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Conserving omnidirectional landscape connectivity under projected land-use change in Borneo

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A R T I C L E I N F O

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A B S T R A C T

Land-use change in tropical regions is rapidly diminishing landscape connectivity and threatening the persistence of forest-dependent wildlife. Identifying priority areas for retaining connectivity amid deforestation and infrastructure expansion is particularly urgent in Indonesian Borneo (Kalimantan), where extensive land-use transformation is projected. We evaluated changes in connectivity for three terrestrial taxa with contrasting habitat preferences and dispersal abilities: lesser and greater mousedeer, *Tragulus*, spp.; Bornean sun bear *Helarctus malayanus euryspilus*; bearded pig *Sus barbatus*. Using camera-trap data from 11 study areas, we applied Bayesian occupancy models to estimate responses to anthropogenic and environmental drivers. Occurrence probability maps were converted into resistance layers and integrated into omnidirectional circuit-theory models to map recent (2021) and predict future (2055) connectivity. We quantified changes in Highly Connected Habitat (HCH; >70th percentile current flow) to identify vulnerable areas and species. Production forests are crucial for connectivity, providing up to 62.1% of HCH. However, these areas face the highest projected losses (up to 15% by 2055). While protected areas remain vital refuges, up to one-third of HCH loss is expected to occur in lowland forest, increasing the isolation of existing reserves. Connectivity near Indonesia's new capital site in East Kalimantan is at high risk of degradation, particularly for wider-ranging species. Further, the Trans-Kalimantan Highway's northern link threatens to bisect the relatively undisturbed interior. Our findings highlight the urgent need to preserve and restore connectivity between lowland forest including protected areas, sustainably manage production forests, and proactively integrate connectivity science into infrastructure planning to prevent irreversible forest fragmentation.

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1. Introduction

Habitat loss, fragmentation, and degradation are among the most pervasive drivers of global biodiversity decline (Tucker et al., 2018). Tropical moist forests are particularly vulnerable as 17% have been lost since 1990 (Vancutsem et al., 2021) and much of the remaining forest is degraded or fragmented by human activities (Grantham et al., 2020). Land-use change poses a major threat to the long-term persistence of forest-dependent species, increasing their vulnerability to both the direct and indirect consequences of forest loss and degradation—particularly reduced landscape connectivity (Haddad et al., 2015). Given the increasing scale and extent of land-use change (Tucker et al., 2018), enhancing connectivity is central to achieving the goals of the post-2020 Global Biodiversity Framework and broader vision for 2050 (CBD, 2022).

Landscape connectivity has both structural and functional attributes (Taylor et al., 2006). While structural connectivity focuses on physical aspects, such as habitat patches and their spatial arrangement, functional connectivity reflects the degree to which a landscape facilitates or impedes the movement of individuals and their genes in relation to dispersal abilities, habitat preferences, and behavioural traits (Taylor et al., 2006). Diminished landscape connectivity can have negative outcomes for wildlife, including reduced access to key resources, restricted gene flow, heightened vulnerability to stochastic events and contact with anthropogenic threats (Dutta et al., 2016; Baral et al., 2021; Wang et al., 2017). Therefore, it is increasingly recognised that the long-term persistence of wildlife populations requires a landscape-scale approach to facilitate movement of individuals among isolated fragments. Yet, due to differences in habitat suitability, dispersal capabilities, home range, and sensitivity to human activities, strategies to enhance connectivity for one species may not be effective for another (Brodie et al., 2015). As such, multi-species connectivity analyses are often necessary to support the design of more effective and ecologically representative conservation strategies.

There are several approaches for evaluating landscape connectivity. Least-cost path calculates the connection path with the lowest cumulative cost (i.e. degree of resistance) between core habitats (e.g., Pullinger and Johnson, 2010), but assumes individuals have perfect knowledge of their environment which has raised questions about biological realism (Balbi et al., 2019). Individual-based models (e.g., RangeShifter, Bocedi et al., 2021) simulate movement based on population dynamics and individual traits within a spatial framework but require detailed information on the target species which is frequently unavailable. Circuit-theory models (e.g., Circuitscape; McRae et al., 2008) bridge the methodological gap by modelling multiple potential movement pathways without the need for extensive species data. Developed as an advancement of graph theory, circuit theory incorporates principles from electrical circuit theory to represent species movement or gene flow as current flowing across a resistance surface (i.e., the landscape) (McRae et al., 2008). Unlike least-cost path models that identify a single optimal route, circuit-theory approaches visualise overall movement flow across all possible pathways, making them particularly useful for complex or highly fragmented landscapes (McRae et al., 2008).

A limitation of traditional applications of circuit theory is the requirement of users to define source and target habitat patches – "cores" – between which connectivity is modelled (Landau et al., 2021). This can introduce bias through user-delineated areas (e.g. political or geographic boundaries such as protected areas) and the assumption that species move toward predefined destinations (Pither et al., 2023). To overcome these limitations, an omnidirectional circuit approach was developed which allows current to flow across a resistance surface from all directions and every cell, without predefining cores (Landau et al., 2021). This method is particularly well-suited for wide-ranging species and those not confined to discrete habitats, better capturing a gradient of ecological conditions (McRae et al., 2016; Phillips et al., 2021). Omnidirectional models are increasingly being used to address a wide range of conservation issues including informing policy (e.g., Biodiversity Net Gain, Martinez-Cillero et al., 2023), mapping regional connectivity for data-sparse species (Hohbein and Nibbelink, 2021), and identifying wildlife movement pathways in response to road expansion (McClure et al., 2017). Despite its utility, omnidirectional circuit models have rarely been applied to Southeast Asia.

Southeast Asia is a rapidly developing region that will benefit from improved integration of landscape connectivity into species conservation programmes (Struebig et al., 2025). The region has experienced some of the highest deforestation rates in the world and ~ 70% of remaining forest cover is within 1 km of a non-forest edge (Haddad et al., 2015). Indonesian Borneo (Kalimantan) has lost nearly one- third of its forest since 1990, mostly from the coastal lowlands (<500 m asl) (Seaman et al., 2025). Forest conversion has been primarily attributed to the expansion of industrial plantations (i.e., oil palm, pulpwood) but also for infrastructure development, timber extraction, mining and fires (Gaveau et al., 2014; Seaman et al., 2025). As a result, Bornean birds and mammals are estimated to have lost an average of 35% of functionally-connected habitat since the 1970s (Ocampo-Peñuela et al., 2020) and many protected areas in the coastal lowlands are considered too small or too isolated to ensure long-term survival of forest-specialist, large mammals (Mathai et al., 2016; Ocampo-Peñuela et al., 2020).

Kalimantan is likely to be further transformed by a new set of challenges emerging from large-scale infrastructural projects (Shira and Associates, 2011). This includes the relocation of Indonesia's capital from the island of Java to East Kalimantan, accompanied by 5220 km of new or upgraded road networks expected to exacerbate deforestation and threaten biodiversity (Alamgir et al., 2019; Spencer et al., 2023). The new capital city – *Nusantara* – is being built within a mosaic of cropland, timber concessions and oil palm plantations, but near important lowland forests (e.g., Sungai Wain Protection Forest) that fall within infrastructure impact zones and are at-risk of becoming further isolated, fragmented or degraded (Spencer et al., 2023). Previous connectivity assessments for Borneo have been limited to single species (e.g., Sunda clouded leopards *Neofelis diardi*; Kaszta et al., 2024), structural connectivity (Alamgir et al., 2019) or coarse distribution modelling assessments identifying climate-change risks to linkages between protected areas (Struebig et al., 2024). It remains unclear how the combined impacts of deforestation and infrastructure development will impact functional connectivity for the terrestrial mammal community across the entire landscape matrix.

Here, we evaluate the effects of projected deforestation and infrastructure development on landscape connectivity in Indonesian Borneo by the year 2055 using three representative mammal taxa with different dispersal capabilities and habitat requirements: mousedeer (lesser and greater mousedeer species; *Tragulus* spp.), sun bear (*Helarctos malayanus euryspilus*), and bearded pig (*Sus barbatus*). We aim to 1) assess patterns in recent landscape connectivity, 2) quantify where and how connectivity could be affected by land-use change by 2055, 3) provide evidence-based recommendations for mitigating connectivity losses in order to protect biodiversity alongside sustainable development and 4) produce a replicable modelling framework for omnidirectional connectivity research using Omniscape software (Landau et al., 2021; McRae et al., 2016).

2. Methods

2.1. Study area

Kalimantan encompasses 533,400 km^2 (73% of Borneo), of which ~287,608 km^2 (54 %) remains intact forest and ~102,522 km^2 (19 %) is degraded forest (Seaman et al., 2025). Forest types include lowland and hill dipterocarp, peat swamp and freshwater swamp forests in coastal and low-lying areas, and montane forests in the interior. Since the 1970s, rapid land-use change has produced a fragmented lowland mosaic dominated by agriculture and plantations, while large contiguous forests persist in mountainous interior regions (Gaveau et al., 2014; Seaman et al., 2025). We collated camera-trap data from 11 study areas spanning a mixture of habitat and management types to inform our connectivity analysis (Fig. 1; Table S1). The Indonesian State Forest Area is categorised into Protected, Production and Conversion zones. The protected zone comprises protected areas (IUCN Category I–VI), as well as watershed protection forest (*Hutan lindung*), while production forests allow for regulated logging, but prohibit deforestation. Conversion forests can be legally cleared for non-forest uses.

2.2. Study species

We focused on forest-dependent, medium-to-large (>1 kg) terrestrial mammals representing a range of ecological requirements, dispersal capabilities, and conservation relevance. Candidate species were restricted to those listed as Vulnerable or higher on the IUCN Red List or under Indonesian protection law (MoEF, 2018), and with sufficient camera-trap detections for model parameterisation. Following these criteria, we selected three case-study taxa (comprising four species): lesser (*T. kancil*) and greater mousedeer (*T. napu*) combined as *Tragulus* spp. (referred to as one species “mousedeer” hereafter for ease), Bornean sun bear (*Helarctos malayanus euryspilus*), and bearded pig (*Sus barbatus*). Mousedeer were grouped due to morphological similarity, overlapping habitat use, and frequent aggregation in biodiversity surveys (Mendes et al., 2024); they represent short-range dispersers (home range estimate 0.056 km^2; Matsubayashi et al., 2003). Sun bears represent intermediate-range dispersers (home range ~ 5 km^2, Fredriksson, 2012; 20.6 km^2, Wong et al., 2004), and bearded pigs as long-range dispersers due to their migratory and nomadic status (Luskin et al., 2017). Further ecological information relevant for the connectivity analysis is in S2.

2.3. Analysis workflow

Landscape connectivity was modelled using Omniscape, an omnidirectional circuit-theory algorithm implemented in Julia (omniscape.jl; Landau et al., 2021). Omniscape iteratively applies a circular moving window across a resistance surface, injecting current from all non-zero source cells toward the central cell, summing current flow across all iterations to produce one cumulative current flow map. Three inputs are required: 1) a *moving window radius* (*mwr*) to represent dispersal capability; 2) a *resistance layer* describing landscape permeability including barriers and impediments to movement; and 3) a *source weight* layer defining the strength of each cell as a source of animal movement (Landau et al., 2021; McRae et al., 2016) (Fig. 2). These input layers can be parameterised with occurrence data and species-specific information to generate more ecologically realistic movement constraints (McRae et al., 2016). Throughout, we processed all spatial layers at 250 m^2 resolution. To minimise false barrier effects, we added a 10-km buffer along the Indo-Malaysian border and populated with values drawn from a truncated normal distribution based on the value distribution within each source weight and resistance raster (Buchholtz et al., 2023).

2.4. Moving window

The moving window radius can be inferred from circular home range size estimates, which capture habitat use and movement, acting as a proxy for dispersal (Landau et al., 2021). Published home range estimates were limited for the focal species and showed inter-individual and inter-study variation (Table S2). In such cases, using the largest reported values is recommended, as these better approximate the minimum core area necessary for population persistence (Martinez-Cillero et al., 2023). Accordingly, moving window radii were not intended to represent precise species-specific dispersal distances, but rather to capture a gradient of dispersal potential across the mammal community. This consideration is particularly important for mousedeer, for which the published home range estimate is smaller than the spatial resolution of the analysis as

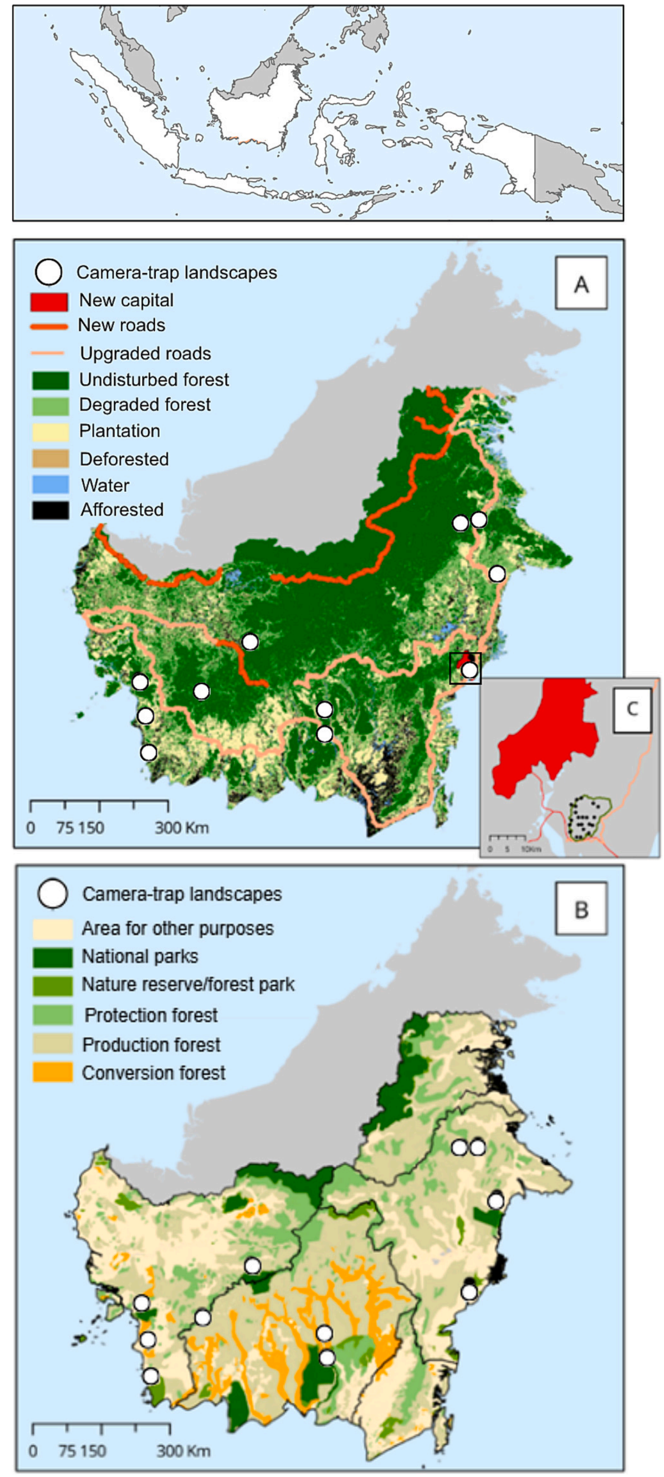

Fig. 1. Study area and survey locations. Maps of Kalimantan including camera-trap study areas within A) landcover classifications from the Tropical Moist Forest Cover (Vancutsem et al., 2021) and planned infrastructure, including the new capital city and roads (i.e. Trans-Kalimantan Highway Northern Link in red near Malaysian Borneo border); B) land use designation (protected, production, conversion) partitioned by the five provinces – clockwise from top: North Kalimantan, East Kalimantan, South Kalimantan, Central Kalimantan, and West Kalimantan; and C) the new capital city zone (red) and nearby Sungai Wain Protection Forest (green boundary) with example of camera-trap locations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

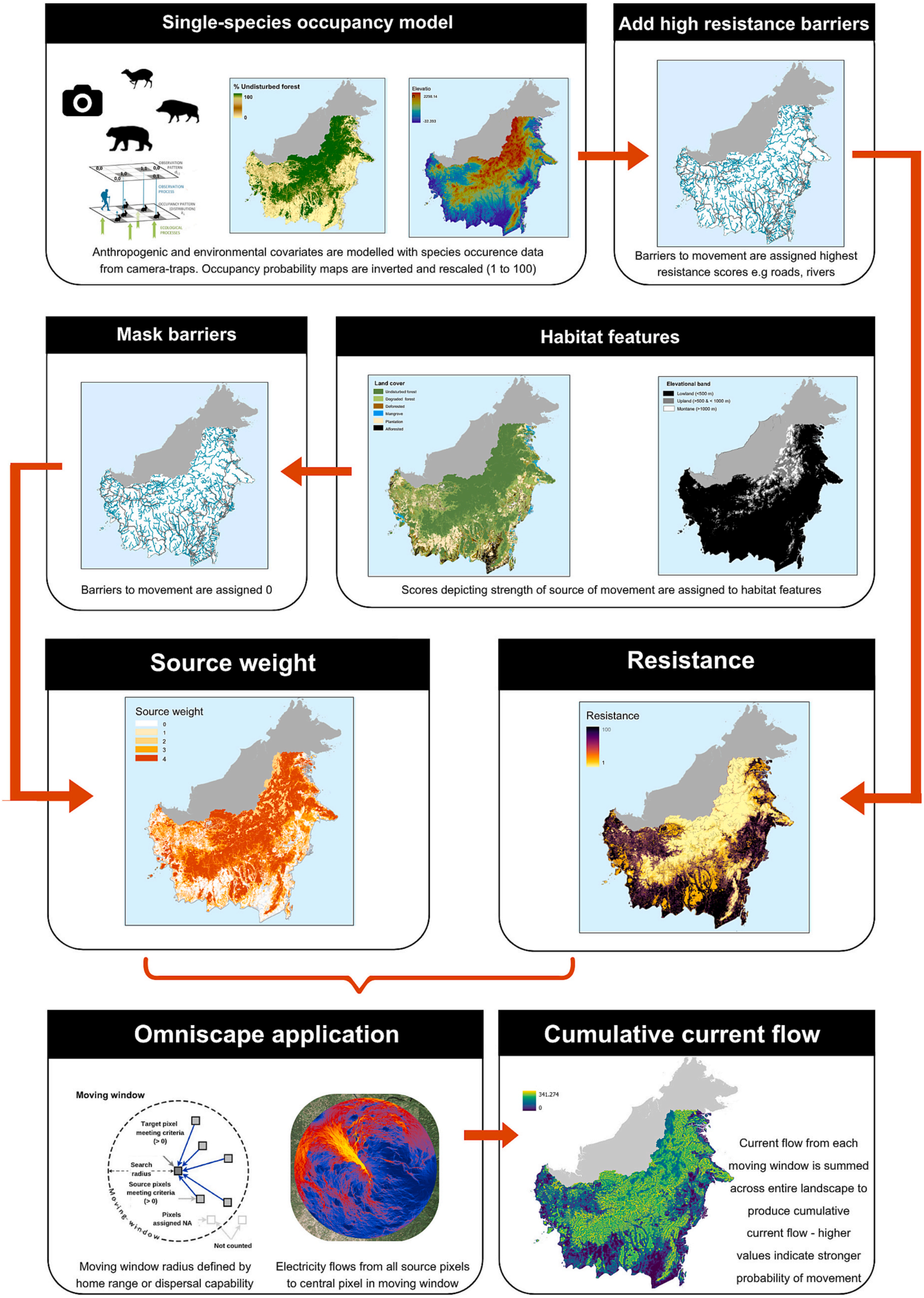

Fig. 2. Workflow for generating resistance and source-weight layers for Omniscape connectivity modelling.

finer resolutions were computationally prohibitive at the extent of Kalimantan. Radii were therefore set at 2.25 km for mousedeer, 5.75 km for sun bear, and 25 km for bearded pig.

2.5. Resistance surface

2.5.1. Occupancy model

To develop species-specific resistance surfaces—representing the relative permeability of the landscape—we inverted (1- occupancy) and rescaled (1 to 100) occurrence probability maps, with post-hoc adjustments to account for known movement barriers. Occupancy (i.e. "the probability that at least one individual of a species occupies a site, accounting for detection error" (MacKenzie and Nichols, 2004), when linked to covariates, can provide underlying information about the suitability of habitat conditions. This approach is supported by previous work (e.g., Phillips et al., 2021; Walpole et al., 2012). However, it assumes the probability of occurrence is correlated with habitat conditions and that landscape resistance to movement is inversely correlated to these conditions (Walpole et al., 2012).

Occurrence was estimated using a single-species, single-season Bayesian occupancy models fitted in spOccupancy (Doser et al., 2022), using camera-trap data from 391 1 km^2 sites across 11 study areas (39,293 trap-nights; Table S1). Where possible, we used pre-2020 camera-trap data to avoid the confounding effects of African Swine Fever, which caused bearded pig population declines across Borneo that year (Lieb et al., 2025). One study area (Rungan) was excluded from the bearded pig analysis as data was collected post-2020. We modelled occupancy as a function of environmental (e.g. % undisturbed forest cover, % undisturbed and degraded forest cover, elevation, biomass t ha^{-1}) and anthropogenic (e.g., human population pressure at three distance decay functions, human accessibility) covariates extracted at the 1 km^2 grid. Detection probability accounted for habitat type and sampling effort. For each species, we used the top-ranked model (lowest WAIC) to generate predictive occurrence maps across Kalimantan. (Full data and covariate processing information in S1 and S2). Throughout we report covariate effects using the mean of the posterior distribution (β) and communicate uncertainty using Bayesian Credible Intervals (BCI) - we infer strong effects if the 95% BCI did not overlap zero and moderate if the 75% BCI did not overlap zero.

2.5.2. Recent and future projections

We generated species-specific occurrence probabilities across Kalimantan by linking posterior model coefficients with forest cover in 2021 (recent) and a business-as-usual deforestation scenario to 2055 (future), summarised as mean posterior maps and masked to the observed covariate range to minimise extrapolation. Future forest cover was projected using a dynamic, spatially explicit forest cover change model developed for Borneo (Seaman et al., 2025). The model uses annual undisturbed forest data from the Tropical Moist Forest (TMF) database (1990–2021; Vancutsem et al., 2021) and incorporates contagious deforestation dynamics, producing 100 Monte Carlo simulations (S3; Table S3). The output raster represents deforestation probabilities (0−100), which we converted to binary forest cover maps for 2055 under three scenarios: low (pixel has >75% chance of loss), moderate (>50%), and severe (>25%) deforestation.

As camera traps were predominantly located in or near forest, values in non-forest cells located >1 km from intact forest were reclassified to zero, reflecting their limited capacity to support populations or facilitate movement (Dutta et al., 2016). We made additional adjustments to reflect barriers to movement. We assigned zero occurrence values to cells intersecting large rivers and major road classes (motorway, trunk, primary, and secondary) derived from OpenStreetMap, while excluding smaller roads (e.g. rural, logging) due to their relatively minor barrier effects. We similarly reclassified mangroves, urban areas, and open land to zero. We did not constrain occurrence predictions to IUCN range polygons because camera-trap detections occurred outside reported ranges. We incorporated future infrastructure expansion by masking (assigned zero) the Northern Link of the Trans-Kalimantan Highway, the proposed toll road connecting the new capital to Balikpapan, and the core urban zone of the planned capital. Because we did not explicitly model indirect effects of urban expansion and secondary road proliferation, future connectivity changes surrounding infrastructure may be underestimated. Finally, we inverted and rescaled the adjusted recent and future occurrence maps to generate resistance surfaces for each species and deforestation scenario.

2.5.3. Source weight

Omniscape allows the user to specify habitat types that function as stronger sources of movement, injecting greater electrical current from those that contribute more to dispersal potential (McRae et al., 2016). We assigned source weight scores using a coreless approach, whereby habitat suitability was informed by camera-trap detections and published literature —rather than the inverse of resistance (Martinez-Cillero et al., 2023). We assigned suitability scores (0–4) to reclassified Tropical Moist Forest Cover Transition Map categories (Vancutsem et al., 2021; Table S4) accounting for elevation (lowland 0–500 m; upland > 500 < 1000; montane > 1000 m) (Table S5). Plantations were assigned a score of 0, not because movement is impossible, but because they are very unlikely to support viable populations or act as demographic sources for forest-dependent species (Yue et al., 2015). For future scenarios, we reassigned source weights to deforested cells based on their overlapping land-use designation. We assigned a non-forest weighting (0) to deforested cells in conversion or non-forest zones to represent total conversion. We assigned a weighting of 1 to deforested cells in protected or production zones to reflect degradation rather than complete clearance (Struebig et al., 2015).

2.5.4. Landscape connectivity assessment

We visually inspected cumulative current-flow maps (hereafter "current flow") using histogram equalisation, which spreads frequent intensity values and enhances low-contrast areas, aiding identification of locations for improving connectivity (Martinez-Cillero et al., 2023). To identify areas contributing most to landscape connectivity, we reclassified current-flow maps using the 70th percentile of the data distribution and designated cells exceeding this threshold as Highly Connected Habitat (HCH; Hohbein and Nibbelink, 2021). We summarised the spatial distribution of HCH as the percentage of total HCH cells within land-use categories, elevational bands, and provinces.

To identify areas of conservation priority where connectivity losses are most severe, we mapped cells classified as HCH in 2021 that were no longer classified as such in 2055 and summarised their spatial patterns as the proportion lost across land-use category, elevational band, and province. Finally, we assessed species-level differences in connectivity patterns using histograms of cell counts across current-flow intensity classes, providing a complementary comparison of habitat isolation that is unaffected by visualisation choices (Martinez-Cillero et al., 2023).

3. Results

3.1. Spatial occurrence

All three species were detected across the 11 study areas, including sun bears in three regions where they were previously considered extirpated (Scotson et al., 2017): Maura Kendawangan (surveyed in 2019) and Pematang Gadung (2019) in West Kalimantan, and Kutai National Park in East Kalimantan (2013). Bearded pigs were detected at the largest proportion of sampled sites (53.3% of 1 km^2 grids), followed by mousedeer (43.0%) and sun bear (31.2%). Mean occupancy probability was 0.68 (75% Bayesian Credible Interval: 0.54 to 0.80) for mousedeer, 0.81 for sun bears (95% BCI: 0.59–0.93), and 0.89 for bearded pigs (95% BCI: 0.52–0.98). Mousedeer occurrence was positively associated with undisturbed forest cover (β = 0.44, 75% BCI:

0.10–0.79) and human pressure (β = 0.77, 95% BCI: 0.25–1.33), and strongly negatively associated with elevation (β = −0.78, 95% BCI: −1.42 to −0.26), indicating persistence in lowland forests near human-modified landscapes. Sun bear occurrence showed a strong positive association with undisturbed forest (β = 1.04, 95% BCI: 0.15–2.31) and a moderate positive association with elevation (β = 0.70, 75% BCI: 0.01–1.53). Bearded pig occupancy declined with elevation (β = −1.02, 95% BCI: −1.79 to −0.37) and unlike the other species, showed no significant relationship with forest cover. Covariate relationships in Fig. S1.

3.2. Recent landscape connectivity

Mapping cumulative current flow revealed extensive, contiguous areas of connectivity for all species the interior regions of Kalimantan, characterised by high forest cover and limited development (Fig. 3). Connectivity declined with elevation for all focal species, most strongly for mousedeer, although uncertainty is higher in montane areas due to limited sampling. Intact lowland comprised of 73.6% (sun bear) to 99.9% (mousedeer) of total HCH across Kalimantan (Fig. 4). However, the coastal lowlands were particularly fragmented, with high current

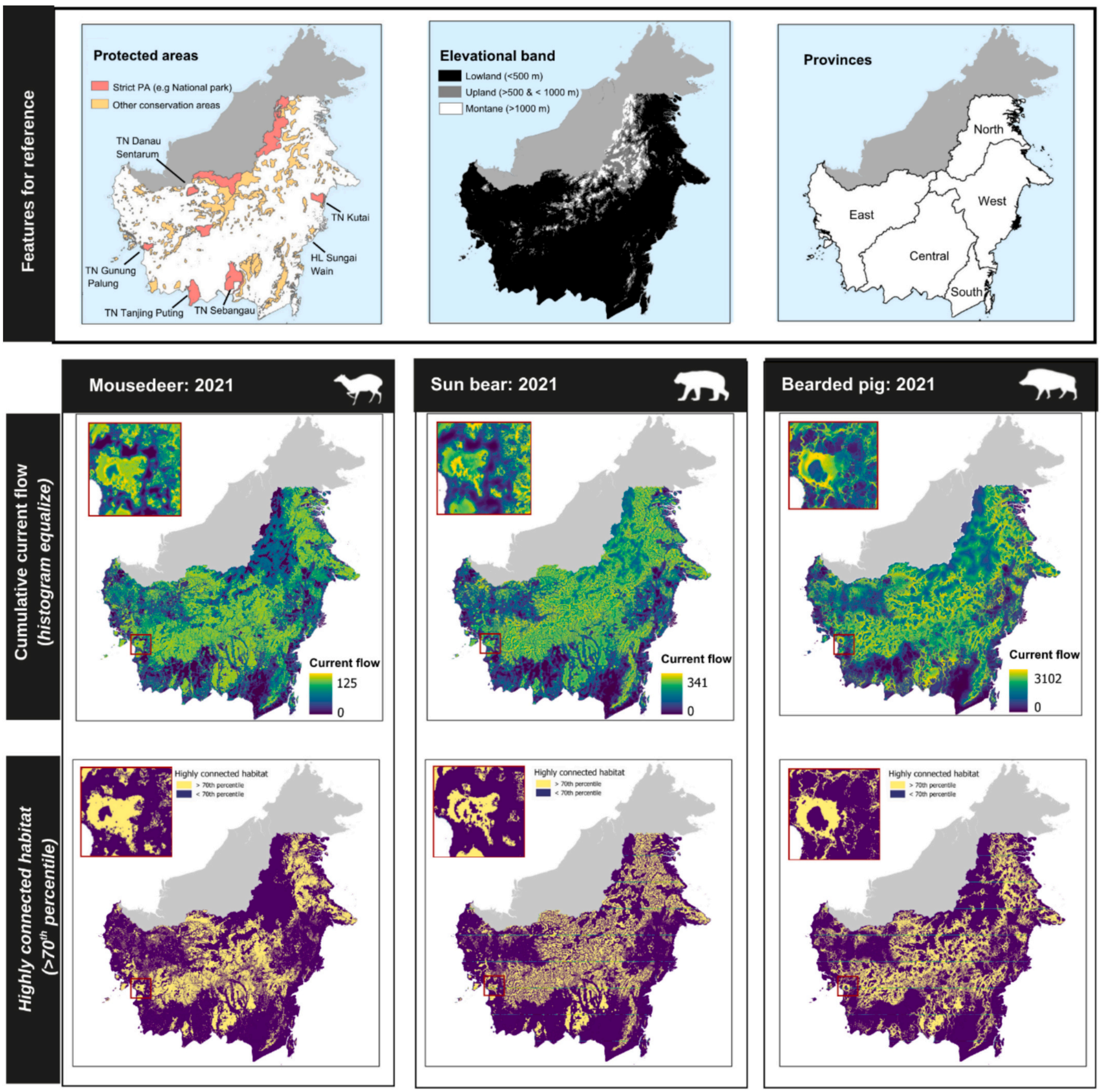

Fig. 3. Upper Panel: Habitat features for reference including protected areas, elevational bands and provinces. Middle Panel: Cumulative current flow for mousedeer, sun bear and bearded pig across Kalimantan in 2021 visualised with histogram equalise to show areas of high and low flow relative for each taxon - dark blue depicting the lowest flow areas for each species and lighter green/yellow depicting highest flow potential. Lower Panel: Highly connected habitat (70th percentile of cumulative current flow) shown in yellow for each taxon, representing areas most important for movement compared to surrounding cells. Inset is of Gunung Palung National Park and surrounding landscape. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

flow typically limited to protected areas, such as Gunung Palung and Tanjung Puting National Parks, which are isolated by surrounding agricultural plantations. Across land-use categories, most HCH occurred within production forests (58.8% sun bear to 62.1% mousedeer), followed by protected areas (19.2% bearded pig to 30.1% sun bear) (Fig. 4).

Differences in dispersal capability strongly influenced spatial patterns of connectivity (Fig. 3). The smallest moving window (mousedeer) highlighted fine-scale, patchy connectivity, particularly in fragmented landscapes such as Kapuas Hulu in West Kalimantan, whereas the largest moving window (bearded pig) revealed broader movement corridors linking extensive forest blocks across otherwise impermeable areas.

3.3. Future landscape connectivity

Projected deforestation and infrastructure development reduced landscape connectivity for all taxa, with the magnitude and spatial patterns varying by dispersal traits and deforestation scenario (Fig. 4; 5). Lowland forests experienced the greatest projected losses, ranging from 16.3% of HCH cells for mousedeer under the low deforestation scenario to 33.9% for bearded pig in the high deforestation scenario (Fig. 4). Very few HCH cells were predicted to be lost from the island's interior under future deforestation scenarios, although the new Northern link of the Trans-Kalimantan Highway introduced a major barrier to movement (Fig. 5).

West, Central and East Kalimantan were predicted to experience the greatest proportional losses of HCH. For example, up to 10.7% of the total HCH for bearded pig was projected to be lost from West Kalimantan by 2055 (Fig. 4). In East Kalimantan, notable losses occurred along connectivity linkages between Sungai Wain Protection Forest, Bukit Soeharto Grand Forest Park and Kutai National Park, the latter also showing substantial declines in HCH (Fig. 5). Protected areas otherwise exhibited the lowest projected losses (1.2% to 3.2% of total HCH), whereas up to 15% was predicted to be lost from production forest.

Bearded pigs (long-range dispersers) experienced the largest reductions, with extensive, continuous areas of HCH disappearing under future scenarios (Fig. 5). In contrast, mousedeer (short-range dispersers) exhibited losses as numerous small, fragmented patches, reflecting their more restricted movement potential and reliance on finer-scale habitat attributes.

Current flow histograms provide further evidence on the level of habitat fragmentation for each species (Fig. 6). For mousedeer, most of the current values are very close to zero, indicating habitat isolation. However, there is an abundance of suitable habitat patches in the landscape matrix, reflected by a relatively large standard deviation. Sun bears show intermediate mobility, demonstrated by higher mean cumulative flow. In contrast, the higher mobility of, and the more general habitat suitability for the bearded pig is well represented in the histogram's flatter distribution and much larger relative mean and standard deviation. For all species, the reduction in mean current flow across future scenarios indicates fewer cells supporting high flow due to habitat loss and increased fragmentation.

4. Discussion

Our landscape-scale assessment underscores the urgency of proactive spatial planning to mitigate the impacts of future land-use change and maintain functional connectivity across Borneo. Using Omniscape to model connectivity across Kalimantan for taxa with contrasting ecological traits, we identify three interlinked priorities for regional conservation planning: (1) protecting and restoring linkages between remnant lowland forests and protected areas, (2) safeguarding and enhancing permeability within production forests, and (3) embedding connectivity considerations into infrastructure and urban development, particularly around Indonesia's new capital city and the Northern segment of the Trans-Kalimantan Highway. Our analytical framework is transferable to other tropical regions experiencing rapid landscape transformation.

Our models of recent connectivity patterns reveal strong contrasts between interior and lowland forests. The interior uplands – largely encompassed by the Heart of Borneo initiative – retain extensive, well-connected forest networks both within and between protected areas, reflecting their relative remoteness and lower historical exposure to land-use pressures (Seaman et al., 2025). However, these higher elevations may be less permeable to predominantly lowland species such as mousedeer (Mendes et al., 2024), and remain comparatively undersampled, limiting our understanding of the assemblages they support. In contrast, lowland forests, despite their exceptional biodiversity, have experienced extensive conversion to agriculture and timber plantations since the 1970s (Gaveau et al., 2014; Seaman et al., 2025) which mirrors broader patterns across Southeast Asia where lowlands offer more favourable conditions for commodity production (Struebig et al., 2025). This has resulted in pronounced fragmentation and isolation of many lowland protected areas, corroborating earlier concerns for Borneo (Curran et al., 2004; Proctor et al., 2011) and aligning with global evidence that fewer than 10% of protected areas are structurally connected (Ward et al., 2020). Such isolation undermines their conservation effectiveness and elevates local extinction risk - as documented in some small reserves of Borneo (Mohd-Azlan et al., 2020) and globally (Williams et al., 2022). Our findings reinforce calls to move beyond simple area-based targets for meeting global biodiversity agendas such as 30 × 30 (CBD, 2022), but instead explicitly account for connectivity, representativeness and habitat quality to ensure their intended outcomes (Ward et al., 2020).

Given that only a fraction of Kalimantan is formally protected for conservation purposes, facilitating species' movement through the broader landscape matrix will be essential for long-term population persistence. Moreover, analyses focusing solely on linkages between protected areas risk overlooking ecologically important areas that remain unprotected, especially in regions where protected area placement is not ecologically representative (Poor et al., 2025). A key advantage of Omniscape is its ability to quantify connectivity across the full landscape matrix, enabling the identification of important regions that may be missed by core- or patch-based models (McRae et al., 2016). Our analyses show that production forests contribute up to two-thirds of Highly Connected Habitat, highlighting their critical role in maintaining landscape permeability. As 57% of Indonesia's forests are designated as production forest (Gunawan et al., 2022), sustainable management of these areas represents one of the most significant opportunities for retaining functional connectivity outside protected areas. Even selectively logged forests can support high biodiversity relative to plantations (Edwards et al., 2014), and function as corridors or stepping stones between intact habitats (Proctor et al., 2011), though their contribution remains vulnerable without effective management.

Projections to 2055 indicate further erosion of connectivity, particularly in East, Central, and West Kalimantan, disproportionately affecting lowland and production forests. Infrastructure remains one of the most immediate and significant threats to biodiversity and landscape connectivity across the tropics, driven by large-scale national and international initiatives (e.g., Belt and Road; Ng et al., 2020). Even under the low deforestation scenario, Highly Connected Habitat linking forests surrounding Indonesia's new capital site is projected to decline sharply for wide-ranging species. Given the importance of nearby Sungai Wain Protection Forest for regional hydrological services (Sukristiyono et al., 2021), fragmentation in this area could generate cascading socio-ecological impacts for both people and wildlife (Ferreira et al., 2019).

Our projections likely underestimate some future impacts as they cannot fully account for secondary deforestation associated with urban and road expansion, but previous research indicates that associated disturbances could extend up to 200 km from the capital development (Spencer et al., 2023; Teo et al., 2020). With the rapid growth of megacities and their associated species threats across Southeast Asia

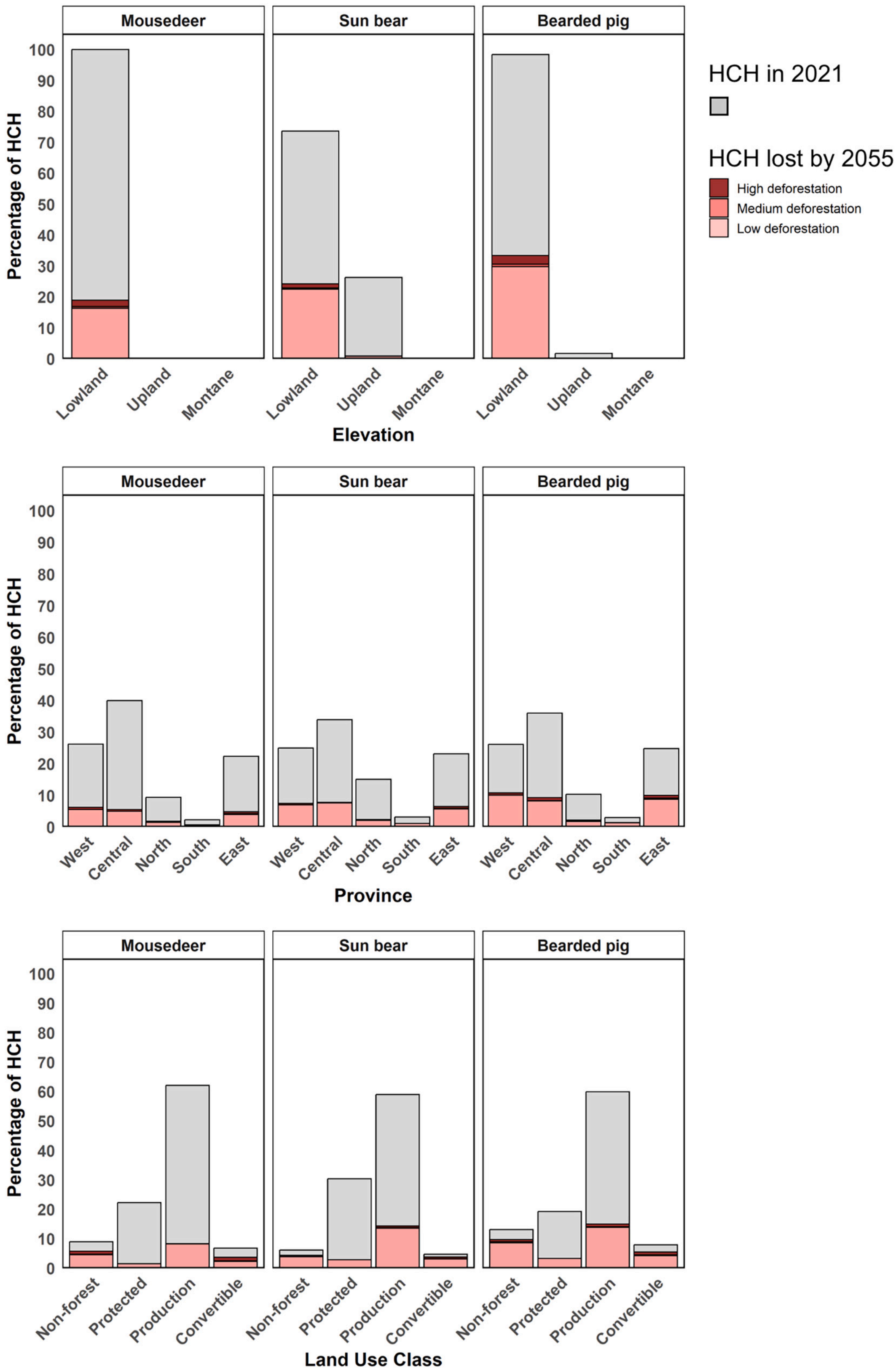

Fig. 4. Percentage of highly connected habitat (70th percentile of cumulative current flow) cells within each category of elevation, province and land-use class in 2021 (grey bars), and the proportion of those cells no longer classified as highly connected within each deforestation scenario by 2055.

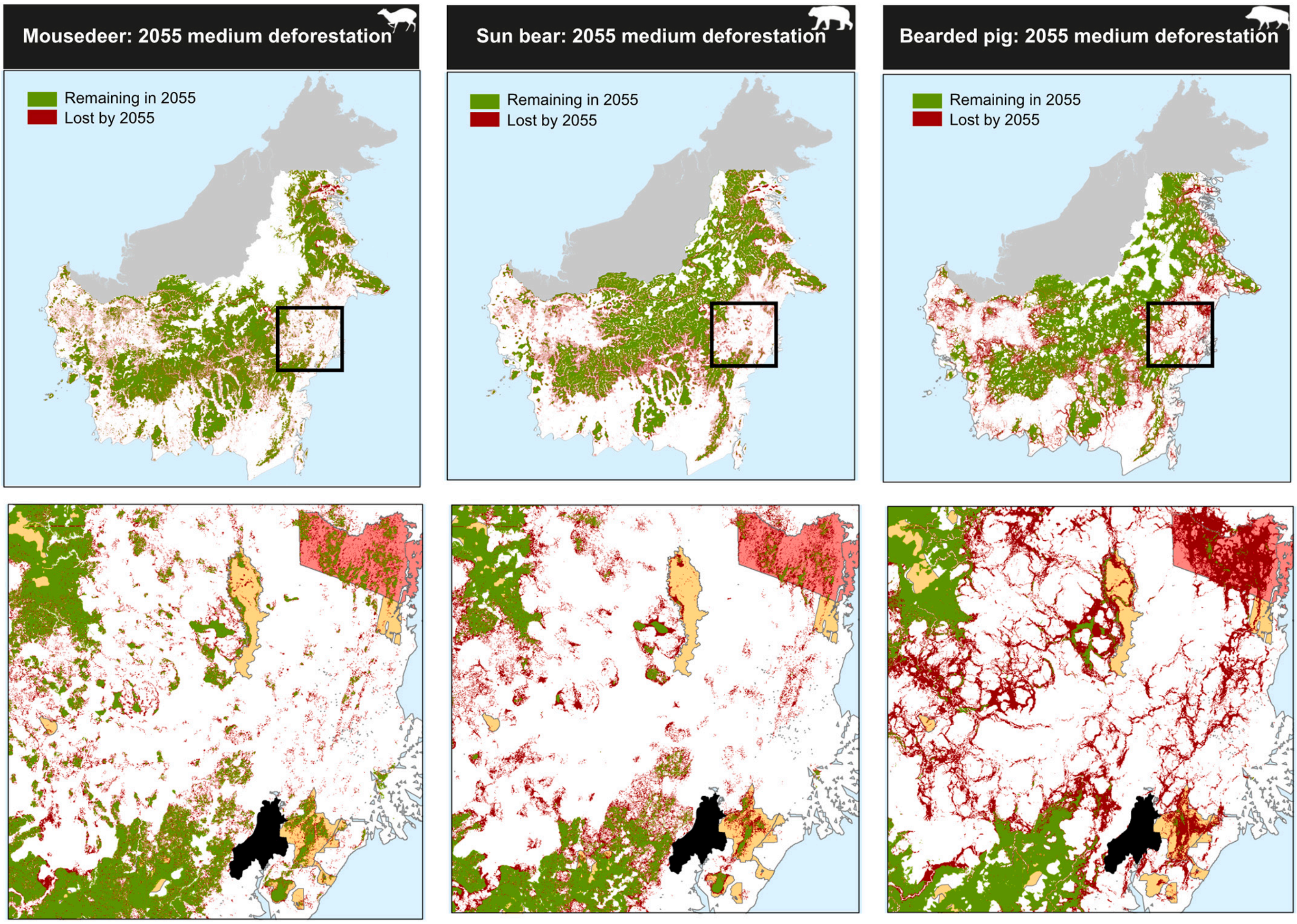

Fig. 5. Connectivity loss maps for each species under the medium-deforestation scenario and accompanying infrastructure development by 2055. Top Panel: Highly connected habitat (>70th percentile of current flow values) present in both 2021 and 2055 (green) and cells identified as HCH in 2021 but no longer by 2055 (red). Bottom panel: Insert zoomed into East Kalimantan near new capital development (black boundary), demonstrating more severe losses for wide-ranging species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Thaweepworadej and Evans, 2023), it will be important to manage urban sprawl and integrate green infrastructure for the new capital to achieve its "smart and sustainable forest city" vision (Nusantara Capital Authority, 2023). New infrastructure through the Heart of Borneo—particularly the Northern link of the Trans-Kalimantan Highway—poses an additional threat by intersecting one of the largest remaining blocks of Highly Connected Habitat. This transboundary region is also increasingly vulnerable to infrastructure expansion in Sabah, Sarawak, and Brunei Darussalam, including new highways and hydropower developments (Sloan et al., 2019). The high risks posed by this new linear infrastructure are consistent with Kaszta et al. (2024), who showed that the Northern segment will intersect a major core area for clouded leopards - potentially severing connectivity between populations in Sabah and Kalimantan. Road-induced deforestation is widespread in the Asia–Pacific, with many roads remaining unmapped in global datasets (Engert et al., 2024), suggesting that connectivity losses could be more severe than projected here.

In line with historical patterns (Seaman et al., 2025), lowland forests are projected to be especially vulnerable, with approximately one-third of all Highly Connected Habitat projected to be lost from these lower elevations. These impacts are likely to be compounded by climate change, as fragmented landscapes limit species' ability to track shifting climatic conditions (Hannah, 2010). Across the tropics, roughly 62% of forests (~10 million km^2) are already unable to support species' climate tracking, particularly in regions with extensive lowland deforestation, such as mainland Southeast Asia, the Brazilian Atlantic Forest, and West Africa (Senior et al., 2019). Key lowland linkages previously identified as critical for climate connectivity in Borneo (Struebig et al., 2025) were projected to lose highly connected status in our analysis, including corridors currently linking protected areas through East Kalimantan. Similarly, areas identified as "forest bridges" (i.e., forest linking otherwise isolated core forest blocks; Alamgir et al., 2019) lost highly connected status in our analysis, raising concerns for the long-term integrity of Borneo's forests.

4.1. Methodological considerations

Our study demonstrates the utility of Omniscape for applied conservation planning in large, heterogeneous landscapes. This approach allows every cell to function as a potential movement source rather than restricting analyses to predefined habitat cores, thereby offering a more ecologically realistic depiction of movement potential (Poor et al., 2025). This whole-landscape perspective reveals the importance of production forests and other non-protected areas that are often overlooked in patch-based approaches (Pither et al., 2023).

A frequent challenge for functional connectivity modelling is the limited availability of species-specific biological information for parametrising models (Keeley et al., 2021). We reduced subjectivity by

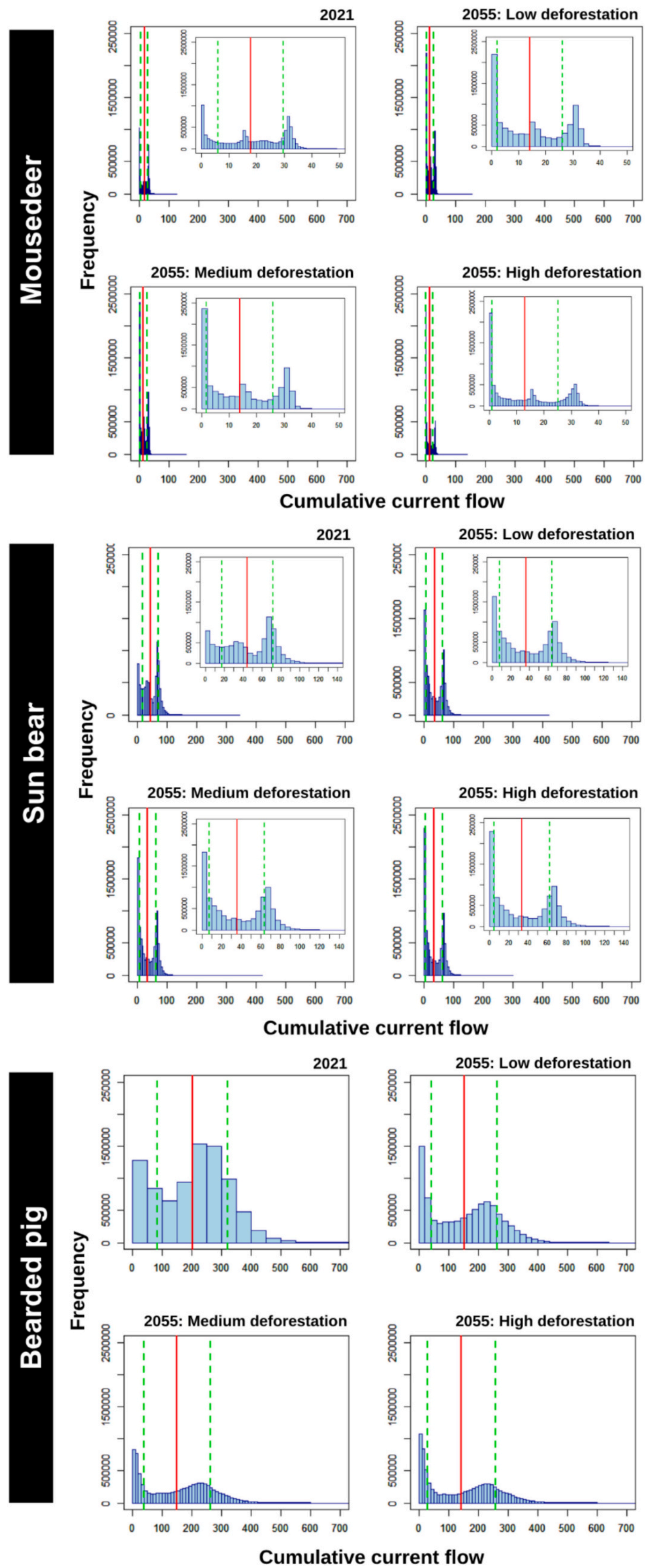

Fig. 6. Histogram representing the cell count (y-axis), against the intensity of cumulative current in each cell (x-axis). The red line represents the mean of current values; the green lines represent the standard deviation. Histograms are presented on the same scale for all species, accompanied by zoomed in figures as necessary. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

drawing on the most comprehensive camera-trap dataset available for Kalimantan, though additional sampling in high-elevation and non-forest habitats would further improve resistance estimates. As new ecological data become available (particularly through GPS and genetic studies), estimates of dispersal distances and source weights should be refined. Consequently, our outputs should be interpreted as relative indicators of connectivity among taxa with differing dispersal abilities and as an initial prioritisation to guide more fine-scale local assessments, rather than species-specific movement probabilities.

Using multi-scale search radii for the moving window enabled us to capture both localised pathways for low-mobility species (e.g., mouse-deer) and broader corridors for wide-ranging taxa (e.g., sun bear, bearded pig), offering local and regional insights essential for designing connectivity strategies to accommodate diverse ecological needs (Belote et al., 2022). Our findings suggest that broad analyses relying solely on large moving windows may risk overlooking locally important areas and stepping stones (Belote et al., 2022). Nonetheless, we also show that wide-ranging species are likely to experience broader swaths of connectivity losses, which reflects their dependence on extensive, contiguous habitat networks and contrasts with shorter-range dispersers that are better able to persist in smaller fragments of forest (Belote et al., 2022). Accompanying histograms of cumulative current flow provide further evidence for our findings as unlike current flow maps, they are not influenced by visualisation techniques, which is often not accounted for when interpreting connectivity maps (Martinez-Cillero et al., 2023). Finally, while finer spatial resolutions may reveal additional small habitat patches or barriers—particularly for short-range dispersers such as mousedeer—computational constraints precluded their use at the extent of Kalimantan. Considering mousedeer home range estimates fall below the spatial resolution of our analysis, results for short-range dispersers should be interpreted with greater uncertainty relative to mid- and long-range dispersers. We therefore encourage replication of this study at finer resolutions and smaller extents using locally relevant data, particularly through provincial or regency-level assessments co-developed with government, NGOs, and academic partners.

4.2. Conservation implications

Meeting global biodiversity targets requires identification, protection, and restoration of key connectivity areas, particularly in regions facing rapid land-use change. Several countries—including Kenya, Tanzania, Costa Rica, and Bhutan—have adopted national connectivity legislation, with similar initiatives proposed in Australia and the United States (Keeley et al., 2019). Given projected land-use changes across Indonesia (Seaman et al., 2025), integrating connectivity science into forest governance, land-use planning, and infrastructure decision-making will also be necessary to support long-term wildlife persistence. Our results highlight three complementary opportunities to mitigate connectivity loss in Kalimantan that are likely relevant across other tropical forest regions.

First, connectivity should be incorporated into protected area planning, particularly in lowland regions where reserves are increasingly isolated. Restoring linkages between small protected areas will be essential for successful dispersal gene flow and climate mitigation (Williams et al., 2022). This will require strengthening protection of buffer zones—often subject to logging or agricultural conversion (Dwiyahreni et al., 2021) — and strategically planning movement corridors that benefit multiple species (Brodie et al., 2015; Struebig et al., 2024). For example, collaboration between NGOs, government and local communities in West Kalimantan has led to an additional buffer zone created between Danau Sentarum and Betung Kerihun National Parks. The initiative helps transfer ownership of forest areas to traditional Indigenous owners, thus avoiding conversion to industrial agricultural plantations (SBL, 2025). Early corridor planning is critical, as the economic cost of linking protected areas is projected to increase by 65% by 2080 (Struebig et al., 2024). Mechanisms such as Other Effective Area-Based Conservation Measures (OECMs) offer additional pathways to enhance connectivity while contributing to 30 × 30 goals (Hughes et al., 2025; Brodie et al., 2025).

Second, production landscapes can play a critical role in maintaining functional connectivity. We found up to two-thirds of Highly Connected Habitat contributed to connectivity within this land-use designation, thus underscoring the importance of sustainable forest management in retaining permeability across logged and mixed-use landscapes. Conservation strategies commonly applied in production landscapes include supply chain certification systems (e.g. Forest Stewardship Council; Roundtable on Sustainable Palm Oil), payment for ecosystem service schemes, and community-based forest management (Struebig et al., 2025). Community forestry initiatives can help reduce deforestation (Santika et al., 2017), contribute to functional connectivity (Hughes et al., 2025), and maintain wildlife populations while also benefiting local communities (Gunawan et al., 2022). Corridors that incorporate production forests and traverse timber production areas, such as Sarawak's Kubaan-Puak corridor in Malaysian Borneo, illustrate how well-managed forestry landscapes can support functional ecosystems benefiting both wildlife and forest-dependent Indigenous communities (WWF, 2025).

Finally, connectivity assessments should be embedded directly into infrastructure and urban planning. Despite aspirations for a "forest city" at Indonesia's new capital, little information is available on how functional connectivity will be maintained beyond the urban core. Scenario-based connectivity modelling—such as Omniscape applications used in other planning contexts (Martinez-Cillero et al., 2023)—could support avoidance, mitigation, and green infrastructure design, helping reconcile sustainable development with biodiversity goals in Indonesia and across the tropics experiencing similar challenges.

CRediT authorship contribution statement

Katie L. Spencer: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nicolas J. Deere:** Writing – review & editing, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Dave J.I. Seaman:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Muhammad Aini:** Data curation. **Namrata B. Anirudh:** Data curation. **Ryan Avriandy:** Data curation. **Gail Campbell-Smith:** Writing – review & editing, Funding acquisition, Data curation. **Susan M. Cheyne:** Funding acquisition, Data curation. **Gabriella Fredriksson:** Data curation. **Robithotul Huda:** Data curation. **Joseph Hutabarat:** Data curation. **Andrew J. Marshall:** Writing – review & editing, Funding acquisition, Data curation. **Yaya Rayadin:** Project administration, Funding acquisition, Data curation. **Karmele L. Sanchez:** Data curation. **Endro Setiawan:** Data curation. **Stephanie Spehar:** Data curation. **Suanto:** Data curation. **Jito Sugardjito:** Supervision, Project administration. **Heiko U. Wittmer:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization. **Jatna Supriatna:** Supervision, Project administration. **Matthew J. Struebig:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111902.

Data availability

The authors do not have permission to share data.

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