



Evaluating Multispecies Landscape Connectivity in a Threatened Tropical Mammal Community

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Abstract: *Habitat corridors are important tools for maintaining connectivity in increasingly fragmented landscapes, but generally they have been considered in single-species approaches. Corridors intended to facilitate the movement of multiple species could increase persistence of entire communities, but at the likely cost of being less efficient for any given species than a corridor intended specifically for that species. There have been few tests of the trade-offs between single- and multispecies corridor approaches. We assessed single-species and multispecies habitat corridors for 5 threatened mammal species in tropical forests of Borneo. We generated maps of the cost of movement across the landscape for each species based on the species' local abundance as estimated through hierarchical modeling of camera-trap data with biophysical and anthropogenic covariates. Elevation influenced local abundance of banded civets (*Hemigalus derbyanus*) and sun bears (*Helarctos malayanus*). Increased road density was associated with lower local abundance of Sunda clouded leopards (*Neofelis diardi*) and higher local abundance of sambar deer (*Rusa unicolor*). Pig-tailed macaque (*Macaca nemestrina*) local abundance was lower in recently logged areas. An all-species-combined connectivity scenario with least-cost paths and 1 km buffers generated total movement costs that were 27% and 23% higher for banded civets and clouded leopards, respectively, than the connectivity scenarios for those species individually. A carnivore multispecies connectivity scenario, however, increased movement cost by 2% for banded civets and clouded leopards. Likewise, an herbivore multispecies scenario provided more effective connectivity than the all-species-combined scenario for sambar and macaques. We suggest that multispecies habitat connectivity plans be tailored to groups of ecologically similar, disturbance-sensitive species to maximize their effectiveness.*

Keywords: animal movement, Borneo, dispersal, fragmentation, habitat corridor, Heart of Borneo, logging, multispecies conservation

Evaluación de la Conectividad de Terrenos Multiespecie en una Comunidad Tropical de Mamíferos

Resumen: *Los corredores de hábitats son herramientas importantes para mantener la conectividad en terrenos cada vez más fragmentados, pero generalmente se ha considerado que solo son usados en estrategias para especies individuales. Los corredores que pretenden facilitar el movimiento de especies múltiples podrían aumentar la persistencia de comunidades enteras con el costo probable de ser menos eficientes para cualquier*

especie dada que un corredor pretendido específicamente para esa especie. Ha habido pocas pruebas de los pros y contras de las estrategias de corredores para una o para múltiples especies. Evaluamos los corredores de hábitat para una especie y para múltiples especies de cinco especies amenazadas de mamíferos en los bosques tropicales de Borneo. Generamos mapas del costo de los movimientos a lo largo del terreno para cada especie con base en las abundancias locales de cada especie, estimadas con modelos jerárquicos de datos de foto-trampas con co-variables biofísicas y antropogénicas. La elevación influyó la abundancia local de las civetas listadas (*Hemigalus derbyanus*) y los osos malayos (*Helarctos malayanus*). La densidad incrementada de carreteras estuvo asociada con una menor abundancia local de leopardos nublados de Sunda (*Neofelis diardi*) y una abundancia local más alta para el venado sambar (*Rusa unicolor*). La abundancia local del macaco cola de cerdo (*Macaca nemestrina*) fue más baja en áreas taladas recientemente. Un escenario de conectividad de todas las especies, con caminos de bajo costo y 1 Km de amortiguamiento generó costos de movimiento total que fueron 27% y 23% más altos para las civetas listadas y los leopardos nublados, respectivamente, que el escenario de conectividad para esas especies individuales. Un escenario de conectividad de múltiples especies carnívoras, sin embargo, incrementó el costo de movimiento por 2% para las civetas listadas y los leopardos nublados. A la vez, un escenario de múltiples especies herbívoras proporcionó una conectividad más efectiva que el escenario de todas las especies combinadas para los venados y los macacos. Sugerimos que los planes de conectividad de hábitats de especies múltiples sean a la medida para grupos de especies ecológicamente similares y sensibles a las perturbaciones, para así maximizar su efectividad.

Palabras Clave: Borneo, conservación multiespecie, Corazón de Borneo, corredor de hábitats, dispersión, fragmentación, movimiento animal, tala

Introduction

As landscapes around the world become increasingly fragmented, conservationists strive to retain or recreate linkages between remnant habitat patches. Strips of high-quality habitat (i.e., corridors) connect remnant patches or protected areas such as national parks (Soule & Terborgh 1999). Meta-analysis confirms the importance of habitat connectivity for maintaining species across systems (Prugh et al. 2008). Habitat corridors may also allow species to track their fundamental niches in geographic space as climate changes (Brodie et al. 2012; Cross et al. 2012). However, most corridor planning initiatives focus on single species (Beier et al. 2008; Beier et al. 2011).

Because so many species are threatened by fragmentation, habitat corridors may more effectively protect regional biodiversity if they are developed to support the movement of multiple species simultaneously, rather than movement of one single species (Beier et al. 2008). However, it remains unclear how to do this. A common approach is to protect patches or corridors that support one or several wide-ranging, often large-bodied, species and assume that conservation of these umbrella species will also facilitate conservation of smaller or less mobile organisms (e.g., Noon et al. 2009; Baguette et al. 2013). For example, landscape models based on graph theory suggest that groups of habitat patches identified for relatively wide-ranging species can support connectivity of species with shorter dispersal distances (Estrada & Bodin 2008). These approaches, however, may not always lead to practical conservation solutions. Small-bodied species may have very different connectivity requirements than larger species (Minor & Lookingbill 2010). Patterns of habitat selection among wide-ranging and more localized

species may be correlated in some cases (Epps et al. 2011) and uncorrelated in others (Brodie & Giordano 2013). An alternative approach is to assess connectivity separately for each species and then overlay the corridor maps to identify locations important to multiple species (Urban et al. 2009). Although this approach seems promising, to our knowledge it has not been empirically evaluated.

No 2 species use or navigate through an area in identical ways. Thus, multispecies connectivity planning strategies are likely to present trade-offs relative to single-species strategies. One advantage of multispecies strategies is that in general they should be more efficient than single species strategies at protecting biodiversity and entire communities (Early & Thomas 2007; Carroll et al. 2010; Schwenk & Donovan 2011). A possible disadvantage of a multispecies strategy is that it could be less effective for a particular species than a strategy designed specifically for that species. But the question is, how much worse?

We assessed the efficacy of single and multiple species connectivity scenarios for threatened mammals in Borneo. Rainforest ecosystems in this region are among the most biologically diverse in the world but are threatened by deforestation, forest fragmentation, and harvest of a variety of species (Corlett 2009). Brunei, Indonesia, and Malaysia, the 3 nations that span the island of Borneo, have many protected areas (e.g., national parks, wildlife reserves) on the island (IUCN & UNEP 2009). But, as in many parts of the world, it is likely that few of these protected areas are big enough on their own to support populations of large-bodied, wide-ranging mammals (Woodroffe & Ginsberg 1998). This is of particular concern given the rapid predicted expansion of oil palm and other monoculture plantations into currently

forested areas in Sarawak (FAO 2002, unpublished data; USDA 2011). Therefore, to prevent the erosion of diversity that occurs in isolated forest patches (Laurance et al. 2011), protected areas in Borneo need to have the connectivity between them maintained. Of course, proper management of the protected areas themselves is also important; unsustainable hunting (Nijman 2004) and illegal road incursion and logging (Curran et al. 2004) are rife in many Bornean parks. Nevertheless, protected areas under proper management can provide crucial habitat for threatened tropical vertebrates (Bruner et al. 2001; Brodie et al. 2009).

Our overall goal was to compare the efficacy of multispecies connectivity scenarios relative to single-species connectivity scenarios in a protected area network in Borneo. We mapped potential dispersal and corridor locations for threatened mammals using empirical estimates of local abundance determined from noninvasive wildlife sampling across the study region.

Methods

Study Region

Our focal region was the Malaysian state of Sarawak and adjacent protected areas (i.e., on the Sarawak border) in Sabah, Indonesia, and Brunei. We used the land cover map of Miettinen et al. (2012) to delimit our study area as that portion of central Sarawak and adjacent protected areas that contained contiguous forest. The study region covered 88,297 km² and ranged from 12 to 2225 m in elevation, 0.627 to 4.920° latitude, and 111.724 to 116.215° longitude (Fig. 1). The study region contained 8 protected areas or groups of adjacent protected areas: a complex consisting of Betung Kerihun National Park, Indonesia (established 1992), Batang Ai National Park, Sarawak (established 1991), and Lanjak Entimau Wildlife Reserve, Sarawak (7871 km² combined); Hose Mountains and Batu Laga, Sarawak (proposed national parks, 497 km²); Usun Apau, Sarawak (proposed national park, 546 km²); Kayan Mentarang National Park, Indonesia (675 km²); Pulong Tau, Sarawak (proposed national park, 676 km²); Gunung Mulu National Park, Sarawak (555 km²); Ulu Temburong, National Park, Brunei (established 1991, 499 km²); and Maligan Virgin Jungle Reserve, Sabah (established 1984, 93 km²).

The study region was in humid tropical rainforest. Forests in Borneo are generally tall (40–60 m canopy) and dominated by dipterocarp trees at low elevations and are shorter and increasingly dominated by Fagaceae, Lauraceae, and Myrtaceae in hills and mountains (Corlett 2009). Average annual rainfall throughout the study region exceeds 2000 mm. Further details on the climate, soils, topography, and biota of the study region, as well as on the protected areas within it, are in Hazebroek and Morshidi (2001). Outside protected areas, selective

logging (hereafter logging) is common within the study region. Extraction data from logging are not publicly available in Malaysia, but harvest is often on the order of 10–15 trees above 60 cm diameter/ha (G. Reynolds, personal communication). There are small-holding oil palm plantings within the study area but few large-scale (>10 ha) plantations.

Field Sampling

We deployed Reconyx and Bushnell digital camera traps in 7 study areas in Malaysian Borneo from 2010–2012 inside and outside of protected areas, with the goal of using detection data to measure habitat use by different mammal species and in turn to assess landscape connectivity. The areas we surveyed were Maliau Basin Conservation Area (Sabah), the Ulu Padas region (unprotected area in Sabah), Hose Mountains, Gunung Mulu, and Pulong Tau National Parks, and the Ulu Baram and Ulu Trusan regions (unprotected areas in Sarawak). We deployed camera traps at 153 locations across these areas. After accounting for camera failures and thefts, we retrieved data from 134 locations. Seventy-eight (58%) of these sites were in protected areas, 56 (42%) were in unprotected areas, 84 (63%) were in unlogged forest, and 50 (37%) were in logged forest. Study areas were accessed by river (via longboat) or road, followed by hiking on foot, often for several days. We selected camera locations to span gradients in elevation and to represent multiple forest conditions (e.g., inside and outside protected areas, logged vs. unlogged forests), while striving for an approximate 1 km minimum spacing between cameras. All camera locations were chosen with no prior knowledge of animal presence, absence, abundance, or diversity. Cameras were generally attached to the base of trees about 30–50 cm aboveground. We set the trigger sensitivity to high for each camera. We did not use baits or lures. Generally cameras were operational for 3–6 months. Camera locations ranged in elevation from 70 to 1815 m.

Out of the >30 mammal species we detected with the camera traps, we selected a subset with which to conduct our connectivity and corridor analyses. Criteria for selection included widespread distribution, which excluded banteng (*Bos javanicus*) and elephants (*Elephas maximus*) with their highly restricted ranges in Borneo; local residents, which excluded bearded pigs (*Sus barbatus*), whose movements to track dipterocarp fruits (Curran & Leighton 2000) could have added substantial unexplained variance to our occurrence data; minimum threshold of conditional detectability, arbitrarily set at 10%; and some threat level on the International Union for Conservation of Nature Red List (IUCN 2013), such as near threatened, vulnerable, or endangered. Based on these criteria, the species for which we analyzed connectivity were the banded civet (*Hemigalus derbyanus*), Sunda clouded leopard (*Neofelis diardi*), pig-tailed macaque (*Macaca nemestrina*), sambar (*Rusa unicolor*), and sun

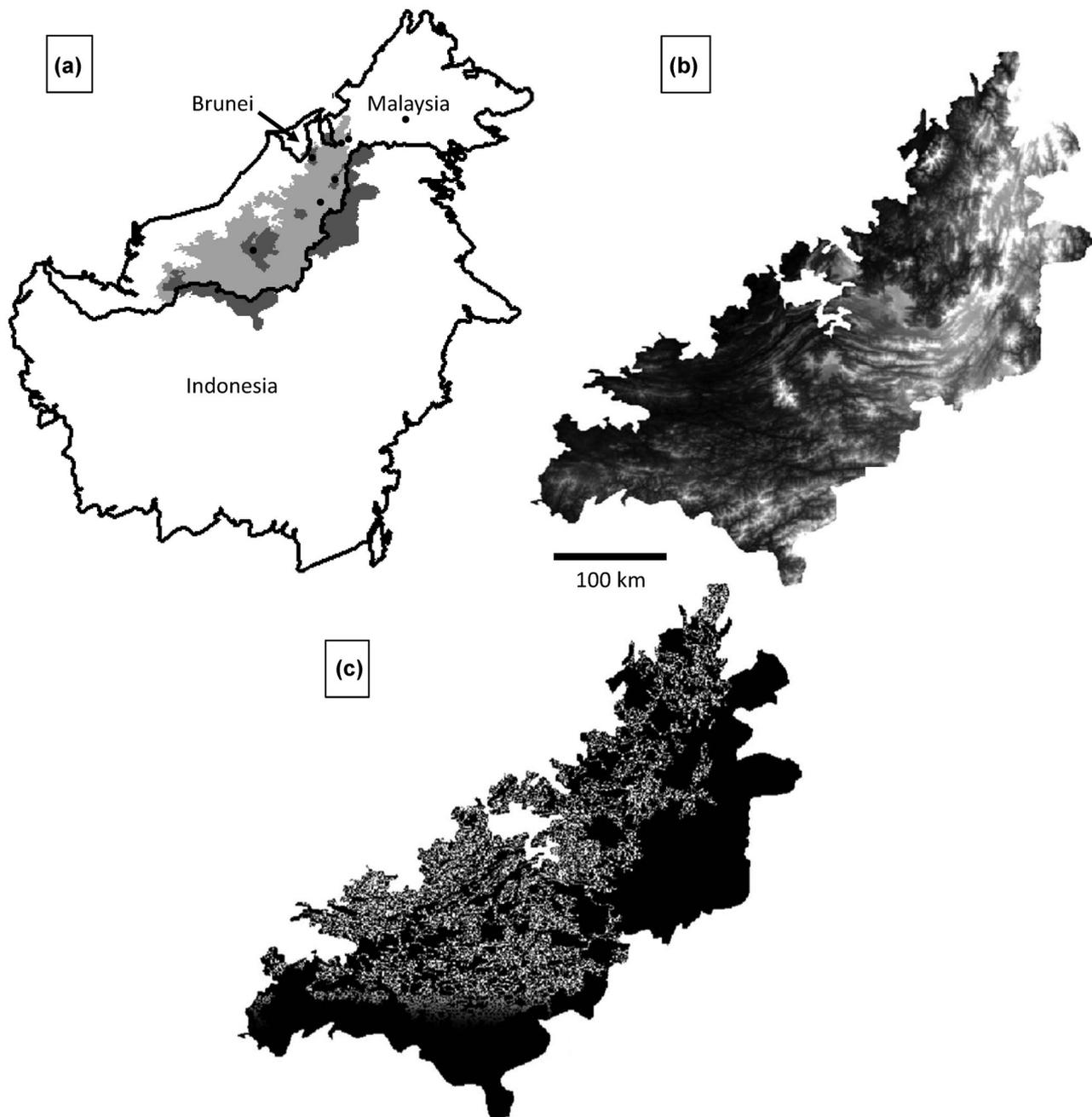


Figure 1. (a) Study region (light gray) and protected areas within it (dark gray) in Borneo (black dots, locations of camera trapping). (b) Elevation within the study region, ranging from <20 m (black) to >2000 m (white). (c) Road density in the study region, ranging from 0 (black) to >1.5 (white) km/km². The 100 km scale bar applies to maps (b) and (c).

bear (*Helarctos malayanus*) (Supporting Information). Each species is listed vulnerable with “decreasing” populations (IUCN 2013).

Local Abundance Analyses

We estimated the average local abundance (number of individuals at each camera trap location) of each species by applying hierarchical *N*-mixture models to the cam-

era trap data to quantify the factors related to local abundance while accounting for imperfect detectability (Royle 2004). These models assume local abundance is proportional to detectability (though both abundance and detectability can covary with other factors as well; we discuss these covariates below) and use the number of detections observed per sampling period to estimate abundance and detection probability. We used elevation, road density, and logging as abundance covariates.

Elevation was included because it is the strongest natural driver of variation in forest composition in the region (Culmsee & Leuschner 2013) and is tightly and negatively related to temperature. We also included a quadratic term for elevation (elevation²) to account for nonlinear responses of abundance to elevation. Road density (km/km²) was estimated from data supplied by World Wildlife Fund Malaysia. Our logging covariate was a binary metric of whether each site had been selectively logged <10 years previously. (In another analysis, we found strong impacts of recent logging on mammal occurrence but substantially weaker impacts of logging that occurred more than a decade ago; J.F.B., unpublished data.) We grouped sampling into 55-day sampling increments to increase detectability (because many of the species were uncommon) and stopped sampling after 6 months (thirty-six 55-d increments). Continuous variables were standardized to have mean = 0 and variance = 1. All models also included study area as a categorical fixed effect (7 levels) to reduce bias from spatial autocorrelation due to our clustered sampling design (Fieberg et al. 2010). We used 4 detection covariates: number of days since camera deployment, number of hours per sampling increment that each camera was operational, camera model (binary for Reconyx vs. Bushnell), and a binary metric of whether the camera was on a game trail.

We used an information-theoretic approach and multimodel inference to assess the effect of environmental factors (covariates) on species-specific local abundance. For each species, we constructed 192 models that represented all combinations of the abundance and detection covariates. We estimated beta coefficients and computed Akaike's information criterion (AIC) for each model. Covariates were considered important factors in local abundance of a particular species if the model-averaged 95% confidence intervals (CI; weighted average across all 192 models) of their coefficients did not include zero.

We developed spatial maps of predicted local abundance for each species with model-averaged beta coefficients. For a lattice of 1 km² grid cells overlaid on the study region, we predicted the local abundance of each species in each cell based on the cell's average elevation and road density and the cell's estimated probability of having been recently logged (i.e., <10 ago) based on discriminant analysis of remote sensing data (Supporting Information). For each cell in each model, predictions were weighted according to the AIC weight of that model.

Corridor Analyses

We used the spatial maps of predicted local abundance to generate least-cost path (LCP) corridors for each species. In this case, LCPs are the paths between 2 protected areas that cost and individual the least to traverse. We used the inverse of local abundance as a measure of movement

cost for each, rescaled from 1 (lowest cost) to 101. We used Linkage Mapper software (McRae & Kavanagh 2011) to determine the position of LCP locations that connected protected areas across the cost landscape. We used the cost-weighted and Euclidean network analysis method and pruned the network to 2 connected nearest neighbors. LCP are one-dimensional, and there are no clear methods to determine the optimum width for corridors (Beier et al. 2008; Sawyer et al. 2011). Therefore, we used 2 corridor width scenarios: we buffered the LCPs by 1 km to define corridors that are narrow relative to their length and 5 km to define corridors that are wide enough to support several territories of wide-ranging species, based on average home range size for mainland clouded leopards (*Neofelis nebulosa*) (Grassman et al. 2005). This latter scenario is considered important for territorial species so that individual territories within the corridor do not take up the entire corridor and prevent use of the corridor by nonresidents (Beier et al. 2008).

We used the single species cost landscapes to quantify connectivity scenarios for combinations of species. We standardized the unscaled costs for each species and then summed these standardized scores into combinations including all carnivores (sum of banded civet, clouded leopard, and sun bear), all herbivores (sum of pig-tailed macaque and sambar), all species except sambar (because sambar had very different responses to forest conditions than the other species; see Results), and all species. We then rescaled these sums to range from 1 to 101. In all cases (single- and multiple-species connectivity scenarios) cost was set to 1 within protected areas and 101 in unforested areas (from Miettinen et al. 2012). While conditions varied even within protected areas (e.g., some have been logged), we assumed that over time forests within protected areas would eventually provide habitat that would not impede the movement of large mammals.

Drawing on the above model sets, we compared the effectiveness of different single- and multispecies connectivity scenarios, defined here as the cumulative cost of grid cells within buffered LCP habitat corridors. To compare the effectiveness of the different connectivity scenarios for each species, we generated metrics of landscape connectivity for each species-scenario combination by calculating the cumulative cost of all cells in all buffered LCPs across the landscape. This allowed us to compare, for example, how the cumulative landscape cost to movement for clouded leopards would change under connectivity scenario designed for all of the species combined as opposed to a scenario optimized for clouded leopards themselves. We pruned the LCP networks to the subset that was common among all species and multispecies combinations. While this approach could underestimate connectivity for a particular species and would not be used in a final corridor planning process, it made it possible to compare the effectiveness of corridor scenarios in a standardized fashion.

Circuit Analyses

To complement the corridor analysis with LCP, we conducted a connectivity analysis based on concepts from electronic circuit theory (McRae et al. 2008). We used the maps of movement cost for each species and multispecies combination discussed above as maps of resistance. We used Circuitscape software (v3.5; McRae & Shah 2011) to assess how individual animals (i.e., current) would move across each landscape and mapped connectivity for each species and multi-species combination. That is, for each resistance map, we calculated the flow of current between each pairwise combination of protected areas and summed overall results to create an estimate of cumulative current across the landscape.

For each species or multispecies combination, we ranked all pixels across the study area in terms of cumulative current flow and selected the top 1% of pixels, 883 km². This figure was chosen arbitrarily, but it is equivalent to a medium-sized national park and therefore seems a reasonable amount of area for additional protection. We then used the sum of the cumulative current across the top 1% of pixels as a measure of landscape connectivity for each species. We assessed how connectivity for a particular species would change when using connectivity scenarios designed for other species, or multispecies combinations, relative to a connectivity strategy optimized for that particular species.

Results

Local Abundance

Elevation affected all 5 species. Banded civet local abundance was lower at middle elevations (~500–1000 m) than in low and high elevations (elevation: model-averaged $\bar{\beta}$ 0.77, 95% CI = 0.20–1.34; elevation²: $\bar{\beta}$ 1.10, CI = 0.68–1.51; Fig. 2). Clouded leopard local abundance increased linearly as elevation increased ($\bar{\beta}$ (0.52, CI = 0.15–0.90), but the effect was slight (Fig. 2). Macaque local abundance peaked at middle elevations (elevation: $\bar{\beta}$ –0.24, CI = –0.40 to –0.07; elevation²: $\bar{\beta}$ –0.27, CI = –0.40 to –0.15). Sambar local abundance was slightly lower at middle elevations (elevation: $\bar{\beta}$ –0.27, CI = –0.63 to 0.09; elevation²: $\bar{\beta}$ 0.27, CI = –0.40 to –0.15). In general, sun bear local abundance increased as elevation increased, but not linearly (elevation: $\bar{\beta}$ 1.23, CI = 0.77–1.70; elevation²: $\bar{\beta}$ –0.30, CI = –0.55 to –0.06).

Roads and recent logging affected species differently. Increased road density was associated with reduced local abundance of clouded leopards ($\bar{\beta}$ (–0.38, CI = –0.75 to –0.01; Fig. 2) but higher local abundance of sambar ($\bar{\beta}$ (0.55, CI = 0.39–0.72). Road density did not have much effect on local abundance of the other species. Newly logged areas had lower average local abundance of macaques ($\bar{\beta}$ (–0.68, CI = –1.10 to –0.27) but was not

highly related to local abundance of the other species. Road density was only weakly correlated with recent logging ($R = 0.25$) and elevation ($R = -0.29$).

Corridor

Maps of landscape cost across the study region differed greatly across species, reflecting their differential responses to environmental covariates. For example, cost maps for clouded leopards and sambar showed clear positive and negative (respectively) effects of road density on cost (Supporting Information). Landscape cost for sun bear was tightly linked to elevation, while macaque cost was fairly constant across the landscape. The multispecies composites of these cost maps resulted in the location of corridors that were fairly consistent between some sets of protected areas but quite variable among other sets of protected areas. For example, the location of the LCP corridor connecting the Hose Mountains and Batu Laga protected area complex to the Betung Kerihun complex was relatively unchanged across multispecies connectivity scenarios (Fig. 3 & Supporting Information), but the corridor connecting Usun Apau to Kayan Mentarang was in almost completely different locations in the all-carnivores versus all-herbivores connectivity scenarios.

In general the multispecies connectivity scenarios increased total cost of the corridors for particular species relative to the connectivity scenarios derived for each species alone (Table 1). Connectivity scenarios based on smaller subsets of species performed better for those species than scenarios based on larger subsets or all of the species. For example, compared with a single-species 1-km buffer-corridor scenario optimized for banded civets the cumulative cost of all corridor pixels increased 27% with the all-species connectivity scenario and increased 2% with the all-carnivores scenario.

Circuit

The results of the circuit analyses were qualitatively similar to those of the LCP corridor analyses. The carnivore multi-species connectivity scenario was more efficient than the herbivores or all-species scenarios at supporting connectivity for each of the 3 carnivore species (Table 2 & Supporting Information). Likewise, the herbivore scenario was more efficient than the other multispecies scenarios at supporting movement for pig-tailed macaques and sambar.

Discussion

Our goal was to assess the relative effectiveness of multispecies connectivity scenarios relative to single-species scenarios in terms of their likelihood of

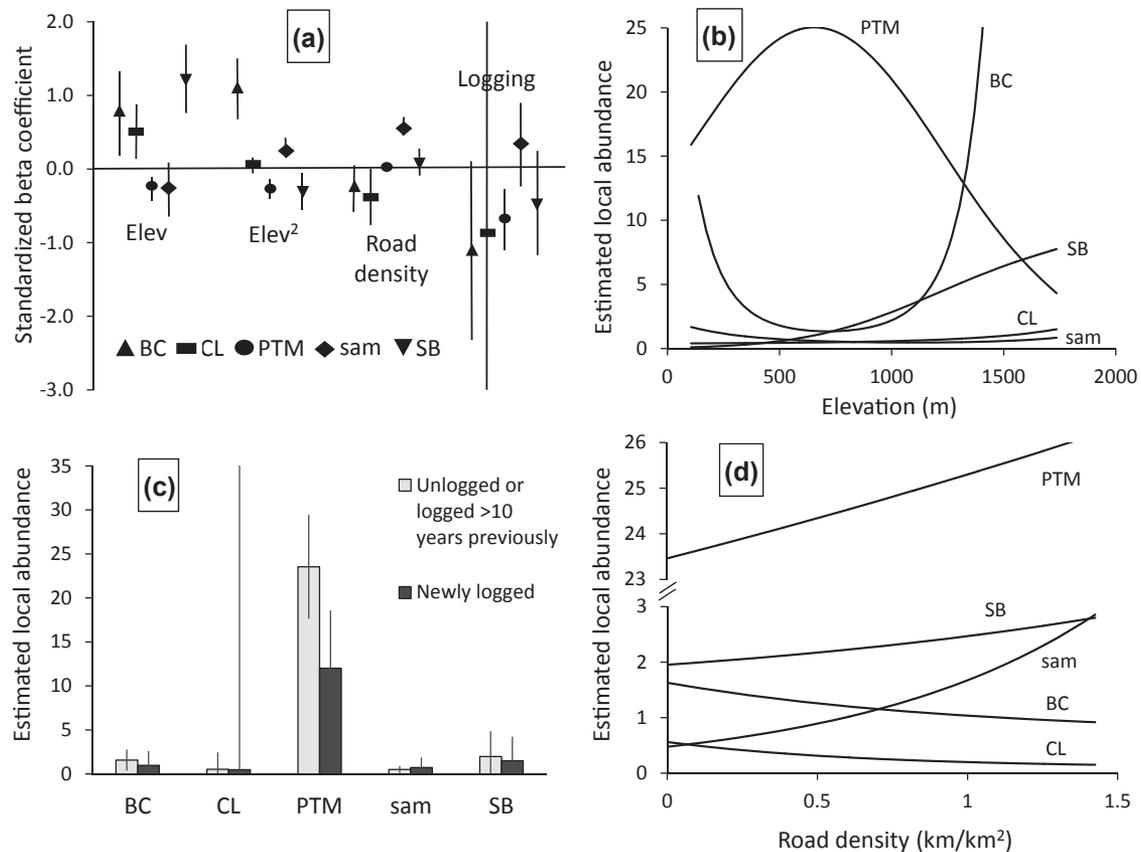


Figure 2. (a) Model-averaged beta coefficients and associated covariate effects of (b) elevation, (c) logging, and (d) road density on estimated mean local abundance of banded civet (BC), clouded leopard (CL), pig-tailed macaque (PTM), sambar (sam), and sun bear (SB).

facilitating movement and dispersal. The all-species-combined corridor scenario generally led to larger increases in total landscape cost for each species than the single-species-optimized scenarios. However, the multispecies scenarios that grouped ecologically similar species were generally more effective. Carnivore connectivity scenarios were nearly as effective as single-species scenarios for banded civet and clouded leopard with 1 km buffers around the LCP corridors.

Our results strongly suggest that umbrella species approaches may fail to conserve community connectivity for threatened species. The carnivore connectivity scenarios did not effectively conserve connectivity for the noncarnivores, a finding that is inconsistent with the umbrella species hypothesis that with protection of carnivore habitat, connectivity for other species is also effectively conserved. Likewise, the herbivore multispecies scenario provided relatively good landscape connectivity, in terms of total cost, for macaques and sambar but did not serve carnivores well. Protected areas designed around the protection of umbrella species can be successful (Caro 2003) or unsuccessful (Roberge & Angelstam 2004) at conserving multiple species, depending

on whether habitat selection and the impact of anthropogenic stressors differ strongly among species. Likewise, for connectivity conservation, our results show that although multispecies connectivity scenarios may often be necessary, if they are implemented improperly (e.g., by selecting only one charismatic umbrella species) they could be ineffective at supporting movement for a particular species relative to connectivity scenarios optimized for that species.

Our results suggest that multispecies connectivity scenarios may be more effective if they are restricted to combinations of ecologically similar species (e.g., carnivores or herbivores), rather than a collection of taxa with very different habitats (Lambeck 1997; Simberloff 1998). To facilitate the choice of which species to assess connectivity for, we suggest that managers focus on species sensitive to human disturbance. In our analysis, the sambar seemed to do well in logged areas and areas with high road densities. Clearly, this species does not require corridors of unlogged forest in order to move through logged areas. However, sambar are quite sensitive to hunting (J.F.B., unpublished data), which can be more intense in areas accessible by roads (Yackulic et al. 2011; Proffitt

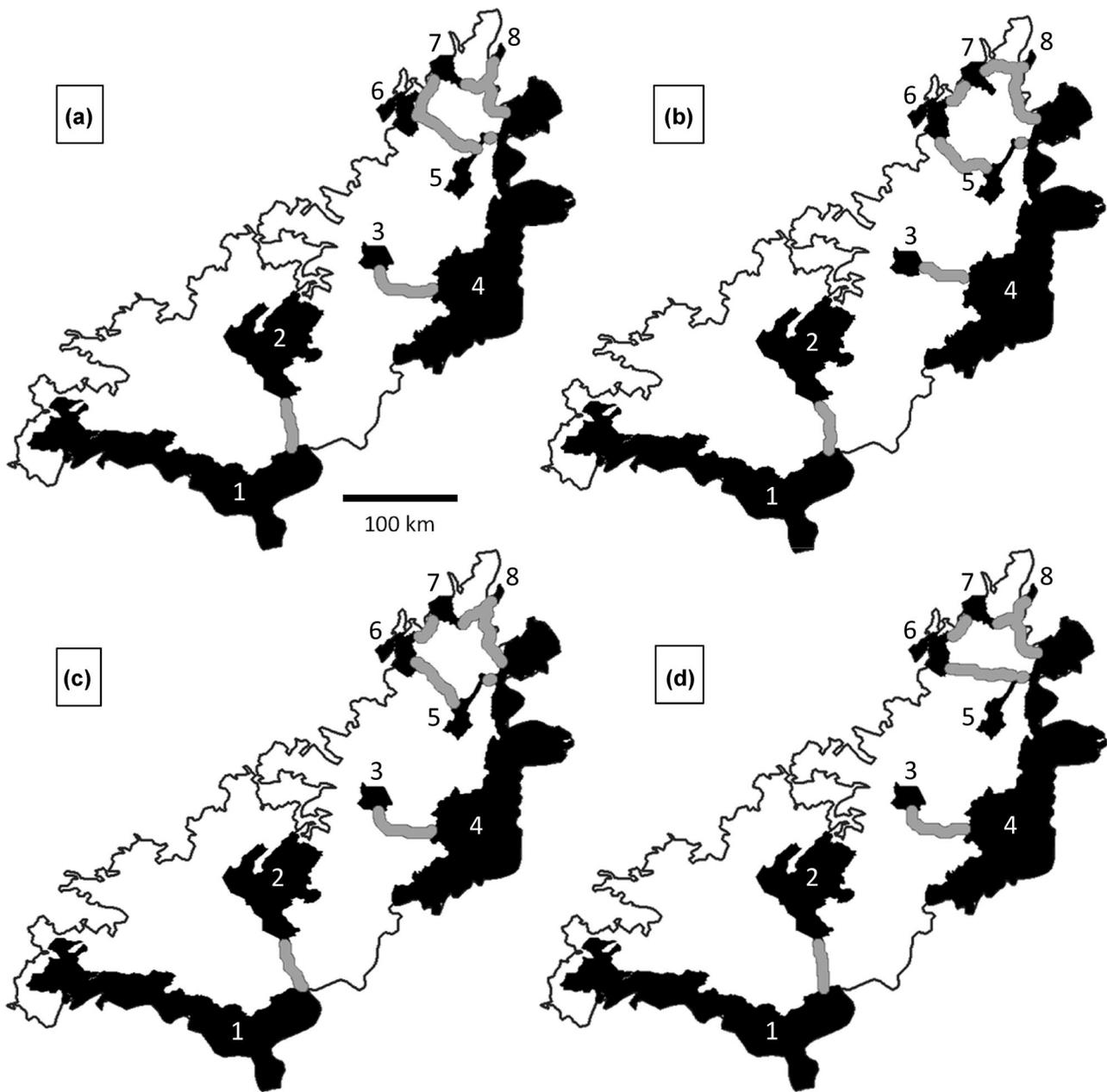


Figure 3. Connectivity across the study region. Protected areas are in black, and least-cost path corridors with 5 km buffers are in gray for (a) all carnivore species (banded civet, clouded leopard, sun bear) combined, (b) herbivore species (macaque and sambar) combined, (c) all species except sambar, (d) and all species combined. Protected areas (in Malaysia unless otherwise noted): 1, Betung Kerihun (Indonesia), Batang Ai, and Lanjak Entimau complex; 2, Hose Mountains and Batu Laga complex; 3, Usun Apau (Malaysia); 4, Kayan Mentarang (Indonesia); 5, Pulong Tau; 6, Gunung Mulu; 7, Ulu Temburong (Brunei); 8, Maligan.

et al. 2013). Thus even if habitat corridors per se are not critically important for this species, unhunted reserves may well be.

The differences between connectivity scenarios changed substantially when using 1 km versus 5 km buffers around the LCP corridors. For example, with a 1 km buffer the all species connectivity scenario increased total movement cost for banded civets by 27% rel-

ative to a scenario designed for banded civets alone. But with a 5 km buffer, the all-species scenario increased total cost for banded civets by 3%. In contrast, the herbivore connectivity scenario lowered total cost for macaques by 25% with the 1 km buffer but increased cost by 5% with the 5 km buffer. These differences highlight the pressing need for better methods of determining optimal corridor width (Beier et al. 2008; Beier et al. 2011; Sawyer

Table 1. Percent change in cumulative landscape cost^a for each species with habitat corridors optimized for other species or multispecies connectivity scenarios relative to corridors optimized for that species.^b

Least-cost path buffer and species for which corridor is optimized	Species present in corridor				
	Banded civet	Clouded leopard	Pig-tailed macaque	Sambar	Sun bear
1-km buffer					
Banded civet	0	4	22	42	36
Clouded leopard	28	0	27	24	54
Pig-tailed macaque	107	45	0	32	103
Sambar	152	100	10	0	132
Sun bear	24	21	16	57	0
Carnivores	2	2	37	42	32
Herbivores	129	79	-25	13	119
All species except sambar	31	16	-24	57	48
All species	27	23	-29	31	42
5-km buffer					
Banded civet	0	20	51	12	18
Clouded leopard	-6	0	1	-5	5
Pig-tailed macaque	12	13	0	0	22
Sambar	29	34	-4	0	39
Sun bear	7	25	44	24	0
Carnivores	0	19	50	9	17
Herbivores	25	25	5	1	37
All species except sambar	11	25	38	13	27
All species	3	21	38	4	20

^aSum of the cost (resistance to movement) for all pixels in the corridor.

^bFor example, compared with a 1-km buffered corridor for banded civets, the cumulative cost to banded civet movement is 2% higher for an all-carnivores corridor scenario and 27% higher with an all-species scenario. Least-cost paths present the best one-dimensional corridor for each species (or species combination), but total corridor cost includes the buffer on either side. So in a few instances corridors optimized for a species combination can be better than those optimized for a single species, resulting in negative values in the table.

Table 2. Percent change in cumulative landscape connectivity^a for each species with habitat corridors optimized for other species or multispecies connectivity scenarios relative to corridors optimized for that species.^b

Species for which corridor is optimized	Species present in corridor				
	Banded civet	Clouded leopard	Pig-tailed macaque	Sambar	Sun bear
Banded civet	0	-20.8	-73.7	-51.1	-17.7
Clouded leopard	-14.5	0	-40.8	-33.7	-6.4
Pig-tailed macaque	-61.9	-36.6	0	-29.5	-40.1
Sambar	-43.5	-29.8	-33.1	0	-22.9
Sun bear	-13.9	-7.7	-48.7	-29.1	0
Carnivores	-5.8	-4.3	-57.2	-38.7	-5.0
Herbivores	-52.0	-31.9	-10.0	-11.1	-29.2
All species except sambar	-29.0	-13.5	-35.4	-39.9	-12.7
All species	-29.2	-14.8	-31.6	-22.7	-7.5

^aSum of cost (resistance to movement) for the top 1% of landscape pixels, based on estimated dispersal of individuals (i.e., flow of electrical current).

^bFor example, compared with a single-species connectivity strategy optimized for banded civets, the total landscape connectivity for banded civets is 5.8% lower with an all-carnivores connectivity scenario and 29.2% lower with an all-species scenario.

et al. 2011). Existing tools (e.g., Pinchpoint Mapper; McRae 2012) can help address this issue by integrating LCP methods and algorithms based on electronic circuit theory. We suggest managers pay special attention to assessing how corridors of different widths affect actual movement (Beier & Loe 1992) and total landscape cost for target species.

The length of potential movement corridors is another critical dimension. Even corridors with low movement

costs may not support animal dispersal if they are too long. It may be that over large landscape scales, connectivity is best supported not by long, narrow (relative to their length) corridors for dispersing individuals but by maintaining habitat patches that support resident individuals.

An important assumption we made is that estimates of local abundance are a suitable proxy for determining optimal corridor locations when direct estimates of animal

movement are unavailable. When designing corridors, it is generally important to account for differences in habitat selection between resident and dispersing individuals and species that move through the corridor quickly versus live within it (Beier et al. 2008). Our data likely integrated information on residents, dispersers, passage migrants, and corridor dwellers because we deployed camera traps in such a wide variety of locations and habitat conditions. Moreover, most of our cameras were placed on movement routes such as game trails, which were likely the routes dispersing individuals used to move from one protected area to another. Finally, for at least some large mammal species, habitat selection by residents and dispersers is very similar (Newby 2011; Sawyer et al. 2011). Our approach and results could be further refined with data on individual movements from global positioning system (GPS) collars. It will likely be years, however, before substantial amounts of GPS-collar data are obtained in Borneo for multiple threatened mammal species. There are also technological hurdles to acquiring accurate GPS locations under the dense and contiguous forest canopy in Borneo (Tobler 2009). Our results highlight that non-invasive sampling, for example use of camera traps, can provide useful data for assessing connectivity at landscape scales, provided sampling is spatially widespread and straddles relevant natural and anthropogenic gradients in habitat conditions.

Some of our proposed corridor locations, and even some of the protected areas, have already been selectively logged. We conducted our analyses to demonstrate a method for determining corridor locations that should be protected from further logging and road development. It may be less expensive to protect areas that have already been selectively logged because most of the economic value from the timber has already been extracted (Wilcove et al. 2013). Moreover, selectively logged forests in Borneo appear to recover their mammal diversity relatively quickly (J.F.B., unpublished data), highlighting their importance to regional conservation. However, many logged forests in Sarawak are subject to conversion to oil-palm plantations (USDA 2011) or inundation behind hydroelectric dams (SCORE 2011). Corridor designation and protection in Borneo (as in many other tropical areas) will be difficult due to uncertainties and disputes over land ownership as well as opaque governmental planning processes. One large-scale habitat connectivity plan exists: World Wildlife Fund's Heart of Borneo Project (Wulffraat & Morrison 2013). Smaller-scale analyses such as ours could help scale down these efforts to identify optimal locations for specific corridors. The protection of corridors where forests are allowed to regenerate is critical to support the long-term, landscape-scale movement of threatened, disturbance-sensitive species. Next steps in the corridor planning process include finalizing a group of target species, determining optimal locations of corridors to support connectivity

for as many of these species as possible, and laying the political groundwork to turn these corridors into legally protected entities.

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Supporting Information

Additional information on the study species, analytical methods, LCP corridors (Appendix S1) and current flow maps for different connectivity scenarios (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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