2, A4). The thin-tailed Rayleigh distribution model did not achieve adequate convergence, suggesting poor fit to the data. For simplicity, we base further inference on the model with lowest DIC, which was the Cauchy kernel distribution.

On average the understory community had a higher probability of moving shorter distances (up to 200 m) in logged versus unlogged forests (Cauchy: logged: mean probability = 0.382, 95% CI = 0.377 to 0.387, unlogged: mean probability = 0.350, 95% CI = 0.350 to 0.351; Figs. 1a, 2). The opposite pattern occurred at distances above 200 m, where the probability of moving larger distances was higher in unlogged compared to logged forests (Cauchy: logged: mean probability = 0.070, 95% CI = 0.067 to 0.073, unlogged: mean probability = 0.0891, 95% CI = 0.0886 to 0.0894; Figs. 1b, 2).

Modelling movement probabilities of species with at least one observation in each habitat type (43 species model set) and the commonest species in the dataset (25 species model set) showed similar results to the full analysis, suggesting that community-level inferences were not sensitive to the inclusion of data-poor species (Table A2, Figs. A3, A5, A6). Again, these models had a higher probability of moving shorter distances (up to 200 m) in logged versus unlogged forests (43 species Cauchy model: logged: mean probability = 0.382, 95% CI = 0.374 to 0.390, unlogged: mean probability = 0.351, 95% CI = 0.350 to 0.353; and 25 species Cauchy model: logged: mean probability = 0.383, 95% CI = 0.371 to 0.396, unlogged: mean probability = 0.351, 95% CI = 0.349 to 0.353) (Figs. A3, A5, A6). They also revealed the reverse pattern at distances above 200 m, with the probability of moving larger distances higher in unlogged versus logged forests (43 species Cauchy model: logged: mean probability = 0.070, 95% CI = 0.065 to 0.075, unlogged: mean probability = 0.0884, 95% CI = 0.0877 to 0.0892; and 25 species Cauchy model: logged: mean probability = 0.069, 95% CI = 0.062 to 0.077, unlogged: mean probability = 0.089, 95% CI = 0.088 to 0.090) (Figs. A3, A5, A6).

At the species level, the results from the 71 species model set concur with those of the 43 species and 25 species model sets. Species-level differences in movement probabilities between habitat types are significant for six insectivorous and one frugivorous species (six of which were in the 25 species model set; Table A1; Fig. A7), where 95% credible intervals for the difference in scale parameter, γ, between habitat types did not overlap zero (BCBAB: *Pellorneum nigrocapitatum*, CWBAB: *Cyanoderma erythropterum*, GHBAB: *Stachyris poliocephala*, HBAB: *Malacocincla sepiaria*, RCBAB: *Malacopteron magnum*, STBAB: *Pellorneum malaccense*, YRFLPEC: *Prionochilus xanthopygius*) (Table A1; Figs. 3, 4, A7).

3.2. Species conservation status, traits, logging sensitivity and trophic position

The most parsimonious models (<2 ΔAICc) explaining between-species variation in the magnitude of their change in movement between habitat types were the null model and the model including only species' body mass ($F = 0.32$, df = 1,69, $p = 0.57$) (Table A3; Fig. A8), indicating that across all 71 species, conservation status, body mass, and foraging guild did not influence movement changes. Species' sensitivity to selective logging (RPA index) was also unrelated to the magnitude of change in movement probability between logged and unlogged forests for all species ($y = 0.003x - 0.0003$, $F = 0.34$, df = 1,69, $p = 0.56$; Fig. A10).

Trophic position data was obtained for 34 of the 71 species included in the model. Overall, species' change in trophic position between logged and unlogged forests was not an important determinant for the extent of change in movement probabilities between logged and unlogged forests ($y = 0.02 - 0.05x$, $F = 2.10$, df = 1,32, $p = 0.16$; Fig. A9).

4. Discussion

Selective logging is the most prevalent disturbance within tropical forests, yet information on how logging impacts mechanistic processes

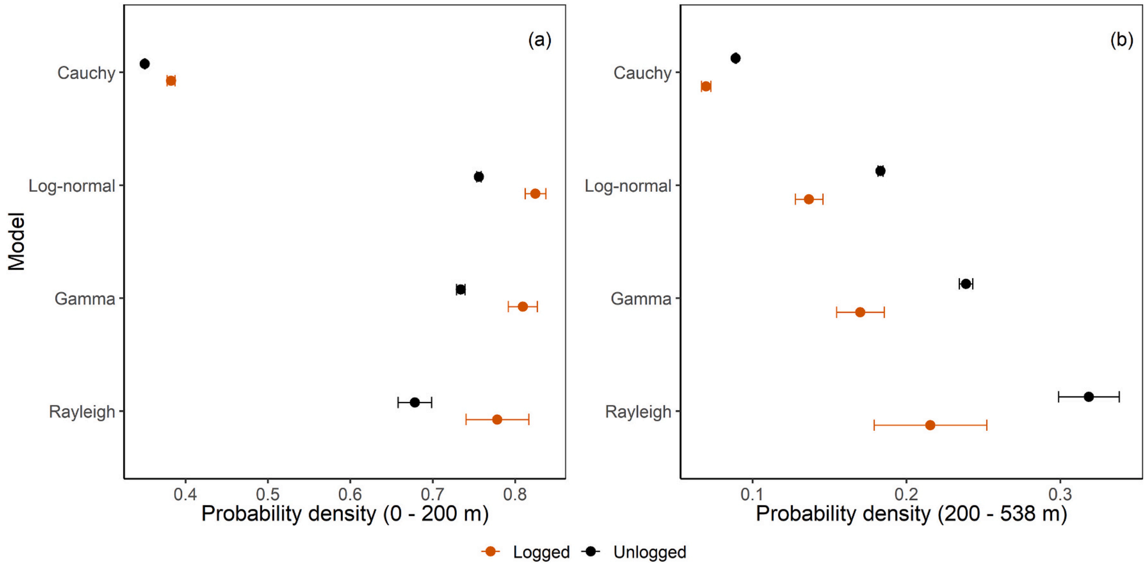

Fig. 1. Mean probability density from all four models (Cauchy, Log-normal, Gamma, Rayleigh) containing 71 species combined for distances between (a) 0 m to 200 m and (b) 200 m to 538 m, with 95% credible intervals. Only the positive half of the Cauchy probability density function was used in the model.

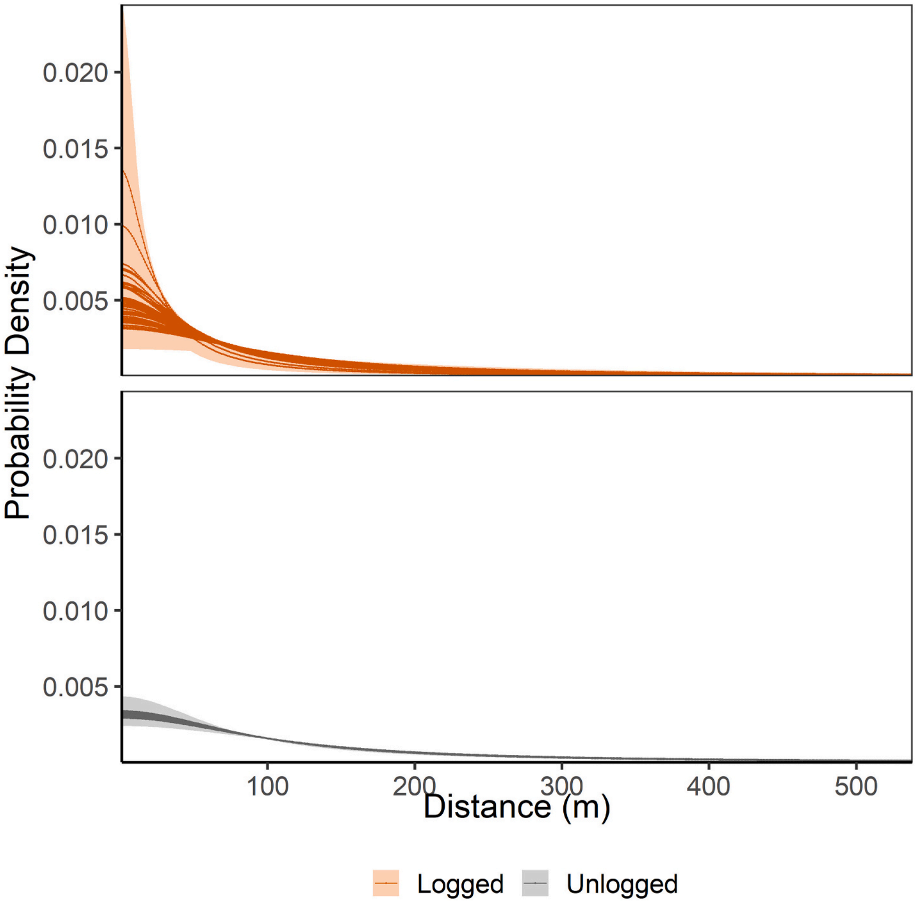

Fig. 2. Posterior means with 95% credible intervals for movement kernels of all species fitted with the Cauchy probability density function in the 71 species model set given a certain maximum distance moved in each habitat type (logged or unlogged). Each line is for a separate species.

that drive biodiversity change is lacking. We found that on average across an understory bird community, individuals had a higher probability of moving shorter distances and lower probability of moving larger distances in logged forests relative to unlogged forests. Changes in movement between logged and unlogged forest were not directly linked to species' conservation status, functional traits, sensitivity or dietary plasticity (Edwards et al., 2013). Moving shorter distances could be indicative of higher fitness due to less energy expanded to obtain resources (Cattarino et al., 2016; but see Doherty et al., 2019) and thus potentially contribute to the persistence of understory species after selective logging. However, it could also indicate less efficient movement or changes in food and breeding resource distributions.

4.1. *Movement patterns*

The higher probability of moving shorter distances in logged forests and moving larger distances in unlogged forests could be due to changed distribution of preferred habitats for understory species. Many understory specialists prefer dense understories (Fagan et al., 2016), which generally occur throughout logged forests but are patchily distributed in unlogged forests, as observed for red-tailed bristlebill (*Bleda syndactyla*) in Uganda (Dale and Slembe, 2005). Furthermore, some species move shorter distances in their preferred habitat, which is likely resource driven (Hansbauer et al., 2008). Conversely, other species, especially forest specialists, tend to avoid even the smallest forest gaps and thus have highly constrained movement patterns within forest interiors, with potential implications on pollination services, seed dispersal, and plant fitness (Volpe et al., 2016; Ibarra-Macias et al., 2011).

Higher predation risk could also increase the likelihood of understory species moving shorter distances in logged forests, as movement behaviour can be highly sensitive to perceived predation pressure (Thiollay, 1999). For instance, lower participation in mixed flocks by understory birds, relative to mid-canopy species, could be explained by the higher availability of predator refugia in the understory, reducing the pressure for cooperative vigilance (Borah et al., 2018). Structural differences in logged forests may also alter predation risk perception and thus flocking propensity (Hua and Sieving, 2016; Kajiki et al., 2018), with consequent impacts on movement. This perceived risk in predation can hinder the movements of understory avian species that are usually able to cross forest gaps (Williamson and Fagan, 2017).

Higher population densities in logged forests can arise through species having smaller home-range sizes (e.g. red-tailed bristlebill, *Bleda syndactyla*; Dale and Slembe, 2005). Logged forests tend to have more understory arthropod prey (Edwards et al., 2012) and small-sized fruits, especially from pioneer trees (Levey, 1988) that are usually spatially clumped (Condit et al., 2002), potentially reducing the need for logged forest understory species to travel far to acquire food. In contrast, home ranges in secondary forests for some Neotropical species are almost twice as large as those in old-growth forests, potentially due to increased predation or reduced resources (Mokross et al., 2018). Forest degradation changes the availability of food sources by limiting the movements of pollinators and seed dispersers (Volpe et al., 2016; Holbrook, 2011). Despite increases in food resources in logged forests (Levey, 1988; Edwards et al., 2012), some species may experience lower survival probabilities (Bailey and King, 2019) due to factors like increased predation risk, greater resource competition, or lower habitat quality. This could lead to logged forests becoming 'ecological traps' (Gilroy and

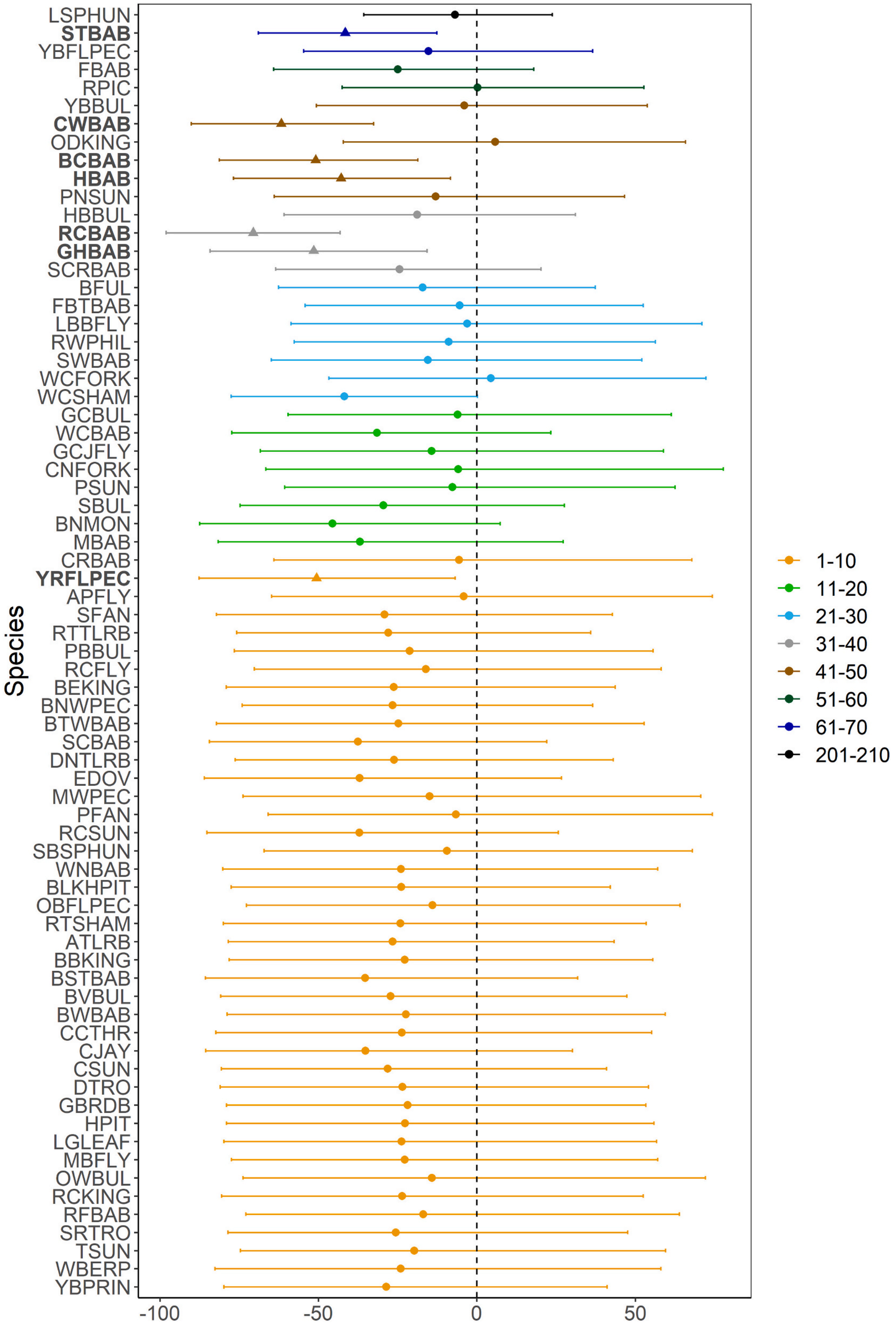

Fig. 3. Posterior distributions (mean and 95% credible interval) for the difference in scale parameter, γ, between habitat types (logged and unlogged), of the Cauchy probability density function in the 71 species model set. 95% credible intervals not overlapping zero are considered to be statistically significant. Species with statistically significant movement changes are highlighted in bold. Sample sizes for each species are colour coded. Species names are substituted with the species' code (species information in Table A1).

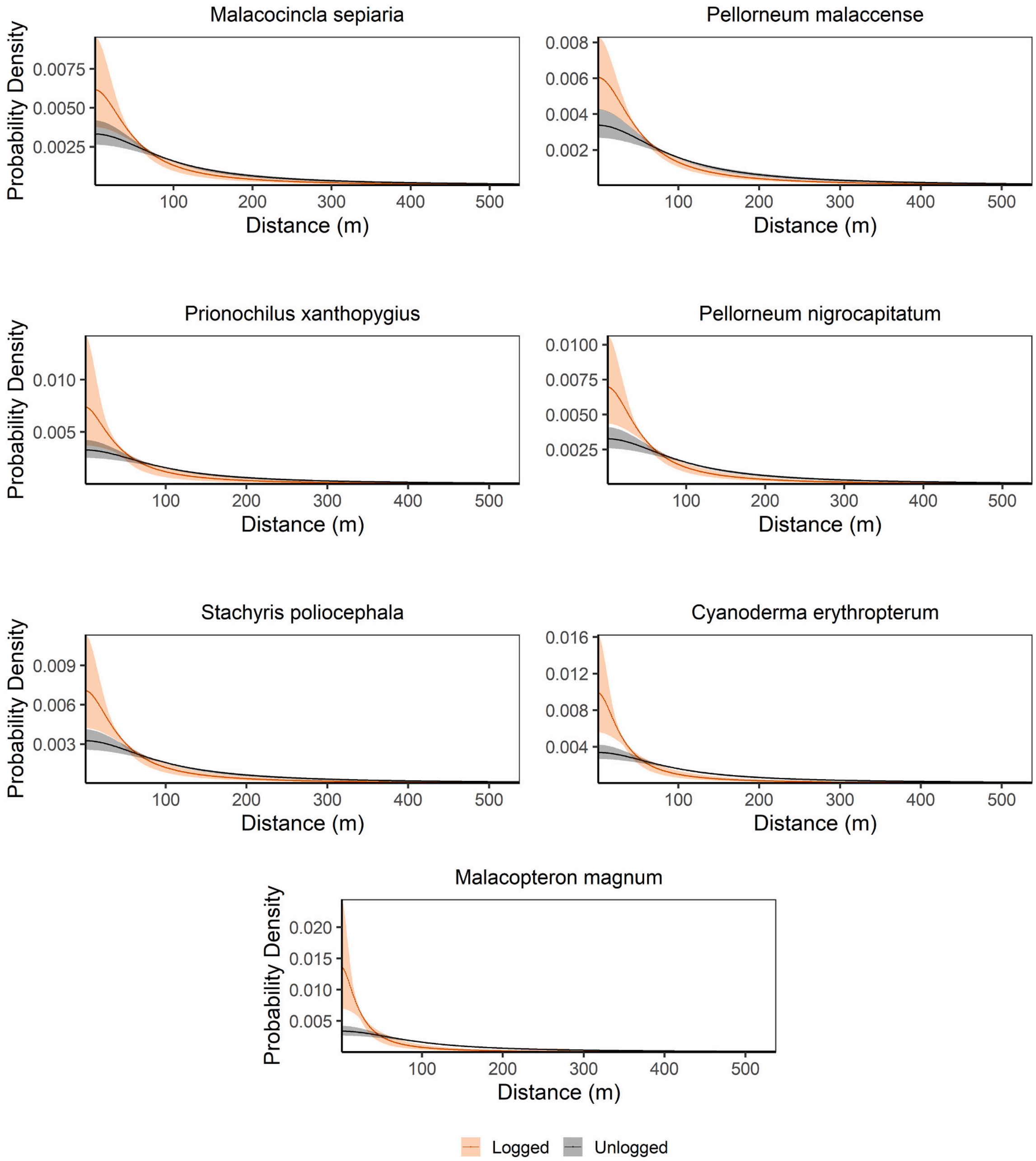

Fig. 4. Posterior means with 95% credible intervals for movement kernels, of species with significantly different movement probabilities between logged and unlogged forests, fitted with the Cauchy probability density function in the 71 species model set given a certain maximum distance moved in each habitat type (logged or unlogged).

Sutherland, 2007) where habitat quality declines without changes in the relative attractiveness of the habitat.

The seven species whose movements most significantly changed in logged forests are six insectivorous babblers and one nectivorous flowerpecker. They also had different degrees of forest dependencies and used a variety of foraging modes, such as foraging flexibly alone or in groups. We therefore find little indication that any particular species traits can be used as predictors of whether species are more likely to be affected by selective logging.

4.2. *Species conservation status, traits, logging sensitivity and trophic position*

We found that (1) species of high conservation concern are equally likely to have similar movement patterns to those of low conservation concern, (2) species' functional traits, such as body mass and foraging guild, did not influence the extent of change in movement, and (3) species more sensitive to logging were not more likely have greater or smaller movement changes compared to species which were more robust to logging. This contrasts with the findings of Ramos et al. (Ramos et al., 2020) where avian species movement patterns in a fragmented landscape were dependent on their body mass and diet. For example, larger species and frugivores moved greater distances, owing to the lack of predictability of fruit resource production (Ovaskainen et al., 2019). The fact that our studied understory community is dominated by species that tend to do well in selectively logged forests (Edwards et al., 2011) may explain the lack of a relationship found in our study.

Understory species in our study community tend to feed at higher trophic levels in logged forests (Edwards et al., 2013) but we did not find a link between the magnitude of trophic position change and movement change. This could indicate behavioural flexibility, as alterations to movement may allow species to keep exploiting the same prey type, despite changes in prey distribution in degraded habitats. Some Malaysian avian species alter their foraging techniques in response to forest structure changes, increasing foraging efficiency (Mansor et al., 2018). Furthermore, Bornean understory birds in logged and unlogged forests have similar levels of glucocorticoid hormones, which regulate feeding behaviour (Messina et al., 2020). In support, these birds also have similar body condition in logged and unlogged forests (Messina et al., 2021). The lack of association with trophic position shifts suggest that movement changes are not associated with changing prey type.

4.3. Management implications

Limited movement in logged forests could have negative implications on the population dynamics of these avian communities. At the landscape level, movement affects the occupancy and extinction rates of species (Irizarry et al., 2016). Hindered movements will also impact gene flow, and thus population resilience and ability to adapt to environmental changes (Bohonak, 1999; Postma and van Noordwijk, 2005). In selectively logged forests, forest gaps and logging roads are not traversable to many species, reducing their ability to move around the landscape (Laurance et al., 2004; Lees and Peres, 2009; Volpe et al., 2016). Through careful spatial planning of logging and application of reduced-impact logging practices the amount and size of forest gaps created by tree felling and logging roads can be reduced (Putz et al., 2008), facilitating movement.

The biodiversity value of logged forest is likely to depend in part on nearby old-growth forests remaining protected, as these can act as source habitats that can help bolster nearby logged forest populations via immigration (Gilroy and Edwards, 2017), as well as promoting gene flow between old-growth and logged forests (Postma and van Noordwijk, 2005; Gilroy and Edwards, 2017). Many studies have shown that the impacts of selective logging on biodiversity are relatively lower if there are neighbouring old-growth forests (Edwards et al., 2014b). Restoring logged forests can also increase the rate of forest regrowth and gap closure. The restoration regime would depend on the goal of restoration (e.g. ecosystem restoration), forest type, degradation level and regeneration ability (i.e. if it requires assisted restoration or not) (Cerullo and Edwards, 2019).

5. Conclusions

Movement probabilities of understory Bornean species were higher at shorter distances in logged forests and movement probabilities were higher at longer distances in unlogged forests. The continued presence of multiple red-listed species within our sample after selective logging may depend on the flexibility of their movement behaviour. More broadly, this underscores the potential for selectively logged forests in the region to retain high conservation value, lending further support for their protection for biodiversity conservation (Edwards et al., 2011). However, we remain unsure if survival and recruitment in logged forest are at, below, or above replacement level, and populations might be sustained by immigration from surrounding ‘source’ unlogged forests, that produce a surplus of dispersing individuals (Gilroy and Edwards, 2017). Future studies should examine how selective logging impacts species survival and recruitment, in combination with movement patterns, especially for rare and endangered species.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability statement

Data will be made available from Figshare upon publication.

CRediT authorship contribution statement

D.P.E., S.T., C.C.P.C. and J.J.G. conceived the ideas and designed methodology; D.P.E., S.T., C.C.P.C., L.N., P.G.C., S.M., M.K., M.F., R.S.M., A.L.S., L.P., B.K., R.F., T.B.H., E.G., J.Y.W.C., E.C., C.Y.Y., T.C.H., R.R.C. and C.C.O. collected the data; C.C.P.C. and J.J.G. analysed the data; C.C.P.C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Appendices. Supplementary data

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