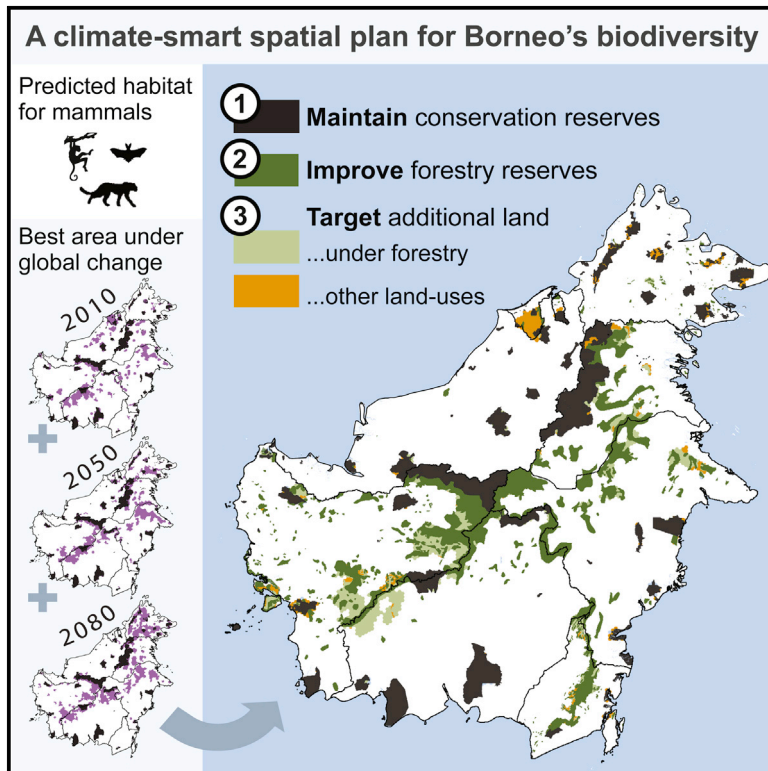


Current Biology

Targeted Conservation to Safeguard a Biodiversity Hotspot from Climate and Land-Cover Change

Graphical Abstract



Authors

Matthew J. Struebig, Andreas Wilting, ..., Kristian Metcalfe, Stephanie Kramer-Schadt

Correspondence

m.j.struebig@kent.ac.uk (M.J.S.), wilting@izw-berlin.de (A.W.)

In Brief

Struebig et al. show the impacts that future changes to land cover and climate could have on Borneo's mammals: a near doubling of species affected compared to the recent past. Mitigation requires improved conservation in non-protected land. Spatial analyses identify upland areas where conservation partnerships with forestry could be most effective.

Highlights

- Land-cover and climate change risk sizeable habitat loss for 49% of Borneo mammals
- These environmental changes could threaten 2× more species than in the recent past
- Better forestry management for conservation in upland areas would curb this loss
- Less land is needed for conservation in the future compared to the present day



Targeted Conservation to Safeguard a Biodiversity Hotspot from Climate and Land-Cover Change

Matthew J. Struebig,^{1,2,*} Andreas Wilting,^{3,*} David L.A. Gaveau,⁴ Erik Meijaard,^{4,5,6} Robert J. Smith,¹ The Borneo Mammal Distribution Consortium, Manuela Fischer,³ Kristian Metcalfe,^{1,7} and Stephanie Kramer-Schadt³

¹Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NR, UK

²School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK

³Leibniz Institute for Zoo and Wildlife Research, 10315 Berlin, Germany

⁴Center for International Forestry Research (CIFOR), P.O. Box 0113 BOCBD, Bogor 16000, Indonesia

⁵Borneo Futures, People and Nature Consulting International, Country Woods House 306, Jl. WR Supratman, Pondok Ranji-Rengas, Ciputat, Jakarta 15412, Indonesia

⁶Australian Research Council Centre of Excellence for Environmental Decisions, School of Biological Sciences, University of Queensland, Brisbane, QLD 4072, Australia

⁷Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, Cornwall TR10 9FE, UK

Summary

Responses of biodiversity to changes in both land cover and climate are recognized [1] but still poorly understood [2]. This poses significant challenges for spatial planning as species could shift, contract, expand, or maintain their range inside or outside protected areas [2–4]. We examine this problem in Borneo, a global biodiversity hotspot [5], using spatial prioritization analyses that maximize species conservation under multiple environmental-change forecasts. Climate projections indicate that 11%–36% of Bornean mammal species will lose $\geq 30\%$ of their habitat by 2080, and suitable ecological conditions will shift upslope for 23%–46%. Deforestation exacerbates this process, increasing the proportion of species facing comparable habitat loss to 30%–49%, a 2-fold increase on historical trends. Accommodating these distributional changes will require conserving land outside existing protected areas, but this may be less than anticipated from models incorporating deforestation alone because some species will colonize high-elevation reserves. Our results demonstrate the increasing importance of upland reserves and that relatively small additions (16,000–28,000 km²) to the current conservation estate could provide substantial benefits to biodiversity facing changes to land cover and climate. On Borneo, much of this land is under forestry jurisdiction, warranting targeted conservation partnerships to safeguard biodiversity in an era of global change.

Results and Discussion

Conservation planning tools can help evaluate protected area effectiveness under climate change [6], advocate new reserves for range-shifting species [4, 7], and incorporate climate adaptation into national assessments [8]. Yet, because few analyses also incorporate the biodiversity impacts of other anthropogenic threats, the ultimate planning needs for environmental change could be underestimated, leading to ineffective targeting of limited conservation resources [2, 4].

Our spatial analyses account for the effects of different climate and land-cover change forecasts on multiple tropical taxa. Borneo ranks among the most vulnerable biodiversity hotspots [9] and exemplifies many of the challenges facing conservation planning [5, 7]: biodiversity decline is predicted by global climate analyses [10] and high rates of habitat loss [11], and reliable distribution data are difficult to obtain. To undertake our assessment, we assembled a comprehensive distribution dataset of 81 mammal species (6,921 records of 13 primate, 23 carnivore, and 45 bat taxa) and developed a framework to model the extent of suitable habitat for each species, utilizing projected climate and land-cover data independently or additively. We identified areas of highest conservation value that could consistently meet minimum areal targets for each species following forthcoming environmental change. To minimize risk of commission and omission errors in our predictions (i.e., a species mistakenly thought to be present or absent, respectively), we accounted for potential sampling bias and incorporated models based on different climate data and presence thresholds, resulting in up to eight possible suitability maps for each species in each time slice (4,698 species-specific maps).

Changes to Suitable Habitat

Although our results demonstrate species-specific responses to environmental change, tracking the extent of suitable habitat between 2010 and 2080 reveals net declines for many species (Figure 1A). When considering climate projections alone (keeping land cover fixed to 2010 conditions), 11%–36% of Borneo's mammal species could lose $\geq 30\%$ of their 2010 habitat by 2080, a trend consistent for each taxonomic group assessed (Figure S2). While comparable losses via land-cover change are not predicted until the end of this century (2%–9% of species by 2050; 26%–41% by 2080), declines will be exacerbated by both processes acting together, resulting in 11%–40% of species losing $\geq 30\%$ habitat by 2050 and 30%–49% by 2080. This suggests that at least 14 carnivore, 4 primate, and 11 bat species could face a heightened risk of extinction by 2080 (<http://www.iucnredlist.org>) (Table S3), almost doubling the proportion of threatened mammals on the island. Habitat loss calculations derived from projections hindcasted to a time before major environmental changes (ca. 1950s) indicate that 16%–26% of species have already been exposed to comparable habitat loss, suggesting that the number of Borneo species affected by projected future changes could be almost double that of the recent past.

*Correspondence: m.j.struebig@kent.ac.uk (M.J.S.), wilting@izw-berlin.de (A.W.)

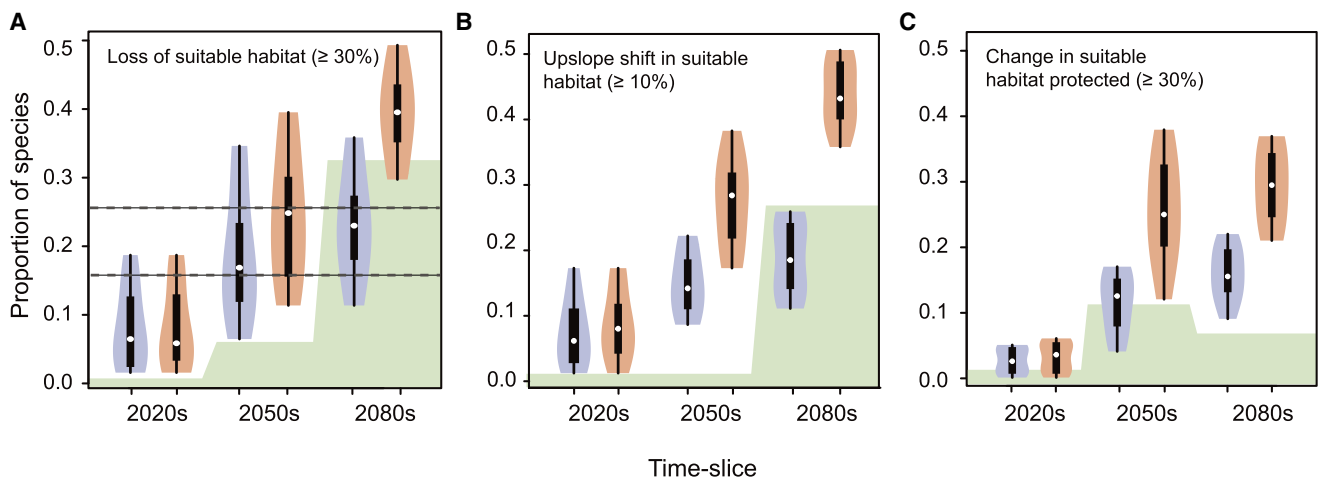


Figure 1. Proportion of Mammal Species Facing a Loss, Upslope Shift, or Increased Habitat Protection by the 2080s under Various Environmental Change Scenarios

(A–C) All changes are relative to areas predicted for 2010 baseline. Violin plots show variation (median, range, kernel density; 25th–75th percentiles) across eight model predictions, each using different climate, emission scenario, and presence threshold data. Blue shading indicates predictions based on climate-only distribution models; red shading indicates climate and land-cover distribution models combined. The green shaded area represents predictions based on land cover only (climate fixed to baseline). Dashed lines in (A) indicate former habitat loss (since ca. 1950s). For (B) and (C), the extent of suitable habitat was determined within 500-m elevation bands and existing conservation areas in baseline and future conditions. See also [Figure S2](#) and [Tables S1, S2, and S3](#).

Increasing Representation in High-Elevation Reserves

Many tropical species responding to climate change experience elevational shifts in suitable habitat conditions, making upslope range shifts and lowland biotic attrition likely [12, 13]. Our analyses suggest that 23%–46% of Borneo mammal species could be affected in this way by 2080 (Figure 1B), a problem particularly acute for carnivores and primates (Figure S2). The number of affected taxa is greater when also accounting for land-cover change because deforestation is projected to disproportionately affect lowlands (Figure S1). However, should species be able to colonize new areas, their representation within existing protected areas will improve over time (Figure 1C) since many of Borneo's largest conservation reserves are at mid to high elevation. Nonetheless, large areas of suitable lowland habitat will remain unprotected.

Spatial Prioritization to Mitigate Environmental Change

To identify the most important areas for biodiversity conservation under the environmental change forecasts, we used a coarse-filter minimum-set framework (to conserve aggregations of species [14]) that prioritized areas in each time slice to meet population targets for each species while minimizing conservation cost. For each environmental scenario, analyses were run separately for each time slice (81 species targets, for baseline, 2050 and 2080) and combined (243 targets). Since species conservation goals have influenced Borneo's reserve design, we considered threat status, population viability, and former range size when setting species-specific area targets (Table S4). This resulted in a target shortfall in existing conservation reserves for 22 species in 2010.

These analyses reveal that more land is required outside reserves if cumulative changes to suitable habitat are anticipated for the future, compared to planning for present-day conditions or for any time slice in isolation (Figure 2A). However, less land is required overall if species' responses to land-cover and climate change are considered together rather

than if the effects of land-cover change are considered alone (Figure 2C), a finding we attribute to greater species representation at higher elevation following climate change.

All patterns are consistent across the scenarios we assessed, but substantial variation in the best area selected is evident across combined models (~82,000–121,000 km²), with much of this discrepancy attributed to the choice of species presence threshold used (Table 1). The greatest differences are evident for the interior lowlands of northern Borneo, although connections between currently small and fragmented reserves are consistently identified (Figure 3). While sub-optimal for any single environmental change scenario, conserving a core area consistently identified by the majority of prioritization models (≥75% consensus) would account for climate projection uncertainty within ~29,000 km² of additional land (Table 1). This represents approximately one-half of the area selected for present-day environmental conditions and incorporates much of Borneo's mid-elevation interior (Figure 3). However, this would still fall short of meeting some species targets, which for present-day conditions would mean underrepresenting 13 species, including eight classified as threatened (<http://www.iucnredlist.org>). The problem would be marginally improved by conserving additional areas of moderate model agreement (50%–74% consensus in ~57,000 km², target shortfall for nine species; Tables 1 and S3), but additional conservation management would still be needed to safeguard remaining taxa.

Where to Target Conservation Investment

Between 21% and 25% of the best areas we provisionally identify under combined climate and land-cover change forecasts are outside conservation reserves but are designated some protection under forestry as permanent natural forest areas. To better understand the potential conservation role of these areas, we reran prioritization analyses with this land use explicitly protected. We found similar trends to our previous assessment (Figures 2B, 2D, and 2F) but with subtle

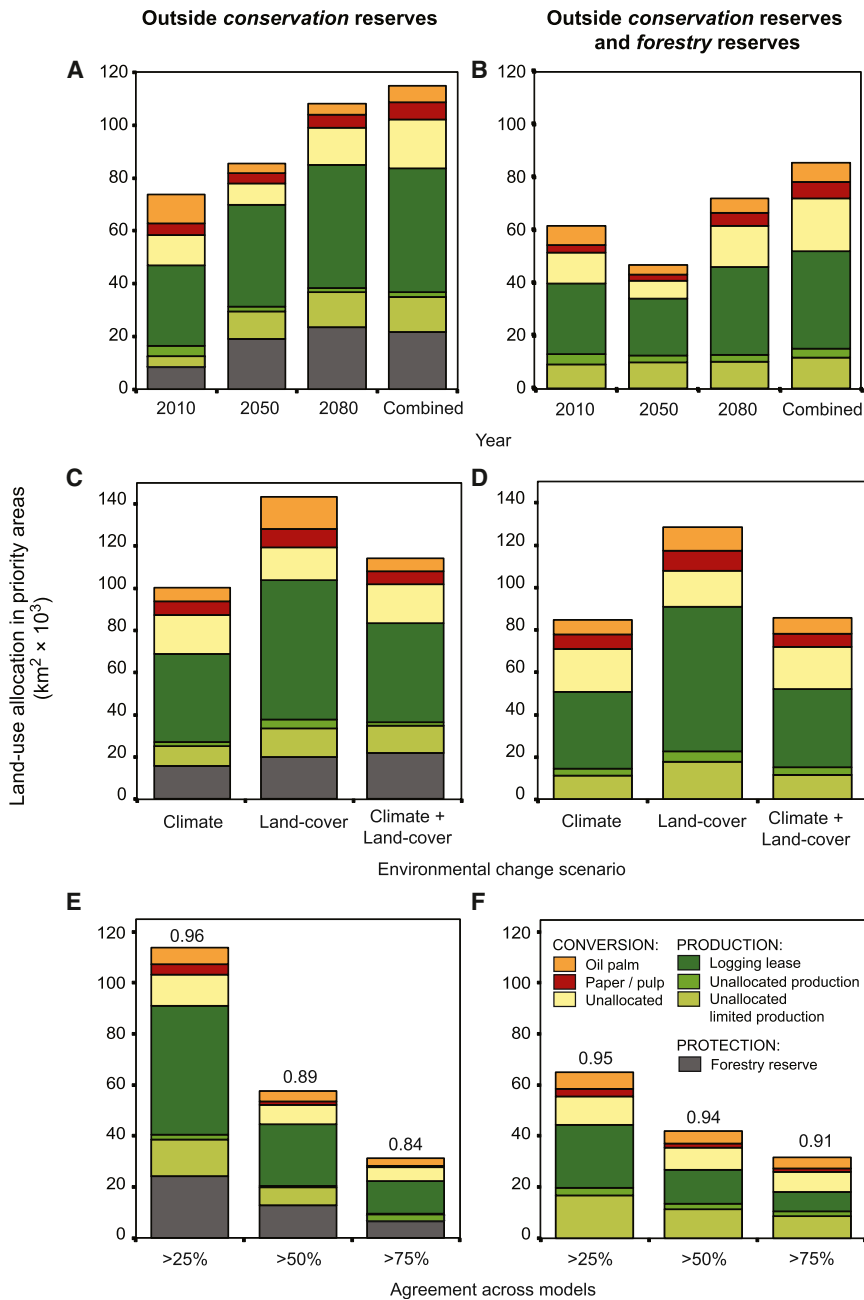


Figure 2. Extent and Land Use within Priority Areas for Borneo Mammal Conservation under Environmental Change Forecasts

(A and B) Meeting species targets across multiple time slices requires more land than each period alone.

(C and D) Accounting for the effects of both land-cover and climate change requires less land than anticipating land-cover change alone.

(E and F) Area of consensus among eight prioritization models based on different thresholds, climate, and emission data; numbers indicate the proportion of baseline targets met.

(A), (C), and (E) consider species representation in conservation reserves before spatial selection. (B), (D), and (F) consider representation in conservation and additional forestry reserves. (A)–(D) are for a single model (CSIROMk2-A2; 25% threshold) but represent trends of others.

partnerships will likely come from the forestry industry in Indonesian Borneo and from plantation and extractive industries in Malaysia and Brunei (Table S5).

Advances and Limitations

Large-scale spatial planning requires strong assumptions about species distributions and ecological processes (e.g., spatial data fully encapsulate a species's environmental niche, and relationships between species and their environment are unchanging over time [2, 7]). Nevertheless, planning outputs can help direct and inform conservation efforts to areas and potential partners that might otherwise be avoided or neglected.

Many forward-looking conservation plans focus on the dynamic nature of climate and assume limited effects of changing land cover [4, 6–8]. By treating the effects of these threats separately, our framework allows for a more realistic assessment of habitat suitability and the costs needed to optimize species representation. While using climate and

differences in area selected (Figure 3C). Conserving the area of greatest consensus under these land-use conditions would meet more species targets in less additional land (Table 1). In at least one-half of the selection models, all but five species could be adequately represented in an additional $\sim 28,000 \text{ km}^2$ (4% of Borneo), primarily under forestry jurisdiction (Figure 2F). Two of these species (otter civet, *Cynogale bennettii*; large flying fox, *Pteropus vampyrus*) are predominantly wide-ranging lowland mammals, and targets would be difficult to meet at high elevation under any prioritization. Hence, this likely represents the optimal spatial plan. Crucial to targeting conservation partnerships is that 46% of this land is already managed as timber concessions or plantations (8%), but 44% is allocated for these land uses but not yet leased (Table 1). Our analyses indicate that the most critical

habitat predictors together in distribution models can improve explanatory power [15], partitioning this information is more appropriate for regions undergoing rapid land-use change (i.e., with a temporal mismatch between land cover and species presence information). Although the land-cover data and expert information required to implement our procedures more broadly across the tropics are increasingly available [11, 16], we advocate further localized assessments so that model outcomes can best inform environmental policy.

We recognize that additional sources of uncertainty from other climate models, emission scenarios, or modeling algorithms could be incorporated into our habitat suitability assessment, allowing us to refine and further quantify variation in our estimates. Refinements also include incorporating demographic processes [17], although we note that for most tropical

Table 1. Land Use in Priority Areas for Borneo's Mammals under Combined Land-Cover and Climate Change Projections between 2010 and 2080

| Model | Fraction Shortfall in Targets | Area (km ²) | Land-Use Allocation of Priority Area (Fraction of Total) | | | | | | |
|---------------------------------------|-------------------------------|-------------------------|--|---------------|---------------------------------|------------------------|-----------------------|---------------------|-------------|
| | | | Production Forest | | | Conversion Forest | | | |
| | | | Forestry Reserve | Logging Lease | Unallocated, Limited Production | Unallocated Production | Paper/Pulp Plantation | Oil Palm Plantation | Unallocated |
| CSIROmk2-A2; 10% | 0.21 (0.09) | 84,146 (48,545) | 0.24 | 0.43 (0.45) | 0.12 (0.24) | 0.01 (0.03) | 0.04 (0.06) | 0.04 (0.05) | 0.11 (0.17) |
| CSIROmk2-A2; 25% | 0.27 (0.13) | 107,330 (75,173) | 0.21 | 0.44 (0.53) | 0.12 (0.15) | 0.02 (0.03) | 0.05 (0.07) | 0.02 (0.03) | 0.13 (0.19) |
| CSIROmk2-B2; 10% | 0.21 (0.07) | 82,388 (39,060) | 0.24 | 0.44 (0.49) | 0.15 (0.24) | 0.02 (0.03) | 0.04 (0.05) | 0.04 (0.04) | 0.08 (0.15) |
| CSIROmk2-B2; 25% | 0.26 (0.12) | 121,036 (91,276) | 0.22 | 0.40 (0.50) | 0.11 (0.14) | 0.02 (0.03) | 0.06 (0.08) | 0.04 (0.05) | 0.15 (0.20) |
| Hadcm3-A2; 10% | 0.21 (0.07) | 83,767 (28,835) | 0.25 | 0.40 (0.40) | 0.14 (0.21) | 0.03 (0.04) | 0.03 (0.06) | 0.05 (0.09) | 0.10 (0.21) |
| Hadcm3-A2; 25% | 0.26 (0.08) | 93,570 (52,518) | 0.21 | 0.47 (0.53) | 0.11 (0.18) | 0.03 (0.04) | 0.05 (0.05) | 0.06 (0.06) | 0.08 (0.14) |
| Hadcm3-B2; 10% | 0.20 (0.07) | 82,233 (30,502) | 0.23 | 0.42 (0.45) | 0.15 (0.21) | 0.04 (0.03) | 0.04 (0.04) | 0.03 (0.06) | 0.09 (0.20) |
| Hadcm3-B2; 25% | 0.25 (0.08) | 90,205 (53,896) | 0.21 | 0.48 (0.57) | 0.11 (0.17) | 0.03 (0.04) | 0.04 (0.03) | 0.04 (0.07) | 0.09 (0.12) |
| High consensus: >75% (7–8 models) | 0.16 (0.09) | 29,074 (15,885) | 0.21 | 0.40 (0.24) | 0.09 (0.27) | 0.01 (0.07) | 0.18 (0.24) | 0.02 (0.04) | 0.10 (0.14) |
| Moderate consensus: >50% (5–8 models) | 0.12 (0.06) | 56,787 (27,854) | 0.25 | 0.46 (0.46) | 0.14 (0.22) | 0.02 (0.04) | 0.02 (0.04) | 0.02 (0.04) | 0.09 (0.18) |

Priority areas are selected after accounting for species representation within existing conservation reserves and represent the optimal solution among Marxan and MinPatch analyses that combined 243 species areal targets for projected suitable habitat in 2010, 2050s, and 2080s. Results are presented for each climate model (CSIROmk2 and Hadcm3 under A2 and B2 emission scenarios) presence threshold (10% and 25% error) combination. Additional prioritization analyses were run that considered land-cover or climate changes in isolation and for each time slice separately (i.e., 81 species targets). Values in parentheses are for priority areas outside of forestry reserves as well as conservation reserves (i.e., assuming forestry reserves also form part of the conservation estate). The shortfall in targets for consensus models is for 81 species in 2010 conditions. See also [Table S5](#).

species, insufficient information is available. Such enhancements would unlikely change our conclusions since prioritization analyses are generally more influenced by cost than by alternative biodiversity features [18]. Even if biodiversity data were changed, we expect upland areas to still be prioritized because development is cheaper at accessible low elevations, and land-cover and climate changes disproportionately affect lowlands.

Conservation Policy Implications

While predicting a pessimistic outlook for Borneo's biodiversity, our analyses indicate that a reevaluation of the conservation estate could be beneficial. To best plan for the effects of land-cover and climate change, we demonstrate that improved conservation outside existing reserves will be necessary to meet biodiversity goals. Protected areas are important for species expanding or shifting ranges under a changing climate [19, 20], a finding supported by increasing species representation in reserves within our projection time frame (Figure 1C). Although there have been some recent steps to designate new conservation reserves in Borneo, land reallocation at the scale required to account for environmental change impacts would be difficult to implement island-wide. Downgrading reserves that underachieve conservation objectives is one way to free up land elsewhere [21], but we find this difficult to justify given additional conservation values inherent to lowland tropical forests (e.g., carbon-rich peatland reserves [22]).

Improved management of forests outside existing reserves could help ameliorate biodiversity losses, as is becoming apparent across the tropics [23]. Forestry, as the dominant land use in our priority areas (Table 1), potentially makes a practical conservation partner since the biodiversity impacts of selective logging can be limited [24, 25]. To be most effective in logging areas, conservation partnerships could promote best management practices [26]. Hunting, which exacerbates mammal declines in Borneo's logged forests [27], would need to be curtailed. Most priority areas identified (89%) are within 5 km of logging roads [28], suggesting that closing roads to

hunters and illegal loggers following operations could prevent biodiversity declines (J.E. Bicknell, D.L.A.G., Z.G. Davies, and M.J.S., unpublished data).

While we demonstrate the importance of buffering existing mid to high elevation reserves in Borneo's interior, several large reserves remain isolated in the coastal lowlands (Figure 3). The ability of lowland species to disperse to upland areas within the pace of global change is therefore concerning, especially for taxa with area targets difficult to meet (Table S4). Additional conservation partnerships in intervening lands could help enhance connectivity between these areas by promoting forested corridors (e.g., northern Borneo [17, 29]) or reduced impact land uses in agricultural mosaics. Although conservation partnerships with agriculture are constrained by the low biodiversity value of tropical monocultures [24], substantial areas of high conservation value have already been allocated for plantation in Borneo (Table 1), making the design of managed landscapes in appropriate areas central to sustaining biodiversity. We identify the key areas and partnerships required with logging and plantation industries to help achieve long-term biodiversity conservation in Borneo and demonstrate a spatial framework to undertake similar appraisals in the world's remaining biodiversity hotspots.

Experimental Procedures

Delineating Climatically Suitable Areas

We applied the maximum entropy algorithm [30] to generate a baseline bioclimatic model for each species from presence data and 25 environmental variables at ca. 1-km² resolution, while accounting for sampling bias and model complexity [31] (Supplemental Experimental Procedures). Each map provided a robust representation of species presence according to model accuracy and expert verification (Table S1). Models were projected into future climates for 2020, 2050, and 2080 time slices, using downscaled data from four scenarios: two global circulation models under two contrasting emission storylines, from the Intergovernmental Panel on Climate Change. Although data from additional climate models would contribute more variation to model projections, the four variants were chosen to reflect a range of values appropriate to the region, time frame, and resolution of the study (Figure S1).

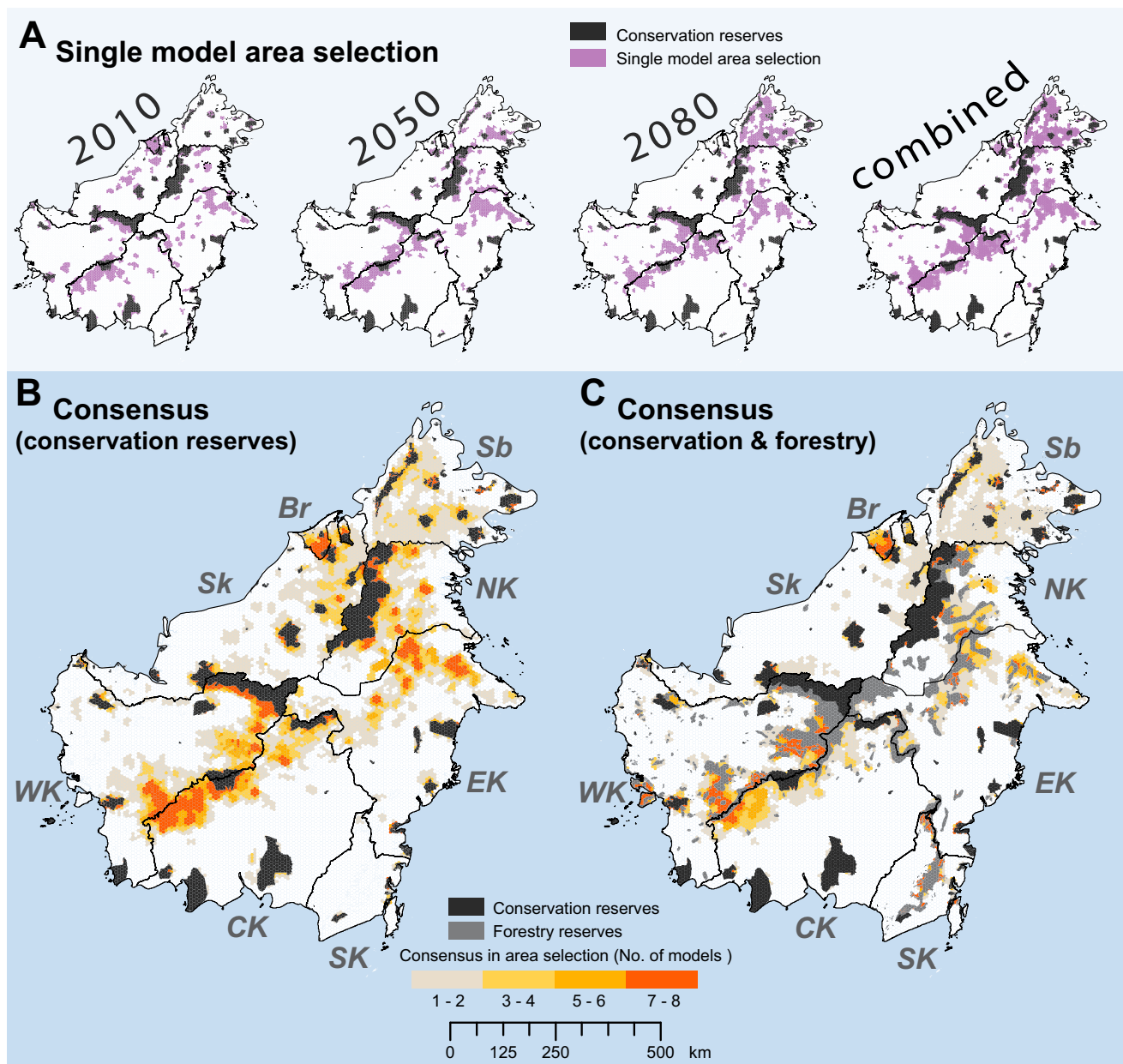


Figure 3. Priority Areas to Direct Conservation Efforts that Safeguard Borneo Mammals from Climate and Land-Cover Change

(A–C) Maps in (A) show the area required for land-cover and climate conditions in each time slice and over the combined projection time frame (i.e., 2010 baseline + 2050 + 2080, with each environmental condition specific to the time slice). Outcomes are according to a single model (CSIROMk2-A2 climate data; 25% threshold) of eight variants, with each utilizing different climate, emission, and threshold data. The priority area is identified after accounting for the proportion of each species range already represented in conservation reserves. Overlaps among these eight model outcomes indicate the greatest consensus in area selection when considering existing species representation in conservation reserves (B) or extending the conservation estate to include forestry reserves (C). State labels are as follows: Br, Brunei; Sb, Sabah; and Sk, Sarawak in Malaysia; and WK, West; EK, East; NK, North; SK, South; and CK, Central Kalimantan in Indonesia. See also [Figure S1](#) and [Table S4](#).

Land-Cover Change Projections

We used a 2000–2010 trajectory of forest loss over Indonesian Borneo to map deforestation [28] and predict the probability of forest loss in any given 1-km² cell using a generalized linear model (binomial error) and ten explanatory landscape variables [32]. Assuming future deforestation would follow recent trends, we reclassified cells with the highest deforestation probabilities for any given year (2020, 2050, 2080) to non-forest classes ([Supplemental Experimental Procedures](#); [Figure S1](#)). Based on the 10-year dataset extrapolated to the whole island, forest conversion would comprise 3.2 million ha by 2020, 12.9 million ha by 2050, and 22.6 million ha by 2080 [32].

Reclassifying CSAs for Habitat Suitability

Land-cover changes were incorporated into distribution models by reclassifying species-specific presence probabilities from climatically suitable areas (CSAs) using a habitat suitability (HS) index modified from [33]: $HS_{i,y} = (M_{i,yc}^2 \times L_{i,y}^3 \times P_i)^{1/6}$. Here, M is the relative presence probability associated with a cell for species, i , in the respective year's climate scenario, yc (i.e., species-specific CSA for each time slice). L is the cells' associated land-cover suitability score for each time slice, yl (derived from deforestation predictions), and P_i is a human population sensitivity score, both defined via an expert-derived scoring exercise for each species (i) ([Supplemental Experimental Procedures](#); [Table S2](#)). We also repeated

analyses to represent the situation prior to major human-induced environmental changes in Borneo (ca. 1950s). We applied two omission error thresholds, strict (25%) or liberal (10%), to convert the resulting HS presence probabilities into binary (suitable, unsuitable) maps.

Spatial Prioritization

We divided Borneo into 50 km² hexagonal planning units and calculated the area of each species in each unit under the different environmental scenarios. Planning units were designated as protected or non-protected. To select the most important areas from those available, we employed a simulated annealing algorithm to identify planning unit portfolios that met minimum area targets for each species in a given time slice at minimum conservation cost.

Species-specific area targets were calculated as home range size multiplied by minimum population size [34], stratified by threat status but capped to a fixed percentage of the former distribution (Supplemental Experimental Procedures; Table S3). We used accessibility as a proxy for conservation cost (planning units with highest cost are closest to settlements), which we calculated as a distance function to human settlements to represent high opportunity costs of agriculture and forestry near infrastructure [35] and the greater threats from hunting and disturbance near populated areas. Our procedures aimed to meet the target shortfall outside protected areas and specific to each time slice by prioritizing additional land connected to the reserve network to avoid prioritizing fragments. For each environmental scenario, analyses were run separately for each time slice and combined. We modified portfolios to ensure selected areas met a minimum size threshold [36] of 250 km² (five planning units; approximating the mean conservation reserve size on Borneo) and maximized connectivity to the existing protected area network. For each scenario, we identified the portfolio with lowest cost as the best solution, overlaid these outputs to determine model consensus, and extracted land-use allocation from 2010 maps [28].

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, two figures, and six tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.11.067>.

Consortia

The members of The Borneo Mammal Distribution Consortium are Tajuddin Abdullah, Nicola Abram, Raymond Alfred, Marc Ancrenaz, Dave M. Augeri, Jerrold L. Belant, Henry Bernard, Mark Bezuijen, Arjan Boonman, Ramesh Boonratana, Tjalle Boorsma, Christine Breitenmoser-Würsten, Jedediah Brodie, Susan M. Cheyne, Carolyn Devens, J. Will Duckworth, Nicole Duplaix, James Eaton, Charles Francis, Gabriella Fredriksson, Anthony J. Giordano, Catherine Gonner, Jon Hall, Mark E. Harrison, Andrew J. Hearn, Ilya Heckmann, Matt Heydon, Heribert Hofer, Jason Hon, Simon Husson, Faisal Ali Anwarali Khan, Tigga Kingston, Danielle Krebs, Martjan Lammertink, David Lane, Felicia Lasmana, Lim Boo Liat, Norman T-L. Lim, Jana Lindenborn, Brent Loken, David W. Macdonald, Andrew J. Marshall, Ibnu Maryanto, John Mathai, William J. McShea, Azlan Mohamed, Miyabi Nakabayashi, Yoshihiro Nakashima, Jürgen Niedballa, Sephy Noerfahmy, Sophie Persey, Amanda Peter, Sander Pieterse, John D. Pilgrim, Edward Pollard, Surya Purnama, Andjar Rafiastanto, Vanessa Reinfelder, Christine Reusch, Craig Robson, Joanna Ross, Rustam Rustam, Lili Sadikin, Hiromitsu Samejima, Eddy Santosa, Iman Sapari, Hiroshi Sasaki, Anne K. Scharf, Gono Semiadi, Chris R. Shepherd, Rachel Sykes, Tim van Berkel, Konstans Wells, Ben Wielstra, and Anna Wong. A full list of affiliations for The Borneo Mammal Distribution Consortium members can be found in Table S6.

Author Contributions

M.J.S. conceived the study, assembled the team, and managed the paper. M.J.S., A.W., and E.M. processed, verified, and georeferenced mammal locality records together with The Borneo Mammal Distribution Consortium. M.F., A.W., and S.K.-S. modeled species habitat suitability, projected into future time frames, and undertook area calculations. D.G. developed land-cover projections, and M.J.S., R.J.S., and K.M. undertook spatial prioritization analyses.

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