# Deforestation projections imply range-wide population decline for critically

# endangered Bornean orangutan

Maria Voigt<sup>1,2,3,1</sup>, Hjalmar S. Kühl<sup>1,2</sup>, Marc Ancrenaz<sup>4,5</sup>, David Gaveau<sup>6</sup>, Erik Meijaard<sup>3,4</sup>, Truly

Santika<sup>3,4,7,8</sup>, Julie Sherman<sup>9</sup>, Serge A .Wich<sup>10,11</sup>, Florian Wolf<sup>1</sup>, Matthew J. Struebig<sup>3</sup>, Henrique M.

Pereira<sup>1, 12, 13</sup>, Isabel M.D. Rosa<sup>14</sup>.

<sup>1</sup> German Centre for Integrative Biodiversity Research (iDiv) Halle – Jena – Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany.

<sup>2</sup> Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany.

<sup>3</sup> Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NR, UK.

<sup>4</sup> Borneo Futures, Bandar Seri Begawan, Brunei Darussalam.

<sup>5</sup> HUTAN-Kinabatangan Orang-utan Conservation Programme, Sandakan, Sabah, Malaysia.

<sup>6</sup> TheTreeMap, Bagadou Bas, 46600 Martel, France

<sup>7</sup> The University of Queensland, School of Biological Sciences, Brisbane, QLD, Australia.

<sup>8</sup> Natural Resources Institute (NRI), Agriculture, Health and Environment Department, University of Greenwich, Chatham Maritime, UK.

<sup>9</sup> Wildlife Impact, PO Box 31062, Portland, OR 97231, USA.

<sup>10</sup> School of Biological and Environmental Sciences, Liverpool John Moores University, Byrom Street, Liverpool, L3 3AF, United Kingdom.

<sup>11</sup> Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, The Netherlands.

<sup>12</sup> CIBIO/InBio, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado Universidade do Porto, Vairão, Portugal.

<sup>13</sup> CEABN/InBio, Centro de Ecologia Aplicada "Professor Baeta Neves", Instituto Superior de Agronomia Universidade de Lisboa, Lisbon, Portugal.

<sup>14</sup> School of Natural Sciences, Bangor University, Bangor, Gwynedd, LL57 2DG, UK.

<sup>&</sup>lt;sup>1</sup> Correspondence: m.ddlvoigt@gmail.com

#### 1 Abstract

2 Assessing where wildlife populations are at risk from future habitat loss is particularly important for 3 land-use planning and avoiding biodiversity declines. Combining projections of future deforestation with species density information provides an improved way to anticipate such declines. Using the 4 5 critically endangered Bornean orangutan (Pongo pygmaeus) as a case study we applied a spatio-6 temporally explicit deforestation model to forest loss data from 2001-2017 and projected future 7 impacts on orangutans to the 2030s. Our projections point to continued deforestation across the 8 island, amounting to a potential loss of forest habitat for 26,200 orangutans. Populations currently 9 persisting in forests gazetted for industrial timber and oil palm concessions, or unprotected forests 10 outside of concessions, were projected to experience the worst losses within the next 15 years, amounting to 15,400 individuals. Our analysis indicates the importance of protecting orangutan 11 habitat in plantation landscapes, maintaining protected areas and efforts to prevent the conversion of 12 13 logged forests for the survival of highly vulnerable wildlife. The modeling framework could be expanded to other species with available density or occurrence data. Our findings highlight that 14 15 species conservation should not only act on the current information, but also anticipate future 16 changes to be effective.

**Keywords:** Biodiversity hotspots, Density distribution model, Future forest loss, *Pongo pygmaeus*, Tropics, Southeast Asia,

# 17 **INTRODUCTION**

Borneo is globally important for biodiversity but experiences some of the highest deforestation rates in the world. Since 1973, the island lost >30% of its original old-growth forest cover to agriculture, plantations, mining, infrastructural development, and forest fires. To reduce these deforestation pressures on the natural environment, land-use planning and conservation should incorporate insights from past patterns and drivers of land-use change and consider potential future deforestation trajectories.

Advances in spatially-explicit and dynamic deforestation modeling offer new ways to study current and expected future forest loss in the tropics (Rosa et al., 2013). In comparison to previous approaches (Lapola et al., 2011; Soares-Filho et al., 2006), these models dynamically project deforestation as a sum of local events, influenced by past patterns of various drivers, rather than imposing a fixed deforestation rate based on historical trends. While deforestation projections have been more commonly applied in South America (Rosa et al., 2013; Silva et al., 2020), there are far fewer assessments available for Southeast Asia despite this being a region of high forest loss (Voigt et al., 2021).

32 Recent increases in the availability of species observation data, as well as advances in computational power and statistical methods, provide improved estimates of range-wide species 33 density distributions (e.g., Strindberg et al., 2018; Wich et al., 2016). A density distribution model 34 35 for the Bornean orangutan (Pongo pygmaeus), for example, indicated that the population declined by 30% (>100,000 individuals) between 1999 and 2015 (Voigt et al., 2018). Large-scale 36 37 deforestation, together with killing in conflict or for food, severely threatens the long-term population viability of this species and stable orangutan populations only persist in landscapes with 38 39 sufficient forest cover (Ancrenaz et al., 2016).

40 Here we use the Bornean orangutan as a case-study to demonstrate how coupling of 41 deforestation projections with density distribution models can help estimate future population 42 impacts of land-cover change on a forest dependent species that has been classified as 'Critically 43 Endangered' by the IUCN (Ancrenaz et al., 2016). We tailored a deforestation model to each Bornean administration within the orangutan range (five Indonesian provinces; two Malaysian 44 45 states - hereafter all referred to as provinces), identified drivers and patterns of land-cover change in 46 the past (2000-2017), and projected them into the future (2018-2032) under a business-as-usual 47 scenario. By identifying the population units most vulnerable to potential future deforestation, our approach can be used to guide pre-emptive conservation efforts and serve as baseline against which 48 49 certain policy interventions can be tested. The approach could be equally as valid for other species and regions where wildlife information and deforestation trends are well documented. 50

# 51 **METHODS**

## 52 Forest maps and deforestation drivers

53 We utilized a previously published dataset specific to Borneo, quantifying natural forest loss

54 between 2001 and 2017 at a resolution of 30 m (Gaveau et al., 2019, Table S1). Forest loss or

55 deforestation is defined as the permanent annual removal of intact or logged old-growth forest that

56 is closed-canopy (>80% cover), and includes high-carbon evergreen dipterocarps on mineral or peat

57 soils, low-biomass pole forests on peat domes, heath forest, and mangroves (Gaveau et al., 2019).

58 Intact and selectively logged forests are similar to "primary" and "secondary" forests on the

Indonesian Ministry of Forestry and Environment's forest maps (MoEF, 2018).

59

60 Patterns of tropical deforestation are shaped by physical and accessibility characteristics, 61 anthropogenic pressures, and land-use (Austin et al., 2019; Curtis et al., 2018). We compiled spatial 62 data on elevation, and distance to roads and rivers, indicating ease of access to the forest; human 63 population density and fire occurrence to represent human pressure; and official land-use designation (Table S1, Supporting Information S1). Land-use was categorized as protected areas 64 (IUCN and UNEP-WCMC, 2017), industrial plantation and logging concessions, as well as 65 unprotected areas outside of concessions (Santika et al., 2015). The selection was based on 66 67 literature describing important drivers of deforestation in the tropics and for Borneo specifically (Austin et al., 2019; Rosa et al., 2013; Struebig et al., 2015). 68

All layers were converted to the Asia South Albers Equal Area Conic projection and
 resampled to the same extent and origin at 1 km<sup>2</sup> pixel size, the highest resolution common to all
 layers, using bilinear interpolation for continuous predictors and nearest-neighbor interpolation for
 categorical predictors. Spatial manipulations and analyses were undertaken in Python (Python
 Software Foundation, 2019), R (R Core Team, 2020) and ArcGIS (Esri Inc., 2014).

### 74 **Deforestation model framework**

We used the modeling approach developed by Rosa et al. (2013) to project the probability of 75 76 future deforestation for each Bornean province. The model accounts for stochasticity of 77 deforestation, and province-wide forest loss rates emerge as the sum of local deforestation events, 78 resulting from the influence of drivers operating in each particular province. Using a forward-79 stepwise model selection, all non-correlated predictors (Pearson's correlation coefficient <0.7) were 80 successively added to a model, which was fitted to five years of forest loss data from 2013–2017 (calibration period). We selected this calibration interval length by considering the trade-off 81 82 between short intervals, potentially reflecting exceptional years, or long intervals, potentially including outdated trends (Rosa et al. (2015). 83

For each province a cross-validation technique was used to assess the predictive power gained by iteratively adding predictors to the model. Half of the data were used to train the model each time and projections were compared to the remaining 50%. After successively adding variables in the order in which they contributed to the highest likelihood, the overall best model was selected for each province (Supporting Information S2, Table S2).

#### 89 Simulations

The highest performing model for each province was used to project the probability of deforestation for each pixel in the five-year calibration period (2013–2017) and the following three five-year periods (2018–2022, 2023–2027, 2028–2032) (Supporting Information S2). We restricted the overall period to 15 years since model-based projections become increasingly uncertain in the future due to uncertainty in socio-ecological and political processes (Schindler and Hilborn, 2015). This period also matches the time-frame in which orangutan data were collected for the abundance model (1999-2015), and deforestation records for training the model were generated (2000-2017).

97 The simulation was based on updating the model and past deforestation for each iteration and time step. Predictor uncertainty was incorporated by drawing the values for the simulations 98 from a Gaussian distribution, using the estimated mean and standard deviation. We subsequently 99 evaluated whether a pixel in a certain period and iteration was lost, by comparing its probability of 100 101 deforestation with a randomly drawn number from a uniform distribution between 0 and 1. We then 102 classified the pixel as deforested if the number was less than the deforestation probability, a procedure which converts probability into binary information with that probability. This also 103 104 introduces stochasticity, which is a key characteristic of observed deforestation patterns (Rosa, et al 2013). This was repeated for all time steps and run 100 times to gauge uncertainty in predictions. 105 106 The resulting binary forest maps were used to calculate projected deforestation and impact on 107 orangutan populations. To characterise the deforestation risk across provinces and land-use classes, 108 the binary maps were aggregated into a summed probability of deforestation.

#### 109 Validation and analysis

110 We validated the projected forest loss maps for each province against observed losses for the

111 calibration time-period (2013–2017), by calculating the perfect match, commission and omission

112 errors. We also calculated the proportion of match between observed and projected forest loss (n =

113 100) within 1, 5 and 10 km neighborhood of a pixel following Rosa et al. (Rosa et al., 2014, 2013).

## 114 Impacts of projected deforestation on orangutan abundance

- 115 We calculated the projected future impact of deforestation on orangutans by overlaying the
- 116 projected forest loss with current orangutan density distribution maps. Orangutan density
- distribution was based on orangutan nest surveys implemented between 1999 and 2015 (4,316 km
- survey effort, median 86 transects per year) and a predictive density distribution model. The model

- 119 considered survey year, climate, habitat cover and human threat predictors to estimate range-wide
- 120 patterns of orangutan abundance (Voigt et al., 2018). We generated a baseline orangutan distribution
- 121 for 2018 by excluding pixels deforested until 2017 (sensu Gaveau et al., 2019) from the density
- 122 distribution layer of 2015.

123 To estimate the total projected loss of orangutans we excluded all pixels with projected forest loss from the orangutan abundance map, and summed the number of affected orangutans. 124 Vulnerability of orangutan populations was assessed by calculating the proportion of orangutans 125 within pixels with either low (0–33%), medium ( $\geq$  33–67%) or high ( $\geq$  67–100%) summed forest 126 127 loss probability. Local orangutan abundance was also classified into low (0.01-0.5 individuals/km<sup>2</sup>), medium (>0.5-2 individuals/km<sup>2</sup>) or high (> 2 individuals/km<sup>2</sup>). Abundance 128 129 thresholds were based on the spread of local densities and expert assessment of what constitutes 130 low, medium or high orangutan density throughout Borneo (Utami-Atmoko et al., 2019). Last, we calculated the loss of forest and vulnerability and loss of orangutans within provinces and land-use 131 categories. Presenting results in this way places a focus on overall orangutan numbers affected by 132 deforestation. However, similarly we could also assess risk to specific populations following other 133 134 criteria, such as genetic distinctness or within certain administrative boundaries. Confidence intervals of the number of orangutans affected were generated by randomly pairing deforestation 135 136 projections (n=100) with bootstraps of orangutan abundance (n=1000) (Voigt et al., 2018). All 137 orangutan numbers were rounded to the nearest 100.

## 138 **RESULTS**

### 139 **Deforestation model**

- 140 In all provinces, previous forest loss, distance to roads and land-use were included in the best model
- 141 (Table S2). Distance to rivers and elevation were included for six of the seven provinces, fire
- 142 incidence for five provinces, and population density for three provinces. Probability of deforestation
- 143 was highest near areas of past forest loss (Figures 1 and 2e).



**Figure 1:** Influence of land-use predictors across Malaysian (MYS) and Indonesian (IDN) provinces on Borneo. Model coefficient values across provinces are summarized in a boxplot (median and 25<sup>th</sup> and 75<sup>th</sup> quartiles as hinges). Predictors with a coefficient smaller than zero (dashed line) were related to lower forest loss, while predictors with a coefficient larger than zero to higher forest loss. The effect of protected areas (PA) and concessions (grey shaded background) is relative to the effect of no protection or designation as concession. Strict PAs are IUCN category 1-3, sustainable use PAs are IUCN category 3-6 or no category and all protected areas recognized in the national land-use plans but not represented in the WDPA database (2017) are included as national PAs (Supporting Information S1 and S2). The intercept and predictors for which all provincial coefficients were close to zero (mean absolute coefficient smaller than 0.05 and a spread smaller than 0.1) were excluded from the figure (elevation, distance to road and rivers, fire incidence, human population pressure). The 95% confidence intervals derived from the 100 model iterations around points are not shown, as they fall within the points.



**Figure 2:** Projected deforestation probability and contextual layers across Borneo. a) Administrative boundaries of Indonesia, Malaysia and Brunei. The position of Borneo can be seen in the inlay. Brunei is excluded from maps b and e, as important predictors did not contain sufficient information for this country. b) Land-use within forested areas (PAs–Protected areas, ITP–industrial timber plantation, IOPP–Industrial oil palm plantation). c) Elevation was derived from a digital elevation model by Jarvis et al. (2008), d) Forest types were derived from Miettinen et al (2016) by combining lowland, lower montane and upper montane evergreen forests to represent forests on mineral soils. e) Observed deforestation and projected summed probability of forest loss on Borneo over time (2018–2032). This value represents the fraction of simulation runs in which the forest in a pixel was lost; i.e. if a pixel was selected to be deforestation in that time period in 50 out of 100 iterations, then it has a 50% probability of deforestation. Observed deforestation and the individual projection time steps are shown in Figure S2. Protected areas experienced low levels of deforestation, with the lowest levels associated with strictly protected areas (Figure 1). Logging concessions were associated with lower probability of forest loss, with the exception of concessions in South Kalimantan. Industrial timber and oil palm plantation concessions had similar levels of deforestation compared to areas without formal management. Although included in the best models, elevation, distance to roads or rivers, fire incidence and population density were weak deforestation predictors, with model effect sizes close to zero.

#### 151 Model validation

- 152 Comparing the projected forest across Borneo for the calibration period, the overall prevalence of
- 153 perfect matches was 94%, false positives (commission errors) was at 5%, and the prevalence of
- 154 false negatives (omission errors) at 6%. When comparing the spatial match of projected
- deforestation a median of 56% of the pixels were in the direct neighborhood (within 1km), 79%
- 156 within 2 km, and 99% within 10 km, of a pixel with observed forest loss, indicating spatial
- 157 concordance (Table S3 and Figure S1)

#### 158 Spatio-temporal deforestation and projections

- Between 2000 and 2017 forests on Borneo decreased by 59,949 km<sup>2</sup>, and by 2032 a further 74,419
  km<sup>2</sup> (95% confidence interval (CI) 74,023–75,157 km<sup>2</sup>) was projected to be lost a 32% decrease
  since 2000 (Figure 2 and 3, Table S4 and Figure S3). Past annual deforestation rates, measured in
  percent forest lost relative to forest cover in 2000, ranged between 0-3% for all provinces, with high
- 163 inter-annual fluctuations (Figure 3b). Projected median annual deforestation rates (2018-2032)
- 164 ranged between 0.55 and 1.72% (Figure 2).
- 165 At the provincial level, projected loss of forest area ranged from 10% in North Kalimantan 166 to 29% in Central Kalimantan in comparison to forest in 2017 (Figures 3b and Table S4).
- 167 Deforestation trends tended to vary among provinces because of differences in drivers and their
- 168 relationship with deforestation, as well as the distribution of clusters with high deforestation
- 169 probabilities (Figure 2e and Figure 3a). In all provinces the projected median deforestation rate was
- 170 within the range of the observed annual rates, indicating a good fit of projections.



**Figure 3:** Observed and projected forest area and loss across Borneo from 2000 to 2032 a) The total forest in the first and last year of the observation period (2000 - 2017, red axis) and the median forest in the last projected five-year period (2028 - 2032, blue axis) for each province. Percent future forest loss from 2018 to 2032 is given above the bars (CI in Table S5). b) Aggregated average percent forest loss before simulation (2001 - 2012) and in the calibration period (2013 - 2017) (red bars with grey filling) was used for model fitting. The annual observed forest loss (red line with black dots) shows inter-annual variability of forest loss in the provinces. Deforestation was simulated for the calibration period and three five-year periods from 2018 - 2032 (blue bars, n = 100, error bars represent CI). The calibration period from 2013-2017 can be compared to the projection of forest loss in the same time interval (difference presented in Table S5). All values in b) given in annual percent loss of forest in 2000, by aggregating over the time-period over which the bar extends and dividing by number of years in interval.

171

Across provinces, protected and high-elevation areas had a high probability of maintaining forest cover until 2032 (Figure 2). Lowland forests, those within industrial timber and oil palm plantations, and forests without protection or concession status, were all associated with a low probability of maintaining forest cover and a high vulnerability to future deforestation.

10

## 176 **Orangutan vulnerability in provinces**

Medium to high (> 0.5 ind/km<sup>2</sup>) orangutan abundances are concentrated in the protected lowlands 177 178 and peatswamp forests in West, Central and East Kalimantan as well as the forests at higher 179 elevations along the border of West and Central Kalimantan (Figure 4). In the unprotected lowland 180 and peatswamp forests of West, Central and East Kalimantan high local orangutan abundances (> 2 ind/km<sup>2</sup>) coincide with high risk of deforestation (i.e. summed probability of projected deforestation 181  $\geq$  67%). In contrast, areas with medium to high orangutan abundance in the central part of West and 182 Central Kalimantan at higher elevations had low deforestation probability (< 33%) (Figure 4a). 183 184 Although fewer orangutans occur in Sabah and Sarawak compared to other provinces, most are projected to experience low levels of forest loss (Figure 4 and Figure S4). In these two states only 185 9% (Sabah) and <1% (Sarawak) of orangutans occurred in areas with high deforestation 186 probabilities. Conversely, in West, Central and East Kalimantan 27%, 23% and 15% of all 187 orangutans were in areas with high deforestation probabilities (Figure S4). Orangutans are only 188 189 present in very low numbers or entirely absent from North and South Kalimantan.

#### 190 **Orangutan vulnerability and land-use**

Orangutans within protected areas and logging concessions were found to be less vulnerable to 191 deforestation than orangutans in industrial plantations and in areas without management. Overall, 192 forests in protected areas and logging concessions harbored 68% (CI: 65-70%) of all orangutans 193 estimated to occur on Borneo in 2018. Most of these orangutans inhabited forests with low 194 deforestation probabilities: 62% (CI: 52–72%) of all orangutans within protected areas and 96% 195 (CI: 95–97%) within logging concessions (Fig S5). Nevertheless, deforestation was projected to 196 affect 7,000 (CI: 4,400–9,800) orangutans in protected areas and 3,700 (CI: 2,600–4,600) 197 198 orangutans in logging concessions.

199 Conversely, a large percentage of the orangutans inhabiting forests allocated for industrial 200 plantations depended on habitat that was highly susceptible to deforestation. Combined these could 201 affect 7,100 orangutans (CI: 5,400–9,700), representing 27% (CI: 25-31%) of the loss of orangutans 202 on Borneo.

203

204



**Figure 4:** Density distribution of orangutans and summed probability of projected deforestation in land-use areas until 2032. Orangutan density is indicated by blue shades and the probability of deforestation by red shades (individual maps in Figure S3). Darker colors identify higher levels of orangutan density and summed probability of projected deforestation. b) Forest of strict, sustainable use, and national protected areas were aggregated to a single category. Similarly, industrial timber and oil palm plantations concessions were combined into a single industrial plantation concession class. The proportion of orangutans in areas with low, medium or high levels of forest loss (pie charts, red shades only) and total projected loss of orangutans until 2032 (number in each panel) differed between land-use classes. Numbers shown are rounded to the nearest 100. Only pixels that were forested in 2017 and that have an estimated density of >0.001 orangutans/km<sup>2</sup> are represented.

205	Areas without formal management supported 19% (CI: 18–21%) of all orangutans in
206	Borneo, and much of this was at high risk of deforestation according to projections affecting 8,300
207	(CI: 6,200–11,100) orangutans (32% [CI: 31–32%] of all loss). Those areas with high vulnerability
208	also harbored high orangutan densities, notably around the Sabangau peatlands in Central

209 Kalimantan and in the Lesan-Wehea landscape in East Kalimantan (Figure S6).

## 210 **DISCUSSION**

Wildlife management is informed by our knowledge about drivers of population declines and our ability to anticipate which measures could effectively curb those losses. For many tropical species, including orangutans, such declines are strongly linked with deforestation. Our modelling of deforestation trends revealed that the forests of Borneo are projected to decline by a further 19% by 2032. Annual deforestation was projected to occur at a rate of 1.54%, which is similar to that experienced in Sumatra since 2001 (Gaveau et al., 2021), but higher than that reported from central Indonesia (1.23% between 2019-2053, Voigt et al. (2021)).

Protected areas and logging concessions are associated with the lowest deforestation risk to the sizeable orangutan populations remaining in these areas, in line with previous research on Borneo (Gaveau et al., 2013; Voigt et al., 2018). Our findings reinforce the value of well-managed logging concessions for biodiversity and the need to control habitat degradation within these forests, as well as preventing conversion and avoiding their degazettement after logging stops (Burivalova et al., 2020).

224 Furthermore, our analysis implies that the largest immediate conservation gains can be made 225 by effectively curbing deforestation in and around plantation landscapes and forests with no formal land-use designation. In these forests around 81% (CI: 78-85%) of orangutan inhabitants could be 226 227 lost otherwise. Sustainability certification schemes, corporate zero-deforestation pledges, moratoria 228 and ecosystem restoration concessions can slow deforestation in areas slated for conversion and are 229 gaining traction in orangutan-range countries (Astari and Lovett, 2019; Rizal et al., 2021; Sills et al., 2014) and the oil palm sector (https://rspo.org/news-and-events/news/uniting-to-deliver-230 231 deforestationfree-sustainable-palm-oil-more-critical-than-ever). Forest patches retained in 232 plantations can provide valuable habitat for wildlife, including orangutans (Deere et al., 2020), 233 although the greatest gains will come from companies not clearing any new forest areas in the first 234 place. The implementation of such tools are thus useful to avoid loss of valuable orangutan habitat 235 and maintain connectivity of forest areas within plantations, mitigating the projected impacts on 236 orangutans in the future (Meijaard et al., 2017).

#### 237 Modelling uncertainties, caveats and future development

With the presented deforestation projections, we created a business-as-usual baseline against which future developments in the Bornean orangutan range can be compared. Although it is likely that the deforestation in coming years is shaped by similar large- and regional-scale drivers than the deforestation in the recent past, it cannot be assumed that future dynamics will perfectly mirror the
past, especially when extending beyond the period of 15 years for which we have projected
deforestation here.

To manage for this uncertainty, a range of scenarios could explore potential future global-244 245 scale changes in resource demand and developments, such as investment in infrastructure projects, further agricultural expansion and the implementation and effectiveness of deforestation mitigation 246 measures. The regional-scale deforestation model could be combined with national or global scale 247 248 econometric models (Busch and Ferretti-Gallon, 2017) that could incorporate drivers such as 249 resource demand. However, as of yet the mechanisms of how these drivers influence deforestation 250 patterns are not yet well established and the data to parameterize such models or scenarios at the scale of Borneo are not freely available. Additionally, changes in political agendas and development 251 252 priorities (e.g., Ferrante and Fearnside, 2019), fluctuation of commodity prices for important agricultural products (Gaveau et al., 2019), global climate or spurious occurrences such as extreme 253 254 weather events, political unrest or the socio-economic effects of the global COVID-19 pandemic and resulting impacts on forests (Brancalion et al., 2020) are difficult to anticipate and thus directly 255 256 include in any model.

257 Different scenarios could be more easily compiled at the local scale, where relevant stakeholders could co-develop potential pathways for their landscapes, and explore expected 258 259 outcomes. In this study we could show that drivers and patterns of deforestation vary for the different provinces, thus highlighting the potential for models that are tailored to the local context to 260 project future change. Orangutans are not only threatened by deforestation, but also suffer 261 considerable declines through hunting, killing in conflict situations and live capture. These threats 262 often remain hidden and are governed by complex socio-economic drivers that remain poorly 263 understood and mapped (Meijaard et al., 2011). This makes it challenging to model the contribution 264 265 of this threat to orangutan vulnerability. The projected orangutan losses thus only represent a proportion of potential future population losses and no-killing policies are an essential cornerstone 266 267 of any conservation approach to succeed at stopping orangutan loss.

## 268 Implications for conservation

We showcased how information on deforestation risk and wildlife density can be combined to draw insights into conservation threats and vulnerability assessment. The information where a reduction in deforestation risk would lead to largest increases in species protection could be used to direct orangutan conservation efforts, for example by contributing to Population and Habitat Viability
Assessments (Utami-Atmoko et al., 2019), national orangutan conservation action plans (Ministry
of Environment and Forestry., 2019) or influencing funding across the species range. In the future,
scenario analysis considering changes in resource demand, planned development efforts or
conservation management, for example, could help to improve landscape-scale planning with
largest benefits for orangutan conservation.

Furthermore, methods that facilitate abundance estimates over large spatial scales, such as integrated modelling that can harness a wider range of data (Bowler et al., 2019) could make abundance estimates more readily available for more elusive or less-well studied species. Valuable information can also be gleaned from inspecting deforestation risk within species ranges or in combination with occurrence probabilities (e.g., Boitani et al., 2011). This would enable the assessment of more general effects of future forest loss on tropical fauna.

Our findings demonstrate that we have a window of opportunity to curb deforestation and its impacts on biodiversity, while highlighting the consequences if we fail to do so. In the context of extensive and rapid changes of land-use, land-cover and climate in this century, increasing efforts to further such approaches and to translate them into effective conservation actions are urgently needed to halt wildlife decline in biodiversity hotspots such as Borneo. Ideally, conservation actions now should not only attempt to act on today's information about deforestation patterns, but also be adaptive to potential changes in drivers and threats.

#### References

- Ancrenaz, M., Gumal, M., Marshall, A.J., Meijaard, E., Wich, S.A., Husson, S., 2016. Pongo pygmaeus. The IUCN Red List of Threatened Species 2016: e.T17975A17966347.
- Astari, A.J., Lovett, J.C., 2019. Does the rise of transnational governance 'hollow-out' the state? Discourse analysis of the mandatory Indonesian sustainable palm oil policy. World Development 117, 1–12. https://doi.org/10.1016/j.worlddev.2018.12.012
- Austin, K.G., Schwantes, A., Gu, Y., Kasibhatla, P.S., 2019. What causes deforestation in Indonesia? Environ. Res. Lett. 14, 024007. https://doi.org/10.1088/1748-9326/aaf6db
- Boitani, L., Maiorano, L., Baisero, D., Falcucci, A., Visconti, P., Rondinini, C., 2011. What spatial data do we need to develop global mammal conservation strategies? Philosophical Transactions of the Royal Society B: Biological Sciences 366, 2623–2632. https://doi.org/10.1098/rstb.2011.0117
- Bowler, D.E., Nilsen, E.B., Bischof, R., O'Hara, R.B., Yu, T.T., Oo, T., Aung, M., Linnell, J.D.C., 2019. Integrating data from different survey types for population monitoring of an

endangered species: the case of the Eld's deer. Scientific Reports 9, 7766. https://doi.org/10.1038/s41598-019-44075-9

- Brancalion, P.H.S., Broadbent, E.N., de-Miguel, S., Cardil, A., Rosa, M.R., Almeida, C.T., Almeida, D.R.A., Chakravarty, S., Zhou, M., Gamarra, J.G.P., Liang, J., Crouzeilles, R., Hérault, B., Aragão, L.E.O.C., Silva, C.A., Almeyda-Zambrano, A.M., 2020. Emerging threats linking tropical deforestation and the COVID-19 pandemic. Perspectives in Ecology and Conservation 18, 243–246. https://doi.org/10.1016/j.pecon.2020.09.006
- Burivalova, Z., Game, E.T., Wahyudi, B., Ruslandi, Rifqi, M., MacDonald, E., Cushman, S., Voigt, M., Wich, S., Wilcove, D.S., 2020. Does biodiversity benefit when the logging stops? An analysis of conservation risks and opportunities in active versus inactive logging concessions in Borneo. Biological Conservation 241, 108369. https://doi.org/10.1016/j.biocon.2019.108369
- Busch, J., Ferretti-Gallon, K., 2017. What Drives Deforestation and What Stops It? A Meta-Analysis. Rev Environ Econ Policy 11, 3–23. https://doi.org/10.1093/reep/rew013
- Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361, 1108–1111. https://doi.org/10.1126/science.aau3445
- Deere, N.J., Guillera-Arroita, G., Platts, P.J., Mitchell, S.L., Baking, E.L., Bernard, H., Haysom, J.K., Reynolds, G., Seaman, D.J.I., Davies, Z.G., Struebig, M.J., 2020. Implications of zerodeforestation commitments: Forest quality and hunting pressure limit mammal persistence in fragmented tropical landscapes. Conservation Letters 13, e12701. https://doi.org/10.1111/conl.12701
- Esri Inc., 2014. ArcGIS. Esri Inc., https://www.esri.com/en-us/arcgis/products/arcgis-pro/.
- Ferrante, L., Fearnside, P.M., 2019. Brazil's new president and 'ruralists' threaten Amazonia's environment, traditional peoples and the global climate. Environmental Conservation 46, 261–263. https://doi.org/10.1017/S0376892919000213
- Gaveau, D.L.A., Kshatriya, M., Sheil, D., Sloan, S., Molidena, E., Wijaya, A., Wich, S.A.,
   Ancrenaz, M., Hansen, M.C., Broich, M., Guariguata, M.R., Pacheco, P., Potapov, P.V.,
   Turubanova, S., Meijaard, E., 2013. Reconciling Forest Conservation and Logging in
   Indonesian Borneo. PLoS ONE 8, e69887. https://doi.org/10.1371/journal.pone.0069887
- Gaveau, D.L.A., Locatelli, B., Salim, M.A., Husnayaen, H., Manurung, T., Descals, A., Arild, A., Meijaard, E., Sheil, D., 2021. Slowing deforestation in Indonesia follows declining oil palm expansion and lower oil prices [WWW Document]. https://doi.org/10.21203/rs.3.rs-143515/v1
- Gaveau, D.L.A., Locatelli, B., Salim, M.A., Yaen, H., Pacheco, P., Sheil, D., 2019. Rise and fall of forest loss and industrial plantations in Borneo (2000–2017). Conservation Letters e12622. https://doi.org/10.1111/conl.12622
- IUCN, UNEP-WCMC, 2017. The World Database on Protected Areas (WDPA) [On-line], Oct 2017.
- Lapola, D.M., Schaldach, R., Alcamo, J., Bondeau, A., Msangi, S., Priess, J.A., Silvestrini, R., Soares-Filho, B.S., 2011. Impacts of climate change and the end of deforestation on land use in the Brazilian Legal Amazon. Earth Interactions 15, 1–29.
- Meijaard, E., Buchori, D., Hadiprakarsa, Y., Utami-Atmoko, S.S., Nurcahyo, A., Tjiu, A., Prasetyo, D., Nardiyono, Christie, L., Ancrenaz, M., Abadi, F., Antoni, I.N.G., Armayadi, D., Dinato, A., Ella, Gumelar, P., Indrawan, T.P., Kussaritano, Munajat, C., Priyono, C.W.P., Purwanto, Y., Puspitasari, D., Putra, M.S.W., Rahmat, A., Ramadani, H., Sammy, J., Siswanto, D.,

Syamsuri, M., Andayani, N., Wu, H., Wells, J.A., Mengersen, K., 2011. Quantifying Killing of Orangutans and Human-Orangutan Conflict in Kalimantan, Indonesia. PLoS ONE 6, e27491. https://doi.org/10.1371/journal.pone.0027491

- Meijaard, E., Morgans, C.L., Husnayaen, Abram, N.K., Ancrenaz, M., 2017. An impact analysis of RSPO certification on Borneo forest cover and orangutan populations. Borneo Futures, Bandar Seri Begawan, Brunei Darussalam.
- Ministry of Environment and Forestry., 2019. Strategi dan Rencana Aksi Konservasi Orangutan Indonesia 2019-2029. Ditjen KSDAE. Kementerian Lingkungan Hidup dan Kehutanan Republik Indonesia., Jakarta.
- MoEF, 2018. The State of Indonesia's Forests 2018. Ministry of Environment and Forestry Republic of Indonesia.
- Python Software Foundation, 2019. Python Language Reference version 3.7.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rizal, A.R.A., Nordin, S.M., Hussin, S.H., Hussin, S.R., 2021. Beyond rational choice theory: multifaceted determinants of participation in palm oil sustainable certification amongst smallholders in Malaysia. FRONTIERS IN SUSTAINABLE FOOD SYSTEMS 5.
- Rosa, I.M.D., Ahmed, S.E., Ewers, R.M., 2014. The transparency, reliability and utility of tropical rainforest land-use and land-cover change models. Global Change Biology 20, 1707–1722. https://doi.org/10.1111/gcb.12523
- Rosa, I.M.D., Purves, D., Carreiras, J.M., Ewers, R.M., 2015. Modelling land cover change in the Brazilian Amazon: temporal changes in drivers and calibration issues. Regional environmental change 15, 123–137.
- Rosa, I.M.D., Purves, D., Jr, C.S., Ewers, R.M., 2013. Predictive Modelling of Contagious Deforestation in the Brazilian Amazon. PLOS ONE 8, e77231. https://doi.org/10.1371/journal.pone.0077231
- Santika, T., Meijaard, E., Wilson, K.A., 2015. Designing multifunctional landscapes for forest conservation. Environ. Res. Lett. 10, 114012. https://doi.org/10.1088/1748-9326/10/11/114012
- Schindler, D.E., Hilborn, R., 2015. Prediction, precaution, and policy under global change. Science 347, 953–954. https://doi.org/10.1126/science.1261824
- Sills, E.O., Atmadja, S.S., de Sassi, C., Duchelle, A.E., Kweka, D.L., Resosudarmo, I.A.P., Sunderlin, W.D., 2014. REDD+ on the ground: A case book of subnational initiatives across the globe. Cifor.
- Silva, A.C.O., Fonseca, L.M.G., Körting, T.S., Escada, M.I.S., 2020. A spatio-temporal Bayesian Network approach for deforestation prediction in an Amazon rainforest expansion frontier. Spatial Statistics 35, 100393. https://doi.org/10.1016/j.spasta.2019.100393
- Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Coutinho Cerqueira, G., Garcia, R.A., Ramos, C.A., Voll, E., McDonald, A., Lefebvre, P., Schlesinger, P., 2006. Modelling conservation in the Amazon basin. Nature 440, 520–523. https://doi.org/10.1038/nature04389
- Strindberg, S., Maisels, F., Williamson, E.A., Blake, S., Stokes, E.J., Aba'a, R., Abitsi, G., Agbor,
  A., Ambahe, R.D., Bakabana, P.C., Bechem, M., Berlemont, A., Semboli, B.B. de, Boundja,
  P.R., Bout, N., Breuer, T., Campbell, G., Wachter, P.D., Akou, M.E., Mba, F.E., Feistner,
  A.T.C., Fosso, B., Fotso, R., Greer, D., Inkamba-Nkulu, C., Iyenguet, C.F., Jeffery, K.J.,

Kokangoye, M., Kühl, H.S., Latour, S., Madzoke, B., Makoumbou, C., Malanda, G.-A.F., Malonga, R., Mbolo, V., Morgan, D.B., Motsaba, P., Moukala, G., Mowawa, B.S., Murai, M., Ndzai, C., Nishihara, T., Nzooh, Z., Pintea, L., Pokempner, A., Rainey, H.J., Rayden, T., Ruffler, H., Sanz, C.M., Todd, A., Vanleeuwe, H., Vosper, A., Warren, Y., Wilkie, D.S., 2018. Guns, germs, and trees determine density and distribution of gorillas and chimpanzees in Western Equatorial Africa. Science Advances 4, eaar2964. https://doi.org/10.1126/sciadv.aar2964

- Struebig, M.J., Fischer, M., Gaveau, D.L.A., Meijaard, E., Wich, S.A., Gonner, C., Sykes, R., Wilting, A., Kramer-Schadt, S., 2015. Anticipated climate and land-cover changes reveal refuge areas for Borneo's orang-utans. Glob Change Biol 21, 2891–2904. https://doi.org/10.1111/gcb.12814
- Utami-Atmoko, S., Traylor-Holzer, K., Rifqi, M.A., Siregar, P.G., Achmad, B., Priadjati, A., Husson, S., Wich, S.A., Hadisiswoyo, P., Saputra, F., Campbell-Smith, G., Kuncoro, P., Russon, A., Santika, T., Voigt, M., Nowak, M., Singleton, I., Sapari, I., Meididit, A., Chandradewi, D.S., Ripoll Capilla, B., Ermayanti, Lees, C.M. (eds.), 2019. Orangutan Population and Habitat Viability Assessment: Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.
- Voigt, M., Supriatna, J., Deere, N.J., Kastanya, A., Mitchell, S.L., Rosa, I.M.D., Santika, T., Siregar, R., Tasirin, J.S., Widyanto, A., Winarni, N.L., Zakaria, Z., Mumbunan, S., Davies, Z.G., Struebig, M.J., 2021. Emerging threats from deforestation and forest fragmentation in the Wallacea centre of endemism. Environ. Res. Lett. 16, 094048. https://doi.org/10.1088/1748-9326/ac15cd
- Voigt, M., Wich, S.A., Ancrenaz, M., Meijaard, E., Abram, N., Banes, G.L., Campbell-Smith, G., d'Arcy, L.J., Delgado, R.A., Erman, A., Gaveau, D.L.A., Goossens, B., Heinicke, S., Houghton, M., Husson, S.J., Leiman, A., Llano Sanchez, K., Makinuddin, N., Marshall, A.J., Meididit, A., Miettinen, J., Mundry, R., Musnanda, Nardiyono, Nurcahyo, A., Odom, K., Panda, A., Prasetyo, D., Priadjati, A., Purnomo, Rafiastanto, A., Russon, A.E., Sihite, J., Spehar, S., Struebig, M.J., Sulbaran-Romero, E., Wilson, K.A., Kühl, H.S., 2018. Global demand for natural resources eliminated more than 100,000 Bornean orangutans. Current Biology 28, 761–769.
- Wich, S.A., Singleton, I., Nowak, M.G., Atomoko, S.S.U., Nisam, G., Arif, S.Mhd., Putra, R.H., Ardi, R., Fredriksson, G., Usher, G., Gaveau, D.L.A., Kühl, H.S., 2016. Land-cover changes predict steep declines for the Sumatran orangutan (Pongo abelii). Science Advances 2 : e1500789.

#### Acknowledgements:

M.V. thanks Sergio Maroccoli and Ana D. de Lima Voigt for comments on early versions of this

manuscript. M.V. and H.K thank the Max Planck Society and Robert Bosch Foundation for funding

and support. M.V. was also funded by the UK Leverhulme Trust via a Research Leadership Award

granted to M.J.S.

# **Author Contributions**

Conceptualization, M.V., H.M.P., M.A., E.M., J.S., M.J.S., S.A.W., H.S.K., and I.MD.R.;

Methodology, M.V., H.M.P., F.W., and I.MD.R.; Software, M.V., F.W., and I.MD.R.; Validation,

M.V., I.MD.R.; Formal analysis, M.V.; Resources, D.G., T.S.; Data curation, M.V.; Writing -

Original draft, M.V.; Writing - Review & Editing, M.V., H.M.P., M.A., D.G., E.M., T.S., J.S.,

M.J.S., S.A.W., F.W., H.S.K., and I.MD.R.; Supervision, H.M.P, H.S.K., and I.MD.R..

# **Declaration of Interests**

The authors declare no competing interests.

## **Supporting Information**

- S1 Spatial layers of deforestation drivers and processing.
- S2 Deforestation model and calibration.
- Table S1: Predictors used in deforestation modelling, including their description, source and year.
- Table S2: Overview over best models and predictor effect sizes for each province.
- Table S3: Validation of observed against projected forest maps for Borneo and provinces.
- Table S4: Province area, forest area and projected proportion of forest loss.
- Table S5: Difference between observed and projected annual deforestation rates for the calibration period 2013-2017.
- Figure S1: Proportion of match between observed and cumulative forest loss within the neighborhood of a pixel for Borneo and each province.
- Figure S2: Observed deforestation and projected probability of forest loss across Borneo (2001–2032).
- Figure S3: Summed probability of forest loss and orangutan density across Borneo.
- Figure S4: Density of orangutans and summed probability of forest loss in provinces
- Figure S5 : Density of orangutans and summed probability of forest loss in land-use areas
- Figure S6: Bivariate map of density distribution of orangutans and summed probability of projected forest loss until 2032 in unprotected areas outside of concessions, Lesan-Wehea Landscape and an area in the periphery of Sabangau National Park.