**Inland Norway
University of
Applied Sciences**

Faculty of Applied Ecology, Agricultural Sciences, and Biotechnology

Darwin Mayhew

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Guardian of the Forest: Do trophic cascade effects of Sunda Clouded Leopards (*Neofelis diardi*) impact Sabah's carnivore community and native pheasant species?

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Authors: Darwin S.G. Mayhew, Inland Norway University of Applied Sciences - Campus Evenstad, (mayhewdarwin@gmail.com); Andrew J. Hearn, WildCRU, Department of Zoology, University of Oxford, (andrew.hearn@zoo.ox.ac.uk); John D.C. Linnell, Norwegian Institute for Nature Research; Inland Norway University of Applied Sciences - Campus Evenstad, (john.linnell@nina.no; john.linnell@inn.no); Olivier Devineau, Inland Norway University of Applied Sciences - Campus Evenstad, (olivier.devineau@inn.no); David W. Macdonald, WildCRU, Department of Zoology, University of Oxford, (david.macdonald@zoo.ox.ac.uk).

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Main Correspondent: Darwin S.G. Mayhew, 826 39th Ave. San Francisco, CA, USA, 94121.
        Contact via: +1-(415)-312-8501, +1-(415)-386-0161; mayhewdarwin@gmail.com.

Abstract:

When apex predators disappear from an ecosystem it can have dramatic consequences including the increase in smaller bodied carnivores whose rise can subsequently impact various prey species, this result better known as mesopredator release. Mesopredator release effects on tropical avifauna has rarely been explored especially in the changing landscape of Sabah, Malaysian-Borneo. Sabah has experienced significant land conversion reducing forest integrity and wildlife habitat. We used a piecewise structural equation model to explore how these changes affect the cascading impacts of various Sunda clouded leopard abundances on both mesopredators and the pheasant communities. While Sunda clouded leopards appear to show a positive relationship with loss of forest integrity, data indicate that they have a limiting effect on some mesopredators who in turn have negative effects on pheasant species. This result suggests that apex predators may be more resilient to landscape alteration without it negating their ability to induce mesopredator release.

Introduction

Understanding the complex interactions that drive ecosystems is at the core of what ecologists strive to explain. However, little is known about the relative strengths, direction, and impacts of the relationships operating in many ecosystems, including in tropical forest. This knowledge gap is perhaps no more evident than in the case of trophic cascade which have seen a variety of definitions over the years (Polis et al., 2000; Hayward et al., 2019). This ecological theory has seen a broad range of applications including the effects of wolves (*Canis lupus*) in Yellowstone National Park, the impact of the decline of large-bodied sharks on rays, the cascading effects of sea otters (*Enhydra lutris*) on sea urchins (*Echinoidea sp.*), and even the effects of declining tigers (*Panthera tigris*) on carnivore communities (Estes & Palmisano, 1974; Ferretti et al. 2010; Steinmetz et al. 2013; Heupel et al. 2014; Ripple et al. 2016). In the process of this concept becoming widely used, its definition has also changed from a simplistic top-down definition to one that focuses on the interrelationships, direct or otherwise, between species (Hayward et al., 2019). Ripple et al. (2016) define trophic cascades as "the indirect species interactions that originate with predators and spread downward through food webs". This concept has various iterations depending on the system or species in question including a form commonly known as mesopredator release. Mesopredator release is often defined as the decline or disappearance in "apex" or top predator populations which in turn results in a population increase of small to medium sized predators (Ritchie & Johnson, 2009; Ripple et al., 2016). The subsequent increase in mesopredator populations is then supposedly followed by a decline in populations of lower trophic level such as small to medium sized mammals or birds (Crooks & Soulé, 1999; Rayner et al. 2007; Sergio et al. 2007).

While mesopredator release has potential for broad ecological impacts, its validity and reliability remain unclear (Lloyd, 2007; Allen et al. 2015; Castle et al. 2021; Rasphone et al. 2021). Studies of mesopredator release face various limitations with factors such as methodology and data limitations often leading to inconclusive results (Lloyd, 2007; Castle et al. 2021; Rasphone et al. 2021). Given the potential biological importance of mesopredator release this dearth of information may be an ecologically important knowledge gap for both ecologists and conservationists alike. Additionally, as the number of apex carnivores in ecosystems around the world continues to decline it is increasingly pressing to understand the affects their disappearance may, or may not, have on their broader habitat (Woodroffe, 2000). Despite the potential impacts of mesopredator release there is mixed evidence supporting this as a universal ecological theory (Allen et al. 2015; Castle et al. 2021). Papers focusing on this topic often investigate large scale correlational trends in populations which fail to show behavioral or mechanistic evidence of mesopredator release (Lloyd, 2007; Cunningham et al. 2020). This is largely due to the difficulties in collecting the necessary data of sufficient precision and extent on elusive species in often wild natural settings (Allen et al., 2011; Hayward et al., 2019). Accordingly, mesopredator release remains controversial at best with new studies being particularly sensitive to criticism over study design, interpretation, and context (Allen et al., 2011; Hayward et al., 2019).

Despite the many pitfalls which the concept of mesopredator release faces, the growing popularity of the theory has sparked numerous studies focused, largely, on terrestrial canine species or invasive mammalian mesopredators (Saggiomo et al. 2021). Despite the trend toward

mammalian systems, research has suggested that incorporating avifauna into mesopredator release models may help reveal relationships between direct predation of birds and nest depredation by mesopredators released during apex predator declines (Crooks & Soulé, 1999; Lloyd, 2007; Sergio et al. 2007; Castle et al. 2021; Saggiomo et al. 2021). This may effectively reduce avifaunal diversity and abundance with knock on effects potentially impacting pollination, invertebrate communities, and even ecotourism activities (Muttaqien et al. 2015; Martínez-Sastre, 2020). However, due to the study design complexities and resource constraints it is difficult to obtain both detailed avifauna and mammalian carnivore data. In addition, the use of data collected by targeting one of these taxa often limits the information of the other available for analysis. Fortunately, camera trapping has been shown to be an effective form of monitoring at least some groups of ground dwelling avifauna such as pheasants in addition to medium and large sized mammalian predators and other prey species (O'Brien & Kinnaird, 2008). Given that camera trapping methods often accrue significant amounts of "by-catch" data from non-target species, this method provides a good opportunity to explore relationships between multiple taxa in an ecosystem using preexisting data.

Mesopredator release is often triggered by external effects on apex predator populations such as reintroduction, persecution, disease, or landscape conversion that radically alters their natural state (Takimoto & Nishijima, 2022). One such location that has undergone significant changes to its landscape in recent years is the Malaysian state of Sabah on the island of Borneo (Cushman et al. 2017; Hearn et al. 2018a). As one of the most biodiverse places in the world, the rapid conversion of primary tropical forest to palm oil plantations has impacted numerous species by reducing habitat, increasing edge effects, and increasing access for poachers

(Cushman et al. 2017; Hearn et al. 2018a). As palm oil continues to be an important economic

resource for local people, including some indigenous communities, it has become critical to

understand how this landscape change affects wildlife communities (Colchester 1993; Hearn et

al. 2019). The potential trophic cascade from the biological community shift in Sabah may have

impacted various species at lower trophic levels that hold ecologically and economically

important roles on the island (Hearn et al. 2018b). To understand the possible effects of trophic

cascades and mesopredator releases in this system we examined the relationship between the

largest obligate carnivore on the island, the Sunda clouded leopard (*Neofelis diardi*), and two of

the most common mesopredator species from our camera-trapping data. The mesopredator in

question are the Sunda leopard cat (*Prionailurus javanensis*), the most common small cat, and

the Malay civet (*Viverra tangalunga*) the most common civet species. These two mesopredators

were selected to simplify our analysis and constrain the complexity of our model in accordance

with our limited data. Unlike previous mesopredator release studies in Borneo, we examined the

cascading effects of the mesopredator community on three species of frequently detected

pheasants: the great argus pheasant (*Argusianus argus*), Bulwer's pheasant (*Lophura bulweri*),

and the crested fireback (*Lophura ignita*) (Brodie & Giordano, 2013). Given the complex nature

of the Bornean ecosystems species of interest were limited to those with enough observations or

ecological significance for our system (Table S1.).

Based on a combination of previous research and predictions inspired by the

mesopredator release hypothesis and trophic cascade mechanics we predicted an a-prior

piecewise structural equation model (Fig 1.). In this model we predict 1: negative effects of

forest integrity loss on the apex predator's detectability corrected index of abundance, 2: varying

degrees of mesopredator release when apex predator abundance decreases, 3: a subsequent

decline in pheasant species abundance hypothetically, resulting from mesopredator release.

Study Area

Camera trap data were collected over 7-years from May 2007 to January 2014 at ten

unique study sites consisting of grids of remote motion sensor camera traps deployed across the

Malaysian state of Sabah on the island of Borneo (Hearn et al. 2018b). This data has been

examined in previous studies which provide a more detailed background of the study area and

history of the data (Hearn et al. 2013, 2018a, 2018b, 2019). Below we provide a broad

description of the habitat, history, and biological nature of this data as it pertains to this study.

The numbers of camera traps used varied between years and study site as did the elevational

range, logging practices, local and broad habitat variables (Miettinen et al. 2012). Camera

trapping grids and camera trap placement were designed to collect Sunda clouded leopard photos

as well as other small carnivore observations. In addition to felid species many other animal

species were recorded and documented for future research. Camera trap locations were separated

in space using a grid of 1 km between points, when possible, to facilitate robust data capable of

being used in for SECR analyses. Two cameras were used at each location positioned across

from one another at shin height to capture 360 degrees of each camera trapping location.

The habitat surveyed spanned an elevational range from 0 to 1600 meters with varying degrees of human disturbance caused by logging, hunting, and agricultural practices (Grantham et al., 2020). Land cover was categorized into thirteen classes based on Miettinen et al.'s (2012) habitat classification. Camera trapping grids were placed around potential Sunda clouded leopard habitat with six out of ten grids located in relatively intact forest habitat, and two out of ten placed in palm oil plantations with the rest located in semi-suitable habitat patches (Hearn et al. 2018b). Camera trapping did not run continuously, however, all seasons were recorded throughout the seven-year period. The peak rainy seasons occurred from February through April and August through October, Temperatures in this region ranged on average from 20.4 to 29.5 °C (Moerman et al. 2013; Sa'adi et al. 2020). Due to the mild variation in climate and relative stability afforded Sabah by its proximity to the equator, climate-related covariates were considered outside the scope of this analysis.

Two-Stage Multivariate Approach

We used a two-stage approach inspired by Cunningham et al. (2020) to analyze our data and create a final piece-wise Structural Equation Model (pwSEM) representing interactions between the carnivore community and pheasant species in Sabah. Justifications for our a-priori SEM can be found in Box 1. We used R studio and QGIS to extract environmental variables, create abundance models, and build our pwSEM (R Core Team, 2020; QGIS Development Team, 2022). The first stage of our analysis calculated environmental variables and modeled an abundance estimate for each species based on our a-priori hypothesis and previous ecological knowledge. These abundance estimates were then used in a subsequent pwSEM to detect the

possible interactions of forest integrity, landcover class, and species abundance on the Sabah

carnivore community structure in the attempt to detect cascading effects that might indicate

mesopredator release.

Environmental Factor Extraction

Two environmental factors were extracted using QGIS which were later incorporated into

our pwSEM as bottom-up and top-down factors (QGIS Development Team, 2022). Both

landcover class and forest loss integrity index values were contained in raster layers sourced

from their respective publications (Miettinen et al., 2012; Grantham et al., 2020). Camera grids

were defined by using a minimum convex polygon (MCP) around the individual camera trap

location vector file without the addition of a buffer (see Fig 2.). The MCP defined in this way

was subsequently used for the calculations performed on both environmental layers to estimate

covariates usable at our sampling level, the camera grid. The bottom-up driver, landcover class,

was included in our model to account for different levels of environmental structure and

productivity among study sites and potentially offset any fine scale climatic influences such as

differing moisture levels. We used the mode of the landcover class from each grid's MCP to

represent the most dominate landcover class in that area. To calculate our top-down driver, forest

loss integrity index (flii), the mean for each camera trap grid's MCP was calculated (see Table

1). However, as flii was specified to range from 0 (low) to 10 (high) missing flii values (as

calculated by Grantham et al., 2020) were truncated to zero. Because the missing flii cell values

were based on forest cover less than 5 meters in height we considered this lack of data equivalent

to the poorest habitat possible. For this reason, we believe the truncation better represents these

urbanized or degraded areas as inhospitable when calculating the mean of the flii for each camera grid.

Abundance Analysis

For each species included in our a priori pwSEM an abundance estimate and standard error (SE) was calculated for each of the ten study sites using the Royle-Nichols or N-mixture model of abundance (Royle & Nichols, 2003; Royle, 2004). Species included in our analysis were included based on both their place in the trophic web and the amount of data available. To prepare our camera trap photos for the abundance models, observations were filtered by 60 minutes using the internal function *assessTemporalIndependence* in the camtrapR package to insure temporal independence in our detections (Niedballa et al. 2016). The filtered detections were in turn used to create a detection history for each species using the *detectionHistory* function (Niedballa et al. 2016). Following this, detection histories were used with the unmarked package *unmarkedFrameOccu* function and *unmarkedFramePCount* function to prepare the data for use in subsequent models (Fiske & Chandler, 2011). Two types of models were used to estimate abundance based on the type of detections available for analysis. For all carnivore species the Royle-Nichols occupancy-based abundance model was used. This model was selected over other possible abundance estimating models as it can account for binary observation data as opposed to group counts. As carnivores tend to be solitary our observation of them (i.e. in each photograph taken) were largely binary presence/absence data making the Royle-Nichols model a better fit. To facilitate this model, observations above one individual detected per event were truncated to one to allow the use of a detection/non-detection-based

abundance model and the associated *occuRN* function from the unmarked package (Royle &

Nichols, 2003; Fiske & Chandler, 2011). Detections of groups of pheasants were more common,

thus allowing for the use of the N-mixture model and the subsequent *pcount* function from the

unmarked package (Royle, 2004; Fiske & Chandler, 2011). As photos showed differing numbers

of pheasants within each 60-minute window, we considered the largest number of pheasants

present in any one photo as the maximum number within that filtered time. The best models

based on AIC scores produced by the Royle-Nichols occupancy-based abundance model and N-

mixture model for each species are listed in Table S2. When multiple models were deemed

equivalent, model-averaging was performed with all models within two delta-AIC points also

shown in Table S2. This process allows for the comparison of study sites by providing

detectability-corrected estimates of abundance from both the N-Mixture and Royle-Nichols

models (Cunningham et al. 2020). Both Royle (2004) and Cunningham et al. (2020) state that

when "sample area is unknown the derived estimates should still serve as a useful measure of

abundance that accounts for detection probability" allowing for the comparison between

different study areas. Thus, we feel it is appropriate to follow the same logic and compare

abundance indices using our camera grids as study sites without calculating actual densities for

each of our study species.

Piece-wise Structural Equation Model

The second stage of analysis took the environmental variables and abundance estimates

produced from stage one incorporating them into a piecewise Structural Equation Model

(pwSEM). The pwSEM analysis used the best abundance models or best averaged models based

on AIC and incorporated them as nodes for the pwSEM. Each species composed a single node connected by a causal pathway with directions determined by previous biological knowledge and natural history traits of the ecosystem. Piecewise SEMs were composed using our species and environmental factors and compared using AIC to determine the most parsimonious model. To construct the pwSEM, individual regressions were used for each of the causal pathways, listed in Table S3. These models are all ordinary least squared models, as the low sample size of points (N = 10 study sites) limits our ability to assess if a different family would be more appropriate. According to Cunningham et al. (2020) as each abundance estimate were calculated at the camera grid level, data was not nested and mixed models were not necessary. However, this simplicity may be less than ideal when taking sample size into account (see discussion for more details). Due to low sample size, we expect that the use of ordinary least square models provides an adequate fit to interpret the data without causing undue bias. The advantage of using piecewise SEM rather than classic SEM is its ability to calculate local estimates using individual regression for each pathway in our hypothesized causal network (Grace et al. 2012; Lefcheck 2016; Cunningham et al. 2020). To determine the most parsimonious model for our pwSEM any variables causing warnings were first removed to determine if they had a negative effect on the AIC. After eliminating any variables causing warnings, we used backward stepwise model reduction removing non-significant pathways (a = 0.05) until only significant pathways remained (for the same approach, see Gordon et al. (2017) and Cunningham et al. (2020)). We calculated our R^2 using the "rsq" package in R. Overall fit was assessed for the final pwSEM using Shipley's test of d-separation (Shipley, 2000, 2009). This tested if all unconnected variables are conditionally independent if Fisher's C has a P > 0.05. Likely due to our small sample size our finial pwSEMs did not meet these criteria but was the most parsimonious based on AIC.

Thereby, this pwSEM was considered worth investigating even if lacking sufficient data to support Fisher's C statistic.

<u>Results</u>

Abundance Estimates and Environmental Factors

For each species a detectablity-corrected estimate of abundance was calculated which was subseqently used in our piecewise structural equation model. Variables used in the Royle-Nichols and N-mixture abundance models are listed in Table S2. Estimates and standard errors of abundance produced from the Royle-Nichols and N-mixture abundance models are contained in Table 1 along with means of forest loss integrity index and the mode of the land cover class calculated for each camera grid using QGIS (QGIS Development Team, 2022). For each camera grid (N = 10) there is one estimate of abundance per species, mean of forest loss integrity index with no data corrected to zero as an index of anthropogenic impact, and the modal value of landcover class as a broad scale representation of ecosystem type. Abundance estimates for all species ranged from 2.3349e-06 to 9.095 with a standdard errors ranging from 0.000413 to 1.466 with abundance estimates approaching zero (i.e. 7.1917e-05) representing non-detection of a species in a given study site.

Piecewise Structural Equation Model

Contrary to our primary prediction the final piecewise Structural Equation Model (Fig. 3) shows a mildly negative impact of higher forest integrity on Sunda clouded leopard abundance.

However, in line with our second prediction of mesopredator release we do see estimates of Sunda leopard cat abundance decline strongly with an increase in Sunda clouded leopard abundance and increased forest integrity (Table 2.). Additionally we see Malay civet abundance increasing with the increased abundances of Sunda clouded leopard but decreasing slightly with higher forest integrity. A cascading effect appears to be present between Sunda clouded leopard abundance, Sunda leopard cat abundance, and our three pheasant species. For instance, great argus pheasant abundance shows a negative response to Sunda leopard cat abundance but responds positively to both Malay civet abundance, increased forest integrity, and Sunda clouded leopard abundance. Similarly, Bulwer's pheasant and crested fireback abundance has a negative relationship with Sunda leopard cat abundance but a postive relationship with Malay civet abundance. Bulwer's pheasants also shows a positive relationship with increasing forest integrity and Sunda clouded leopard abundance but crested firebacks do not. Crested fireback, unlike the other two pheasent species, show a negative relationship with Sunda clouded leopard abundance.

Discussion

To our knowledge this is the first study to use a piecewise structural equation model to examine the relationship between mesopredator release and the avifaunal community in a tropical ecosystem. The use of a cross-taxa analysis such as this may help improve our understanding of the complex food webs that make up the diverse and varied ecosystems of tropical ecology. The avifaunal community serve an important role in both natural systems and local economic processes by promoting ecotourism, pollination, and pest control. Understanding how mammalian communities indirectly impact these factors can facilitate more complex and

inclusive management strategies in addition to understanding how they effect avifaunal communities directly. Finally, by understanding how species assemblages are composed, it may be possible to create multi-species conservation strategies that are both financially and logistically strategic.

Within our final piecewise structural equation model our predictions met mixed results, potentially representing separate unmeasured drivers affecting our study species. For instance, the negative relationship between Sunda clouded leopards and forest integrity was counter to our first prediction where we expected decreasing forest integrity due to recently logged or oil palm plantation areas to reduce abundance estimates (Hearn et al., 2018b). However, the increased openness in the forest structure due to logging and tourism trails may have increased larger prey species abundances in lower integrity forests leading to a subsequent increase in the apex predator's abundance (Wearn et al. 2017). Additionally, the result suggests that while the integrity score accounts for increased poaching access the actual poaching pressure may either be lower than expected, less impactful then predicted, or less mechanistically linked to access than expected. Future research should investigate whether the relationship between the forest loss integrity index accurately represents the finer landscape scales that make it up. Another issue that could affect the results is the temporal distance between when our camera traps were set and when the forest integrity index was calculated (6 to 13 years depending on the grid). This mismatch may be the reason for the estimate provided by the linear model being relatively small when compared to our expectations and the strength of other relationships within our pwSEM. The possibility also remains that our grids with low to medium integrity scores act as refuges in an otherwise disturbed landscape, possibly demonstrating higher abundance then that habitat

normally would without the highly disturbed matrix around them. The mild negative effect that forest integrity has on Sunda clouded leopards indicates that the loss of forest integrity, at least to a point, is not the driver of trophic cascades further down in the carnivore community. However, this result does not take into account varibles not included in this model which may better explain forest integrities postive effects on pheasant species but negative effect on Sunda clouded leopards, Sunda leopard cats, and Malay civets.

Similarly, to the effects of forest integrity on Sunda clouded leopards we also see a slightly mild negative relationship with Malay civets. This relationship, like the Sunda clouded leopard, is likely linked to increases in food availability in more mixed forest structures and within palm oil plantations (Evans et al., 2021). The general diet of the Malay civet is composed largely of invertebrates and fruit with a larger proportion of fruit consumed in unlogged forest then in logged forest (Colon & Sugau, 2012). This dietary difference could imply the relationship seen is one that is driven by diversification of food sources rather than increased density of prey like the Sunda clouded leopard. We also see a positive relationship between Malay civet and all three pheasant species. This runs counter to our second prediction that nest predation by civets would reduce pheasant abundance. However, this is potentially explained by civets' dietary preference for fruit in higher integrity forests benefiting pheasants, possibly even outweighing the negative effects of nest predation (Colon & Sugau, 2012). As civets consume larger amounts of fruit in higher integrity forest they may not only act as seed dispersers, increasing seedlings and fruit tree abundance, but also create disturbance in fruiting trees causing fruit to fall to the ground where pheasants can access it thus benefiting pheasants both directly through increasing resource accessibility and indirectly through seed dispersal.

Unlike Sunda clouded leopards and civets, Sunda leopard cats show a much stronger preference for lower integrity forest likely due to their preference for hunting small mammals that often occupy these anthropogenic influenced matrix habitats at higher densities (Hearn et al. 2018b). The relatively strong negative relationship between Sunda leopard cats and Sunda clouded leopard begins to show a possible mesopredator release effect that cascades down into the negative effects Sunda leopard cats seem to have on all three pheasant species. Even though Malay civets have been recorded eating birds, we suspect an obligate carnivore like the Sunda leopard cat would have a larger direct predation impact on these ground dwelling birds. Despite how rare it might be for Sunda leopard cats to take a full-grown pheasant; their increased presence may have additional effects on pheasant behavior that reduces survival.

In addition to the cascading relationships that appears to be an example of mesopredator release, the association between both great argus pheasants and Bulwer's pheasant with Sunda clouded leopard reinforces our hypothesis that this is a cascading effect structured by apex predator abundance. Crested firebacks on the other hand, unlike our other pheasant species, showed no significant response to forest integrity and a negative relationship with Sunda clouded leopards. This negative relationship with Sunda clouded leopards may be a function of exploitation competition as Sunda clouded leopards have a positive effect on our two other pheasant species possibly increasing intraguild competition. We suggest future research focus on niche partitioning and relationships within the avian community as these fine scale mechanisms are outside the scope of this research.

Despite the large number of camera traps used at each study site and relatively long periods the cameras ran, our analysis was ultimately limited by the number of camera grids itself. With only ten grids it is difficult to build reliable and robust models. In addition, the design of the grids was largely organized to facilitate previous fine-scaled studies at the camera trap level. This methodology did not provide an even spread of grids across land cover classes or levels of forest integrity at the broader landscape level. These limitations added to the difficulties of examining the degradation of Sabah forests and the effects of conversion of land to palm oil plantations as a predictive element in our models. Structural equation models and our pwSEMs are very data hungry and thus need large numbers of points to facilitate complex models and even more to accurately represent complex systems such as tropical ecosystems. Originally our study design planned to use estimates from the camera trap level to compare trends in either occupancy or abundance providing over 450 points of references. However, the Royle-Nichols abundance models and N-mixture models require repetition within an area to estimate abundance, thus this methodology cannot be reliably used at the camera trap level. We attempted to use single-season occupancy models, as opposed to abundance models, to increase sample size by examining the data at a finer spatial scale. However, the differences between the covariates used in the best model for each species varied, seemingly causing issues when comparing these occupancy estimates in the final pwSEM. To address these issues, we believe it may be possible to sub-divide camera trap grids and use mixed effect models to increase sample size in future iterations of this project design. Alternatively, the use of a multispecies occupancy model may

provide a finer scale and robust way to estimate the effects of mesopredator release in this community.

While our results suggest the presence of mesopredator release for some of the species in Sabah, Malaysia, we believe the removal of landcover class, due to the warnings within R and lower AIC value after its removal, may have affected these results. We believe the exclusion of landcover class as a bottom-up driver is necessary due to our low sample size. However, incorporating bottom-up effects in the analysis most notably effected the relationship between Sunda clouded leopard abundance and Sunda leopard cat abundance changing it to a non-significant result. We wish to highlight that while we did not have enough data to incorporate landcover class, its impacts may significantly impact the relationships in our ecosystem. The reduction in model complexity by removing landcover class was driven by the belief that a more simplistic model would be appropriate given our data limitations. In future models with more data, we suggest that landcover class be maintained if data can support it and be removed only following the backwards stepwise model reduction method described above. This correlational analysis approach could not document the mechanistic links in such ecological interactions, but it is possible that the theory might not even be applicable to ecosystems like ours (Brodie & Giordano, 2013). However, the empirical results provide novel insights into the links between land use changes and community structure in Sabah, Malaysia that we believe help create a foundation for future studies.

In guiding future research, we propose the continuation of large-scale camera trapping be focused on the urban-wildland and agricultural-wildland interface to better assess how these

human modified landscapes effect the carnivore community of Sabah. In addition to monitoring the anthropogenic extreme of Sabah's ecosystem more focus on the lower and upper mountain regions of the island may aid in our understanding of how these various forest types and elevational gradients influence community structure. While previous camera trapping through this project has used larger grid sizes to enable accurate assessments of a contiguous landscape, we suggest smaller, still robust, camera grids to cover several areas at once rather than one large relatively similar landscape type. We also recommend combining projects across ecological specializations to better address missing pathways in the tropical ecosystem. Specifically, by incorporating fine scale botanical and entomological surveys at the camera trap level. These taxa are difficult to estimate using camera trapping but serve as fundamental pillars in the trophic web making up large percentages of mesopredator diets (Grassman et al., 2005; Colon & Sugau, 2012; Welti et al., 2020). Coordinating multiple projects can be difficult but the detailed snapshot it could provide across landscapes altered by both natural and anthropogenic factors may reveal a much more detailed view of how these changing forests are affecting life in Sabah, Malaysia.

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Tables:

Table 1. Abundance (± SE) measurements derived from the Royle-Nichols and N-mixture abundance models for each focal species in each study site. Camera grids are listed by alphabetic order, forest loss integrity index is the mean of each grid on a scale from 0 (Low) to 10 (High) based on Grantham et al. (2020), Major Landcover class was the mode of landcover for each grid based on Miettinen et al. (2012).

Camera Grid	Major Landcover Class	Forest Loss Integrity Index	Sunda Clouded Leopard	Sunda leopard cat	Malay Civet	Great Argus Pheasant	Bulwer's Pheasant	Crested Fireback
Crocker	Lower montane forest	8.754478	0.6537 (0.1805)	0.5207 (0.1505)	1.593 (0.2560)	2.8873 (0.3737)	0.9091 (0.2018)	0.3776 (0.1199)
Danum Palm	Large-scale palm plantation	5.751941	7.1917e-05 (0.0021)	9.095 (1.466)	4.083 (0.6005)	0.2765 (0.1382)	7.2924e-06 (0.000798)	1.9747 (0.3637)
Danum Valley	Lowland forest	9.791994	0.1979 (0.07116)	1.0928 (0.2030)	0.6623 (0.1130)	0.0769 (0.04452)	1.5990e-05 (0.000705)	1.5687 (0.2038)
IJM	Large-scale palm plantation	2.227400	0.2401 (0.1084)	1.0832 (0.2795)	1.5603 (0.2777)	0.3722 (0.1410)	2.3349e-06 (0.000413)	1.8129 (0.2982)
Kinabatangan	Plantation/ regrowth	3.742337	1.00116 (0.17783)	2.7240 (0.3644)	3.0937 (0.3193)	1.4391 (0.1880)	0.3768 (0.1080)	2.3681 (0.2301)
Malua	Lowland forest	9.318820	0.9641 (0.3534)	0.2537 (0.1162)	3.8147 (0.6195)	9.0873 (0.8767)	2.2897 (0.5084)	4.5735 (0.5778)
Sepilok	Lowland forest	6.659003	0.7987 (0.2243)	1.1871 (0.3081)	4.4884 (0.5912)	6.5553 (0.6725)	0.8570 (0.2904)	2.7906 (0.3973)
Tabin	Lowland forest	8.793230	0.4946 (0.1101)	0.4754 (0.1084)	2.5300 (0.2678)	3.1784 (0.2980)	6.4864e-06 (0.00042)	3.2039 (0.2833)
Tawau	Lowland forest	8.669084	0.7553 (0.1299)	0.4846 (0.0913)	3.2534 (0.2970)	4.1403 (0.3092)	1.4791 (0.1885)	0.4921 (0.09001)
Ulu Segama	Lowland forest	9.150120	0.8259 (0.2890)	0.2770 (0.1243)	2.6464 (0.4831)	7.3419 (0.7523)	1.3537 (0.3493)	1.4792 (0.2868)

Table 2. Piecewise structural equation model's results of the local estimates for each linear regression model that compose the global model. All models were built using Ordinary least squared regressions. Estimates are standardized and P-values are marked as significant at an a = 0.05.

Models	Coefficient (SE)	P-value
Sunda Clouded Leopard Abundance: OLS		
(Intercept)	0.7256	< 2e-16 ***
Forest Loss Integrity Index	-0.0166	0.00378 **
Sunda leopard cat Abundance: OLS		
(Intercept)	5.4782	<2e-16 ***
S. Clouded Leopard Abundance	-2.2211	<2e-16 ***
Forest Loss Integrity Index	- 0.3692	<2e-16 ***
Malay Civet Abundance: OLS		
(Intercept)	1.8241	<2e-16 ***
S. Clouded Leopard Abundance	2.1608	<2e-16 ***
Forest Loss Integrity Index	-0.0690	7.04e-05 ***
Great Argus Pheasant: OLS		
(Intercept)	-3.4750	<2e-16 ***
Sunda Clouded Leopard Abundance	0.7188	0.0074 **
Sunda leopard cat Abundance	-0.7303	<2e-16 ***
Malay Civet Abundance	1.9783	<2e-16 ***
Forest Loss Integrity Index	0.3252	<2e-16 ***
Bulwer's Pheasant: OLS		
(Intercept)	-0.8845	<2e-16 ***
Sunda Clouded Leopard Abundance	1.0331	<2e-16 ***

Sunda leopard cat Abundance	-0.1609	<2e-16 ***
Malay Civet Abundance	0.4433	<2e-16 ***
Forest Loss Integrity Index	0.0803	5.87e-15 ***
Crested Fireback Abundance: OLS		
(Intercept)	1.1258	<2e-16 ***
Sunda Clouded Leopard Abundance	-0.5301	0.0363 *
Sunda leopard cat Abundance	-0.0578	0.0376 *
Malay Civet Abundance	0.3779	6.46e-16 ***

Figures:

Figure 1. Forest integrity has declined rapidly due to palm oil plantations and related human influences across Southeast Asia. This graph depicts our, *a-prior* Structural Equation Model and the potential restructuring of the Sabah carnivore community following forest integrity loss and its subsequent effects on pheasant species community.
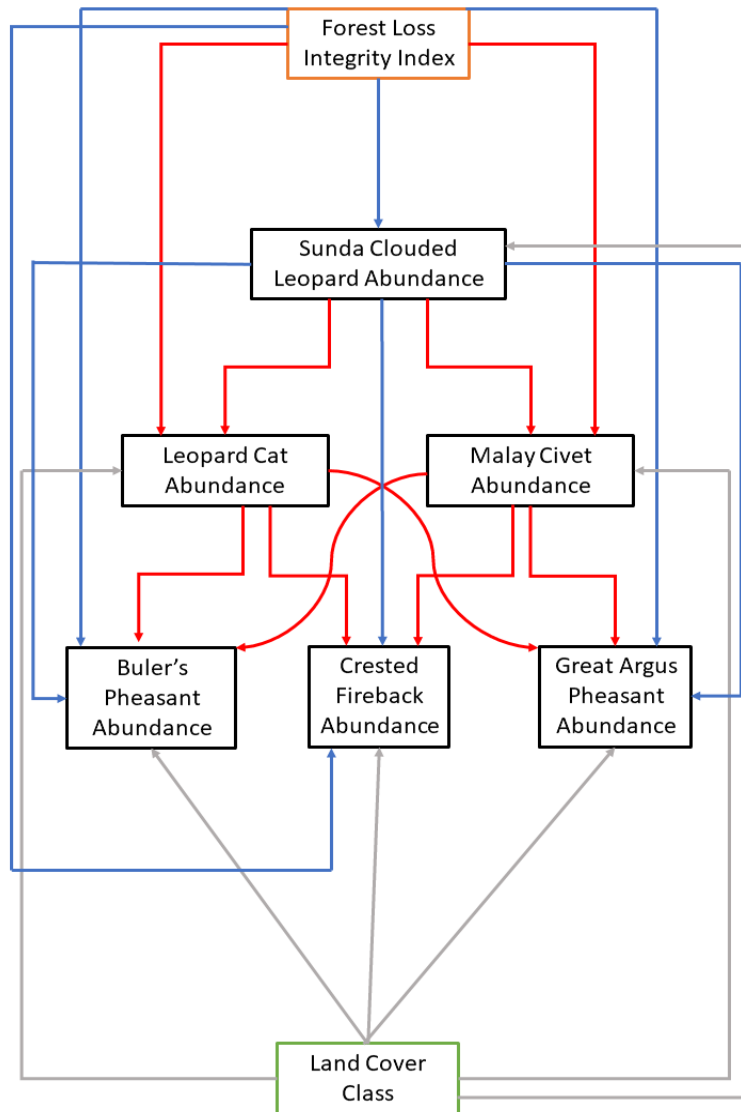
Figure 2. Camera trap grid regions are depicted as red outlines. Grids names are as follows: 1.

Crocker, 2. Danum Palm, 3. Danum Valley, 4. IJM, 5. Kinabatangan, 6. Malua, 7. Sepilok, 8.

Tabin, 9. Tawau, 10. Ulu Segama. Land cover classes are based on the Miettinen, J., Shi C., Tan

W.J. and Liew S.C. 2012. 2010 land cover map of insular Southeast Asia in 250m spatial

resolution. Remote Sensing Letters 3: 11-20. DOI: 10.1080/01431161.2010.526971.
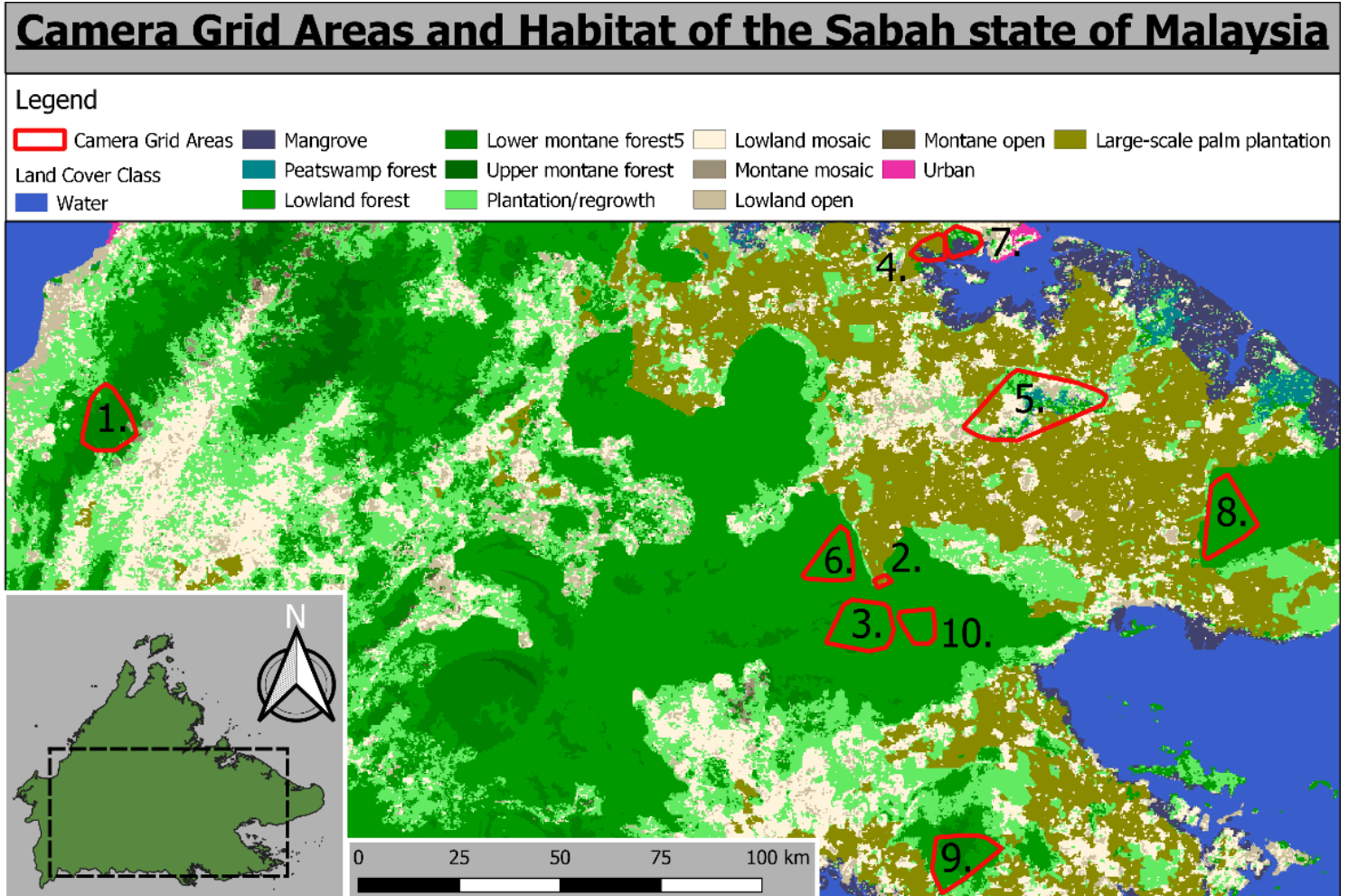
Figure 3. Our finial piecewise structural equation model showing Sunda clouded leopards and forest integrity have a trophic cascading effect on Sunda leopard cats and subsequently pheasant species. Nodes are our species of interest and the forest loss integrity index extracted from Grantham et al.'s (2020) study on global forest integrity. All lines represent significant pathways from our most parsimonious pwSEM at an alpha level of a = 0.05, with blue lines representing positive relationships and red lines representing negative relationships. Line thickness increased with coefficient size and stars representing p-value significance. P < 0.05 *, P < 0.01 **, P < 0.001 ***. Raw coefficients for each species modeled in our pwSEM are listed in Table 1.
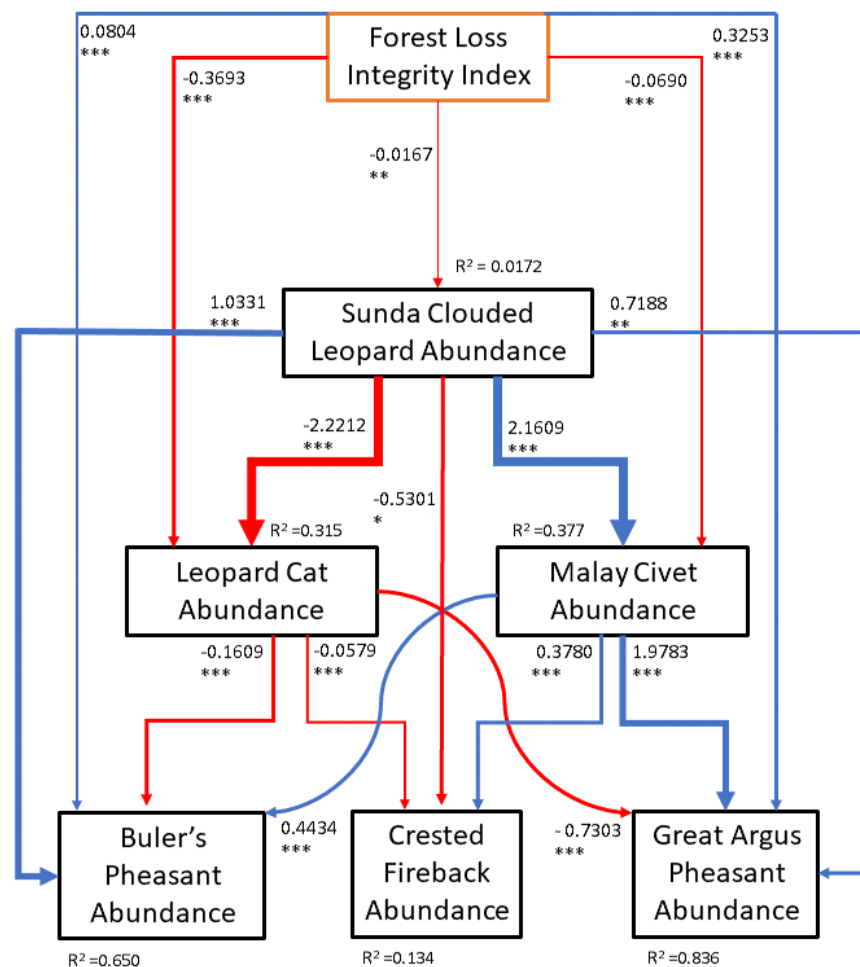
Text Boxes:

Box 1. Sabah's carnivore ecosystem and its effects of pheasants. An *a priori* prediction of the community structure governing possible mesopredator release.

Based on the mesopredator release hypothesis and trophic cascade theory we predict that a decline in Sunda Clouded Leopards (12 - 26 kg) abundance, triggered by a reduction in forest integrity, will have a cascading effect on both Sunda leopard cats (2–3.6 kg) and Malay civets (5.6 - 6.6 kg) who are the most common species in each of their respective guilds occurring on our camera traps (Grassman et al., 2005; Jennings et al., 2010; Hearn et al., 2013;). Subsequently we expect a cascading impact on great argus pheasant (1.59 -1.7 kg), Bulwer's pheasant (0.916 - 1.8 kg), and crested firebacks (1.6 – 2.6 kg) reducing their respective abundances through direct predation and nest predation (Duffey, 1996; Bulwer's pheasant, 2022; Crested Fireback, 2022). Sunda leopard cats strongly prefer habitat with low forest integrity which suggests that as forest integrity declines, we expect higher Sunda leopard cat abundance predating on a naive prey base. Malay civets as one of the most common and adaptable civets' species have been documented predating on birds among more common prey suggesting they may also pose a threat to ground dwelling pheasants. We do not believe Sunda leopard cats and Malay civets will directly impact each other's abundance as they are in relatively the same weight class that minimizes intra-guild predation and civets tend to be more omnivores reducing possible resource competition.

Land cover class and forest integrity index were included to account for top-down disturbance as well as bottom-up productivity differences between study sites on species abundance estimates.

Landcover class may also help account for moisture and elevational differences in study sites which could affect primary producers, prey densities, and subsequent predator abundances.

Selection of species was based primarily on number of observations which allowed accurate estimates of abundance and secondly on providing representatives from important guilds without overwhelming our model. We also wanted to included species we knew were both obligate carnivores in addition to omnivores to distinguish how these two diets impacted possible mesopredator release. Malay civets were also favored in our species selection as possible nest predators who could represent a common widespread effect on reproductive success to pheasants.

Supplementary Tables:

Supplementary Table 1. The number of individual photos for species within the carnivore community broken up by guild and trophic level. Species occurrence across all cameras varied by relative rarity which is represented by how many photos were accumulated over the seven-year period.

Common Name	Scientific Name	Trophic Level	Family	Number of Independent Photos
Sunda Clouded Leopard	*Neofelis diardi*	Apex Predator	Felidae	518
Sun Bear	*Helarctos malayanus*	Apex Predator	Ursidae	807
Domestic Dog	*Canis familiaris*	Apex Predator	Canidae	5
Sunda Leopard Cat	*Prionailurus javanensis*	Mesopredator	Felidae	1811
Marbled Cat	*Pardofelis marmorata*	Mesopredator	Felidae	188
Bay Cat	*Catopuma badia*	Mesopredator	Felidae	40
Domestic Cat	*Felis catus*	Mesopredator	Felidae	27
Flat-headed cat	*Prionailurus planiceps*	Mesopredator	Felidae	3
Malay civet	*Viverra tangalunga*	Mesopredator	Viverridae	5586
Banded Palm Civet	*Paradoxurus hermaphroditus*	Mesopredator	Viverridae	2245
Masked palm civet	*Paguma larvata*	Mesopredator	Viverridae	215
Hose's civet	*Diplogale hosei*	Mesopredator	Viverridae	211
Banded linsang	*Prionodon linsang*	Mesopredator	Viverridae	99
Binturong	*Arctictis binturong*	Mesopredator	Viverridae	51
Banded civet	*Hemigalus derbyanus*	Mesopredator	Viverridae	6
Small-toothed palm civet	*Arctogalidia trivirgata*	Mesopredator	Viverridae	6
Short-tailed mongoose	*Herpestes brachyurus*	Mesopredator	Mustelidae	674
Yellow-throated Marten	*Martes flavigula*	Mesopredator	Mustelidae	278

Collared Mongoose	*Herpestes semitorquatus*	Mesopredator	Mustelidae	143
Malay weasel	*Mustela nudipes*	Mesopredator	Mustelidae	29
Ferret badger	*Melogale everetti*	Mesopredator	Mustelidae	8
Malay badger	*Mydaus javanensis*	Mesopredator	Mephitidae	413

Supplementary Table 2: Abundance model selection using both the Royle-Nichols model of abundance for Sunda clouded leopard, Sunda leopard cat, Malay civet and N-mixture model of abundance for great argus pheasant, Bulwer's pheasant, and crested fireback. Both model types estimate abundance as well as detection probability. We present models for each species with ΔAIC less than 2, as well as the null model.

Species	Detection	Abundance	Number of Parameters	AICc	ΔAICc	AICc Weight
Sunda Clouded Leopard: Royle-Nichols						
	~ Effort + Forest Road	~ Camera Grid	13	1819.363	0.000	4.103902e-01
	~ Effort	~ Camera Grid	12	1819.999	0.636	2.985181e-01
	~ Effort + Forest Road + Ridge	~ Camera Grid	14	1820.967	1.604	1.839805e-01
	~ 1	~ 1	2	1874.015	54.652	0.0000
Sunda leopard cat: Royle-Nichols						
	~ Effort	~ Camera Grid	12	1973.810	0.000	4.864236e-01
	~ Effort + Forest Road	~ Camera Grid	13	1975.183	1.373	2.448015e-01
	~ Effort + Ridge	~ Camera Grid	13	1975.787	1.977343	1.809839e-01
	~ 1	~ 1	2	2211.578	237.768	0.0000
Malay Civet: Royle-Nichols						
	~ Effort + Ridge	~ Camera Grid	13	6177.291	0.000000	4.169403e-01
	~ Effort	~ Camera Grid	12	6178.381	1.090316	2.417213e-01
	~ Effort + Forest Road + Ridge	~ Camera Grid	14	6178.677	1.386740	2.084237e-01
	~ 1	~ 1	2	6490.977	313.686	0.0000
Great Argus Pheasant: N-Mixture						

~ Effort	~ Camera Grid	12	6411.104	0.000000	4.717765e-01
~ Effort + Forest Road	~ Camera Grid	13	6412.291	1.187138	2.605868e-01
~ Effort + Ridge	~ Camera Grid	13	6413.093	1.988980	1.745158e-01
~ 1	~ 1	2	7137.238	726.134	0.0000
Bulwer's Pheasant: N-Mixture					
~ Effort + Forest Road + Ridge	~ Camera Grid	14	2024.15	0.000	5.3e-01
~ Effort + Ridge	~ Camera Grid	13	2024.35	0.20	4.7e-01
~ 1	~ 1	2	2304.464	280.314	0.000
Crested Fireback: N-Mixture					
~ Effort + Ridge	~ Camera Grid	13	4710.765	0.000	5.575849e-01
~ Effort + Forest Road + Ridge	~ Camera Grid	14	4711.294	0.529	4.279885e-01
~ 1	~ 1	2	5062.078	351.313	0.000

Supplementary Table 3. Model structures of pathways that compose the finial piecewise structural equation model. Model types were restricted to ordinary least squared models only as the sample size was too small for other model types to be used. These models represent the most parsimonious models for our data given our limited flexibility.

Response Variable	Predictor Variable	Model Type
Sunda Clouded Leopard Abundance (SCL Abund)	Forest Loss Integrity Index Grid Mean (flii)	Ordinary least squares
Sunda leopard cat Abundance (LC Abund)	SCL Abund + flii	Ordinary least squares
Malay Civet (MC Abund)	SCL Abund + flii	Ordinary least squares
Great Argus Pheasant	SCL Abund + LC Abund + MC Abund + flii	Ordinary least squares
Bulwer's Pheasant	SCL Abund + LC Abund + MC Abund + flii	Ordinary least squares
Crested Fireback	SCL Abund + LC Abund + MC Abund + flii	Ordinary least squares