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Citation for final published version:

Voigt, Maria, Wich, Serge A, Ancrenaz, Marc, Meijaard, Erik, Abram, Nicola, Barnes, Graham L, Campbell-Smith, Gail, d'Arcy, Laura J, Delgado, Roberto A, Erman, Andi, Gaveau, David, Goossens, Benoit, Heinicke, Stefanie, Houghton, Max, Husson, Simon J, Leiman, Ashley, Sanchez, Karmele Llano, Makinuddin, Niel, Marshall, Andrew J, Meididit, Ari, Miettinen, Jukka, Mundry, Roger, Nardiyono, Musnand, Nurcahyo, Anton, Odom, Kisar, Panda, Adventus, Prasetyo, Didik, Priadjati, Aldrianto, Purnomo, A., Rafiastanto, Andjar, Russon, Anne E, Santika, Truly, Sihite, Jamartin, Spehar, Stephanie, Struebig, Matthew, Sulbaran-Romero, Enrique, Tjiu, Albertus, Wells, Jessie, Wilson, Kerrie A and Kuhl, Hjalmar S 2018. Global demand for natural resources eliminated more than 100,000 Bornean orangutans. *Current Biology* 5 , pp. 761-769. 10.1016/j.cub.2018.01.053  
file

Publishers page: <http://dx.doi.org/10.1016/j.cub.2018.01.053>  
<<http://dx.doi.org/10.1016/j.cub.2018.01.053>>

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# Global demand for natural resources eliminated

## 2 more than 100,000 Bornean orangutans

### 4 Authors:

Maria Voigt<sup>1,2,39\*</sup>, Serge A. Wich<sup>3,4,\*</sup>, Marc Ancrenaz<sup>5,6</sup>, Erik Meijaard<sup>5,7</sup>, Nicola Abram<sup>7,8,9,10</sup>,  
6 Graham L. Banes<sup>1,11,12</sup>, Gail Campbell-Smith<sup>13</sup>, Laura J. d’Arcy<sup>14,15</sup>, Roberto A. Delgado<sup>16</sup>, Andi  
Erman<sup>17</sup>, David Gaveau<sup>18</sup>, Benoit Goossens<sup>19,20,21</sup>, Stefanie Heinicke<sup>1,2</sup>, Max Houghton<sup>3</sup>, Simon J.  
8 Husson<sup>22</sup>, Ashley Leiman<sup>23</sup>, Karmele Llano Sanchez<sup>13</sup>, Niel Makinuddin<sup>24</sup>, Andrew J. Marshall<sup>25</sup>,  
Ari Meididit<sup>26,27</sup>, Jukka Miettinen<sup>28</sup>, Roger Mundry<sup>1</sup>, Musnanda<sup>24</sup>, Nardiyono<sup>29</sup>, Anton Nurcahyo<sup>30</sup>,  
10 Kisar Odom<sup>31</sup>, Adventus Panda<sup>27</sup>, Didik Prasetyo<sup>32</sup>, Aldrianto Priadjati<sup>33</sup>, Purnomo<sup>24</sup>, Andjar  
Rafiastanto<sup>34</sup>, Anne E. Russon<sup>35</sup>, Truly Santika<sup>5,7,8</sup>, Jamartin Sihite<sup>31,33</sup>, Stephanie Spehar<sup>36</sup>,  
12 Matthew Struebig<sup>37</sup>, Enrique Sulbaran-Romero<sup>1,2</sup>, Albertus Tjiu<sup>38</sup>, Jessie Wells<sup>7,8</sup>, Kerrie A.  
Wilson<sup>7,8</sup>, Hjalmar S. Kühl<sup>1,2</sup>

14

### Affiliations:

16 1 Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig,  
Germany.

18 2 German Centre for Integrative Biodiversity Research (iDiv) Halle – Jena – Leipzig, Deutscher  
Platz 5e, 04103 Leipzig, Germany.

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1 Lead contact

2 Correspondence: Maria.Voigt@idiv.de (M.V.) and Sergewich@gmail.com (S.A.W.)

- 20 3 Research Centre in Evolutionary Anthropology, and Palaeoecology, School of Natural Sciences  
and Psychology, Liverpool John Moores University, Byrom Street, Liverpool, L3 3AF, United  
22 Kingdom.
- 4 Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904,  
24 1098 XH Amsterdam, The Netherlands.
- 5 Borneo Futures, Bandar Seri Begawan, Brunei Darussalam.
- 26 6 HUTAN-Kinabatangan Orang-utan Conservation Programme, Sandakan, Sabah, Malaysia.
- 7 ARC Centre of Excellence for Environmental Decisions, The University of Queensland, Brisbane,  
28 QLD, Australia.
- 8 The University of Queensland, School of Biological Sciences, Brisbane, QLD, Australia.
- 30 9 Living Landscape Alliance, 5 Jupiter House Calleva Park, Berkshire, RG7 8NN, United  
Kingdom.
- 32 10 Forever Sabah, H30 Gaya Park, Lorong Muntahan 1C, Penampang Road, 88300, Kota Kinabalu,  
Sabah, Malaysia.
- 34 11 School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue,  
Aberdeen, AB24 2TZ, United Kingdom.
- 36 12 CAS-MPG Partner Institute for Computational Biology, 320 Yue Yang Road, Shanghai, 200031,  
People's Republic of China.
- 38 13 Yayasan IAR Indonesia, Bogor, 16001, Indonesia.
- 14 Borneo Nature Foundation, Jalan Bukit Raya No. 82, Bukit Raya, Palangka Raya 73112,  
40 Indonesia.
- 15 Zoological Society of London, London, United Kingdom.
- 42 16 Departments of Anthropology and Biological Sciences, Program in Integrative and Evolutionary  
Biology (IEB), University of Southern California, Los Angeles, USA.

- 44 17 GFA/KWF, Kapuas Hulu Program, West Kalimantan, Indonesia.  
18 Center for International Forestry Research, P.O. Box 0113 BOCBD, Bogor 16000, Indonesia.
- 46 19 Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University,  
Cardiff, United Kingdom.
- 48 20 Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma Muis, 88100, Kota  
Kinabalu, Sabah, Malaysia.
- 50 21 Sustainable Places Research Institute, Cardiff University, Cardiff, United Kingdom.  
22 Orangutan Tropical Peatland Project, The Center for International Cooperation in the Sustainable  
52 Management of Tropical Peatlands (CIMTROP), University of Palangka Raya, Central Kalimantan,  
Indonesia.
- 54 23 Orangutan Foundation, London, United Kingdom.  
24 The Nature Conservancy (TNC) Indonesia, Jakarta, Indonesia.
- 56 25 University of Michigan, Department of Anthropology, Department of Ecology and Evolutionary  
Biology, Program in the Environment, and School for Environment and Sustainability, Ann Arbor,  
58 MI 48109, USA.  
26 Biology Faculty, Universitas Nasional (UNAS), Jakarta, Indonesia.
- 60 27 World Wide Fund for Nature-Indonesia (WWF-Indonesia), Central Kalimantan Program,  
Indonesia.
- 62 28 Centre for Remote Imaging, Sensing and Processing (CRISP), National University of Singapore  
(NUS), Singapore 119076.
- 64 29 Austindo Nusantara Jaya Tbk, Jakarta 12910, Indonesia.  
30 College of Arts and Social Sciences, The Australian National University, Canberra, ACT,  
66 Australia.  
31 Borneo Orangutan Survival Foundation (BOSF), Indonesia.

- 68 32 The Indonesian Association of Primatologists (PERHAPPI), Bogor, Indonesia.  
33 Restorasi Habitat Orangutan Indonesia (RHOI), Bogor, West Java, Indonesia.
- 70 34 Flora and Fauna International-Indonesia, Ragunan, Jakarta, Indonesia.  
35 Psychology Department, Glendon College of York University, 2275 Bayview Avenue, Toronto,  
72 M4N 3M6, ON, Canada.  
36 Anthropology Program, University of Wisconsin Oshkosh, Oshkosh, WI, USA.
- 74 37 Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation,  
University of Kent, Canterbury CT2 7NR, UK.
- 76 38 World Wide Fund for Nature-Indonesia (WWF-Indonesia), West Kalimantan Program,  
Indonesia.

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## Summary

80 Unsustainable exploitation of natural resources is increasingly affecting the highly biodiverse  
tropics [1,2]. Although rapid developments in remote sensing technology have permitted more  
82 precise estimates of land-cover change over large spatial scales [3–5], our knowledge about the  
effects of these changes on wildlife is much more sparse [6,7]. Here we use field survey data,  
84 predictive density distribution modeling, and remote sensing to investigate the impact of resource  
use and land-use changes on the density distribution of Bornean orangutans (*Pongo pygmaeus*). Our  
86 models indicate that between 1999 and 2015 half of the orangutan population was affected by  
logging, deforestation or industrialized plantations. While land clearance caused the most dramatic  
88 rates of decline, it accounted for only a small proportion of the total loss. A much larger number of  
orangutans were lost in selectively logged and primary forests, where rates of decline were less  
90 precipitous, but where far more orangutans are found. This suggests that further drivers,

independent of land-use change, contribute to orangutan loss. This finding is consistent with studies  
92 reporting hunting as a major cause in orangutan decline [8–10]. Our predictions of orangutan  
abundance loss across Borneo suggest that the population decreased by more than 100,000  
94 individuals, corroborating recent estimates of decline [11]. Practical solutions to prevent future  
orangutan decline can only be realized by addressing its complex causes in a holistic manner across  
96 political and societal sectors, such as in land-use planning, resource exploitation, infrastructure  
development, and education, and by increasing long-term sustainability [12].

98

## Results

### 100 Bornean orangutan field survey data

To model Bornean orangutan density distribution and derive metapopulation abundances we  
102 compiled orangutan field surveys. Estimates of orangutan density and abundance are usually  
derived from the observation of their nests [13,14] on line transects [15]. A total of 36,555  
104 orangutan nests were observed on 1,491 ground and 252 aerial transects that were surveyed  
between 1999 and 2015 throughout the Bornean orangutan range, with a total survey effort of 4,316  
106 km (ground: 1388 km, aerial: 2928 km), and a median of 86 transects (interquartile range (IQR): 28  
– 156 transects) per year. The cumulative area of land surveyed contained 1,234 km<sup>2</sup>. During the  
108 study period, the average yearly encounter rate significantly decreased from 22.5 to 10.1 nests/km  
(parameter estimate = -0.06, SE = 0.02,  $z = -2.25$ ,  $p = 0.04$ . The model contained the log-  
110 transformed mean nest encounter rate per year as response, weighted by the number of transects per  
year and the year as predictor).

112

### Estimating change in Bornean orangutan density distribution

114 We built a predictive density distribution model to estimate Bornean orangutan abundance. The full  
model included survey year, climate, habitat cover and human threat predictor variables (see  
116 methods and key resources table) and explained orangutan density significantly better than the null  
model including only the intercept (likelihood ratio test,  $\chi^2 = 1,440$ ,  $df = 13$ ,  $p < 0.001$ ). Mean  
118 temperature, lowland and peatswamp forest cover had a significant positive relationship with  
orangutan density (Figure S1, Table S2). Study year, rainfall variability and human population  
120 density negatively affected orangutan density (Figure S1, Table S2). Intermediate levels of rainfall  
in dry months were related to higher densities of orangutans. Topsoil organic carbon content,  
122 estimate of orangutan killing and percentage of the population with hunting taboos were not  
significantly correlated with orangutan density. While the orangutan density was lower in areas with  
124 more montane forest cover, the cover of deforested areas around transects was slightly positively  
correlated, but its confidence limits included zero.

126 With the aim of minimizing model uncertainty in spatial model predictions, we used multi-model  
inference and evaluated all possible combinations of covariates included in the full model (Table  
128 S2). The complete set of all fitted models was then used to estimate the orangutan density  
distribution across the range. The estimated distribution was mapped to metapopulations delineated  
130 by experts at the Population and Habitat Viability Assessment Workshop (PHVA) for Bornean  
orangutans. In this context, the term "metapopulation" was used to identify larger entities which are  
132 bound by dispersal barriers, such as rivers, major roads and areas without forests and include one or  
more orangutan subpopulations. Only 38 out of 64 identified metapopulations retained more than  
134 100 individuals and can thus be considered to contain viable subpopulations [16].

The three largest metapopulations were found in Kalimantan, the Indonesian part of Borneo and  
136 have experienced a strong decline over the studied 16-year period (Figure 1).

Western Swananer, the largest metapopulation, lost an estimated 42,700 individuals (95%  
138 confidence interval (CI): 12,700 – 73,400) since 1999, with 40,700 (95% CI: 30,000 – 57,200)  
remaining in 2015. The second largest population, Eastern Swananer, lost 20,100 individuals (95%  
140 CI: 7,200 – 33,500), and was estimated to contain 16,800 (95% CI: 12,100 – 23,100) in 2015. In  
Karangan, the third largest population, 8,200 individuals (95% CI: 1,900 – 15,400) were lost and  
142 9,000 (5,900 – 14,200) remained in 2015. The total estimated loss of Bornean orangutans between  
1999 and 2015 amounted to 148,500 individuals (95% CI: 48,100 – 252,300).

144 We used predictions of forest cover from Struebig et al. [17] for 2020 and 2050 to project future  
orangutan decline (Figure 2). To this end, we assumed that orangutans cannot survive in areas  
146 without tree cover. The orangutan abundance in the three largest populations was projected to drop  
further and reach 31,100 individuals (95% CI: 22,500 – 44,000) in the Western Swananer  
148 metapopulation area, 14,700 individuals (95% CI: 9,600 – 19,600) in Eastern Swananer and 6,100  
individuals (95% CI: 3,800 – 10,000) in Karangan by 2050. The total future loss for all  
150 metapopulations was projected to be 45,300 (95% CI: 33,300 – 63,500). This projected future  
decline is only based on the direct consequence of habitat loss. It does not consider the effects of  
152 orangutan killing for food and in conflict and is therefore most likely an underestimate. All  
estimates are rounded to the nearest hundred.

154

## Linking remotely sensed resource use and density distribution

156 To identify possible causes for the estimated orangutan loss, we compared absolute abundance and  
density from the beginning and the end of the survey period between land-use types, and assessed  
158 differences in change over time. We differentiated areas, in which resource use had altered the  
environment and areas in which land-use remained unaltered during the study period. For land-use  
160 changes we considered deforestation, conversion to industrial plantations (oil palm and paper pulp)



and selective logging in natural forests. As stable land-use we considered primary and montane  
162 primary forest, regrowth forests, industrial plantations established prior to the study period and  
'other', comprising non-forest areas.

164 By 2015, 50% of the orangutans estimated to have occurred on Borneo in 1999 were found in areas  
in which resource use had altered the environment. A comparison of distinct regions revealed that  
166 50%, 60% and 10% of the orangutans were affected by transformation into industrial oil palm or  
paper pulp plantations, deforestation, or selective logging in Kalimantan, Sabah and Sarawak,  
168 respectively. Rates of orangutan decline were highest in areas deforested or converted to plantations  
(63 - 75% loss) in both Kalimantan and Sabah (Figure 3). In Sarawak, there were almost no  
170 industrial plantations and deforested areas within the orangutan metapopulation range, together  
affecting only 0.4% of area and 2% of the orangutan population. Industrial plantations and  
172 deforestation contributed 7% (Kalimantan), 2% (Sabah), and less than 1% (Sarawak) to the overall  
estimated loss of orangutans in each of the three regions.

174 Both Kalimantan and Sabah had the highest orangutan abundance in selectively logged forests,  
followed by primary forest. In Sarawak, the highest orangutan abundance was found in primary  
176 forests. The rate of orangutan decline across the three regions and these two land-use classes was  
less precipitous, but still high (49 – 56%). The loss of orangutans in primary and selectively logged  
178 forests between 1999 and 2015 accounted for 67% of the total loss in Kalimantan (93,000  
individuals, 95% CI: 26,500 - 162,300), 72% in Sabah (6,100 individuals, 95% CI: 2,400 – 10,000)  
180 and 83% of the total loss in Sarawak (900 individuals, 95% CI: 250 – 1,600).

## 182 **Discussion**

The unsustainable use of natural resources has caused a dramatic decline of Bornean orangutans.  
184 Only 38 out of 64 remaining metapopulations have more than 100 individuals, the assumed  
threshold for viability of Bornean orangutan populations [16]. Our findings suggest that more than  
186 100,000 individuals have been lost in the 16 years between 1999 and 2015. All three analytical  
approaches employed in this study, based on field survey data, spatial covariate modeling, and  
188 remote sensing, corroborated the concluded impact of resource use and resulting decline of Bornean  
orangutans. The results are also very consistent with the genetic signature of a recent collapse found  
190 in an orangutan population in Sabah [18] and evidence of large annual losses of orangutans through  
hunting and conflict killing in Kalimantan [8–10]. Our results substantiate the percentage loss  
192 estimated by Santika et al. [11] and reinforce the recent uplisting of the Bornean orangutan as  
Critically Endangered on the IUCN Red List [19]. The numbers reported here are larger than past  
194 estimates [11], but are in line with findings reported for other great ape taxa [20–23].

We have established the density distribution of Bornean orangutans with a model-based approach  
196 which uses the relationships between predictor variables and observed orangutan abundance to  
predict abundance for unsurveyed sites. These predictions are useful for deducing trends at the  
198 regional to landscape scale [24], but may be limited at a local scale, where additional demographic  
and behavioral drivers can influence orangutan density distribution, e.g., ranging behavior in  
200 response to local food resources or conspecifics. Thus, our findings reveal patterns at large spatial  
scales, but great care should be taken when inferring from predictions at specific sites.

202 Another aspect of our study that requires critical assessment is the inference of orangutan  
abundance from nest counts. Nest decay time, an essential parameter to translate nest density into  
204 orangutan density, varies between survey sites. Although factors like rainfall, wood density and  
complexity of nest architecture are known to influence nest decay time [13,25,26], additional  
206 variability in decay time between sites is not fully understood [27]. We addressed this issue by using

all available datasets on orangutan nest decay, comprising information on the life span of more than  
208 thousand nests (see methods) across Borneo. If our findings of orangutan decline were an artifact of  
severely biased nest decay times, this would require nest decay time to have halved over the course  
210 of the study period. However, we found no indication of this, and so do not consider this to be a  
limitation of our study.

212 Contrary to our expectations, the model coefficient for deforestation indicated a slightly positive  
relationship between deforestation in years prior to the survey and orangutan abundance. There are  
214 several possible explanations for this observation, suggesting that the model coefficient does not  
capture a causal relationship. First, surveys tend to be biased towards areas with known orangutan  
216 occurrence. Thus, our dataset possibly lacks sufficient variance for detecting the true impact of  
deforestation on orangutan density. Second, some studies have suggested that the number of  
218 orangutans in areas adjacent to deforested areas are temporally inflated, due to the displacement of  
individuals and subsequent refugee crowding [28,29]. Third, high dietary flexibility allows  
220 orangutans to be resilient in the face of some levels of disturbance [30,31]. This may delay the  
effects of deforestation on the observed density for several years, before populations eventually start  
222 to decline [28]. Irrespective of this, when we compare spatial model predictions and remotely  
sensed land-use change, the highest rates of orangutan decline were detected in areas with habitat  
224 removal (deforestation and conversion to industrial plantations). This shows that the predictive  
density distribution model has indirectly captured the deleterious effects of deforestation on  
226 orangutan abundance. Our finding suggests that deforestation and industrial oil palm and paper pulp  
plantations are responsible for about 9% (14,000 individuals) of the total loss of orangutan  
228 abundance. Whereas in the early years of the study it was mainly degraded land with low orangutan  
density that was converted to industrial plantations, after 2005 the conversion of forests to oil palm  
230 plantations has been increasing dramatically [32]. Some studies have suggested that orangutans can

occur in oil palm or paper pulp plantations, when they are managed well and adjacent forest  
232 fragments are maintained [33–35]. However, it is unclear whether this is just a transient effect or  
whether orangutans can indeed persist over the long-term [33–35].

234 The highest orangutan abundances were found in selectively logged forests in Kalimantan and  
Sabah and in primary forests in Sarawak. This finding is consistent with studies reporting that  
236 orangutans can occur in selectively logged or regenerating logging concessions, depending on the  
type and intensity of logging operations [36–39]. Consequently, successful orangutan conservation  
238 is necessarily situated in multi-functional landscapes [36,40], and recognizes the importance of  
degraded and logged forests as well as forest fragments in plantation matrices [33,34].

240 Effective partnerships with logging companies, whose concessions harbor the majority of  
orangutans, are essential to curb orangutan loss [41]. Similarly, partnerships with oil palm and paper  
242 pulp producers are important to promote best practice guidelines for management [33,35,42]. Such  
partnerships have already been reported e.g. by Meijaard et al. [43], and could potentially provide  
244 co-benefits for biodiversity conservation in general [37]. The Roundtable on Sustainable Palm Oil  
(RSPO) and the Forest Stewardship Council (FSC) are examples of certification schemes that  
246 incentivize these partnerships, by enabling consumers to favor responsible natural resource  
management [42].

248 The pervasive decline of orangutans in more intact habitat is consistent with various studies  
identifying hunting as the main driver of biodiversity loss in the tropics [44,45], including Southeast  
250 Asia [2]. More specifically, our observation is supported by the results of extensive interview  
surveys in Kalimantan that show that, per year, on average 2,256 orangutans were hunted or killed  
252 due to conflict with humans [8–10]. The estimate of orangutan killing in the model is based on a  
Borneo wide projection of hunting pressure derived from these interview surveys [10]. In the model  
254 this predictor did not show an influence on orangutan density. Possibly, our dataset lacks sufficient

variance for detecting the impact of killing on orangutan density or the available layer does not  
256 represent well the actual hunting pressure. Human population density, on the other hand, had a  
significant negative influence on orangutan densities in the model and may have already captured  
258 the effect of orangutan killing. Orangutans are also present in the national and international wildlife  
trade. Traded orangutans are usually young orphans, and for each orphan adult individuals have  
260 been killed [46]. Due to the low reproductive rate of the species, even very low offtake rates of  
reproductive females (~1% per year) will drive populations to extinction [16,47]. In the absence of  
262 plausible alternative explanations for the observed loss of orangutans in seemingly intact habitats,  
such as the occurrence of widespread and highly lethal infectious diseases as observed among  
264 African apes [48], killing is the most likely explanation. From this perspective, our prediction of a  
further loss of 45,300 orangutans over the next 35 years, based solely on projections of forest cover  
266 change is most likely an underestimate. Furthermore, many individuals currently occur in  
fragmented, small populations which are assumed not to be viable and will most likely disappear in  
268 the near future.

Knowledge about the density distribution of key species is essential to explore the consequences of  
270 land-use change, exploitation of natural resources, development of infrastructure, and climate  
change. It is also needed to evaluate which conservation interventions are most effective in reducing  
272 decline and loss of biodiversity.

In essence, natural resources are being exploited at unsustainably high rates across tropical  
274 ecosystems, including Borneo. As a consequence, more than 100,000 Bornean orangutans vanished  
between 1999 and 2015. The major causes are habitat degradation and loss in response to local to  
276 global demand for natural resources, including timber and agricultural products, but very likely also  
direct killing. Our findings are alarming. To prevent further decline and continued local extinctions  
278 of orangutans, humanity must act now: biodiversity conservation needs to permeate into all political

and societal sectors and must become a guiding principle in the public discourse and in political  
280 decision-making processes.

## 282 **Acknowledgements:**

We would like to thank the governments of Indonesia and Malaysia, and their forest and  
284 environmental departments, for supporting this research. We also thank Herlina Hartanto, Purwo  
Kuncoro, Isabelle Lackman, Kisar Odom, Dessy Ratnasari, Adi H. Santana, Eddy Santoso, Iman  
286 Sapari, Ahmat Suyoko, Sri Suci Utami-Atmoko, Carel P. van Schaik and the field staff for  
collecting and contributing data, and all funding organizations for funding these surveys. We further  
288 thank Dirk Sarpe and Christian Krause for help with the scripts and implementation on the high-  
performance cluster. We thank Florian Wolf for help with GIS programming. We thank Dr.  
290 Henrique Pereira and Dr. Isabel M. D. Rosa for helpful discussions and Sergio Marrocoli for  
providing comments on the manuscript. We thank the Max Planck Society and Robert Bosch  
292 Foundation for funding and support.

## 294 **Author Contributions**

Conceptualization, M.V., S.A.W., M.A., E.M., and H.S.K.; Software, M.V., S.H., R.M., and H.S.K.;  
296 Methodology, M.V., R.M., and H.S.K.; Formal analysis, M.V., R.M., and H.S.K.; Investigation,  
M.V., S.A.W., M.A., E.M., G.L.B., G.C.S., L.J.A., R.A.D., A.E., B.G., M.H., S.J.H., A.L., K.L.S.,  
298 N.M., A.M., R.M., M., N., A.N., K.O., A.P., D.P., A.PR., P., A.R., A.E.R., J.S., S.S., A.T., and  
H.S.K.; Resources, N.A., D.G., J.M., T.S., M.S., and J.W.; Data curation, M.V., S.A.W., and E.S.R.;  
300 Writing – Original\_draft, M.V.; Writing - Review & Editing, M.V., S.A.W., M.A., E.M., N.A.,

G.L.B., B.G., S.H., M.H., A.J.M., J.M., R.M., M., A.E.R., T.S., M.S., E.S.R., K.A.W., and H.S.K.;

302 Supervision, S.A.W., M.A., E.M., R.M., and H.S.K.

## 304 Declaration of Interests

The authors declare no competing interests.

306

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308

## Figure Legends

310 **Figure 1: Abundance of the three largest orangutan metapopulations between 1999 and 2015**  
311 **and projected abundance for 2020 and 2050.**

312 Orangutan abundance was estimated for the three largest metapopulations with a multi-model  
313 approach over the study period (1999 to 2015). Estimates of future orangutan abundance were  
314 based on forest cover projections for 2020 and 2050 by Struebig et al. [17] and are indicated by a  
315 hashed line. Shaded areas and error bars represent the 95% confidence intervals. On the y-axes the  
316 number “10,000” is highlighted in blue to show the scale difference between the three populations.  
317 The map shows all identified metapopulations in grey. The three largest metapopulations are  
318 indicated by their color. State labels are as follows: Br, Brunei; Sb, Sabah; and Sk, Sarawak in  
319 Malaysia; WK, West; EK, East; NK, North; SK South; and CK, Central Kalimantan in Indonesia.  
320 See also Figures S1, S2 and Tables S1, S2 and S3.

322 **Figure 2: Spatial distribution of estimated orangutan densities on Borneo for the year 1999**  
323 **and 2015, and projections to 2020 and 2050.**

324 Bornean orangutan density per 1 km<sup>2</sup> in the beginning and the end of the study period and for 2020  
325 and 2050. Between 1999 and 2015 high density areas (dark green) disappeared, while medium  
326 density areas (light green) declined. Low density areas (beige and purple) expanded. Future  
estimates are based on projected forest loss [17], therefore map representations between model

328 estimates and future projections differ. Areas in which forest was projected to be lost, also lose the  
resident orangutans. Hence, maps between 2015 and 2020 seem to lose many fragments inhabited  
330 by orangutans, but they already had low density before. Between 2020 and 2050 further areas were  
projected to lose forest, but the loss is less visible. See also Figures S1, S2 and Tables S1, S2 and  
332 S3.

334 **Figure 3: Linking remotely sensed resource use and density distribution.**

Percent area affected by resource use in orangutan metapopulations during the study period, forest  
336 and non-forest classes (pie charts), their spatial distribution (map) and total orangutan abundance  
and its change between the first study year (1999) and last study year (2015) (bar-charts). Total  
338 areas per province in km<sup>2</sup> is given in the lower right corner of the pie charts. Areas had either been  
transformed into plantations (oil palm and paper pulp), deforested or selectively logged between  
340 1999 and 2015, were covered with forest (regrowth, primary or montane primary forest), were  
plantations already before the study period or another unspecified non-forest class. The percent  
342 orangutan abundance loss in comparison to 1999 is highlighted in rectangles. The error bars  
indicate the 95% confidence interval. On the x-axes the number '2000' is highlighted in blue to  
344 show the scale differences between the three areas. See also Figure S3.

346 **STAR methods**

**CONTACT FOR REAGENT AND RESOURCE SHARING**

348 **Further information and requests for resources should be directed to and will be fulfilled by  
the Lead Contact, Maria Voigt (Maria.Voigt@idiv.de).**

350

**METHOD DETAILS**

## 352 Study area and orangutan data

For this study we compiled three types of data: 1) line transect nest count data; 2) nest decay time  
354 data; and 3) polygons representing areas inhabited by orangutan metapopulations. Bornean  
orangutan (*Pongo pygmaeus*) nest count line transect data were compiled from surveys undertaken  
356 across Borneo between 1999 to 2015. Researchers reported the number of orangutan nests observed  
along line transects, which were either walked or flown with a helicopter (aerial and ground  
358 transects), respectively. The datasets were converted to a standard format to include the number of  
observed nests, total transect length, year of survey, and start and/or end coordinates of surveyed  
360 transect line. All ground transects with perpendicular distances (ppd) to nests were used for the  
Distance analysis [49] (number of nests = 15,858, 64% of total), to estimate truncation distance and  
362 effective strip width (ESW), that is, the perpendicular distance from the transect, below which an  
equal number of nests was missed as seen beyond [14]. For the predictive density distribution  
364 model we also considered aerial and ground transects without ppd and assumed estimated ESW to  
be representative. The cumulative area of land surveyed was calculated as the transect length  
366 multiplied by two times the effective strip width, excluding repeat sampling.

There were only few transects from areas on Borneo in which orangutans are known to be absent.  
368 Thus, we added ‘virtual’ transects with zero nests randomly to expert-delineated areas of orangutan  
absence [50] to balance this bias in sampling. For each survey year, we set the number of transects  
370 in the area of known absences to 50% of the number of surveyed transects in the orangutan range in  
the given year. We tested the effect of varying the number of absence transects (30%, 50% and 80%  
372 density of surveyed transect), but the model proved to be robust and the resulting orangutan  
abundance estimate did not differ substantially (30% absence density in comparison to 50%:  
374 correlation coefficient  $> 0.99$ , maximum percent difference = 5.6%; 80 % absence density in

comparison to 50%: correlation coefficient  $> 0.99$ , maximum percent difference = 3%;  $n = 16$   
376 years).

We compiled nest decay information from four sites. For two locations (Sabangau in Central  
378 Kalimantan and Lesan in East Kalimantan) nest decay datasets included information from repeated  
visits about nest status from construction to disappearance. The dataset from Lesan included 88  
380 nests, which were visited between February 2005 and September 2006. In Sabangau 423 nests were  
visited between July 2001 and April 2011. For two other sites (Kinabatangan, Sabah and Gunung  
382 Palung, West Kalimantan) we used information about nest decay time, estimated by Ancrenaz et al.  
and by Johnson et al. [25,51].

384 At the PHVA for Bornean orangutans held between the 24<sup>th</sup> and 27<sup>th</sup> of May 2016 in Bogor,  
Indonesia, 41 orangutan experts mapped 64 Bornean orangutan metapopulations [16]. The resulting  
386 metapopulation polygons covered areas between 6 and 58,157 km<sup>2</sup>, amounting to a total area of  
333,250 km<sup>2</sup>. Predictions were extrapolated to this area, and although only a small proportion was  
388 actually sampled (0.37%), the surveys were distributed well across the area. Only 23% of the  
metapopulation area was located outside the 95 % minimum convex polygon of transect locations.

390

## Predictor variables of orangutan abundance

392 We selected predictor variables based on their presumed importance for orangutan ecology, while  
guaranteeing data availability for the whole range and minimizing the correlation between them  
394 [24]. The final predictor variable set comprised layers depicting climate (mean daily temperature,  
yearly variation in rainfall, rainfall in dry months (May - September), habitat (topsoil organic  
396 carbon content, peat swamp, lowland and lower montane forest cover), and anthropogenic pressures  
on orangutans (deforestation, human population density, orangutan killing estimates, and percent  
398 population with religious hunting taboos). The predictor for orangutan killing estimates was based



on a Borneo wide model of orangutans killed in years prior to interview surveys [8] by Abram et al.  
400 [10]. We included percent Muslim population as a proxy for the proportion of the population that  
has hunting taboos, because it had been shown that hunting pressure on primates is lower in areas  
402 inhabited by a majority of Muslims [9,52].

Before extraction, we reprojected all predictor layers to the Asia South Albers Equal Area Conic, to  
404 allow for accurate representation of metric distances. The layers were resampled to the same extent,  
origin and a resolution of 1 km, the coarsest available. Nearest neighbor resampling was used for  
406 categorical predictors.

We extracted climate and habitat variables within a radius of 1 km around each transect, resulting in  
408 an area of at least 3.14 km<sup>2</sup>, depending on the transect length. This approximates the size of the  
home range of female orangutans on Borneo and ensures that climatic and ecological predictors that  
410 have an effect on the population are appropriately represented. Variables indicating anthropogenic  
pressures were obtained within a distance of 10 km, approximating the distance over which human  
412 influence is most likely (E. Meijaard, unpublished observation).

Information about habitat cover was available for three time points (2000, 2010 and 2015 [53,54]).  
414 We used the habitat cover information from 2000 for all transects surveyed between 1999 – 2005,  
the layer from 2010 for all transects surveyed between 2006 and 2012, and the layer from 2015 for  
416 transects sampled in 2013 to 2015. At the time of the analysis, deforestation maps were available for  
each year between 2000 and 2014 [3]. For each transect, we considered the percent area deforested  
418 in the years prior to the survey in a 10 km-buffer around the transect.

When the start or the end-point of a transect was unknown, we extracted the predictor variables  
420 with a radius of half the transect length [sensu 55]. We determined the proportion of each class  
within the neighborhood for categorical and the mean value for continuous predictor variables.

422 We repeated the extraction for a 1 x 1 km grid covering the metapopulation areas, to enable the  
estimation of orangutan abundance over the whole range. It was visually verified that all predictors  
424 had an approximately symmetrical distribution, and human population density was subsequently  
log-transformed. We also ensured that the range of variable values extracted for the transect  
426 observations was broad enough to meaningfully allow prediction to the range of values extracted for  
the metapopulation areas by comparing the distribution of both. We found that the majority of  
428 predictors covered more than 75% of the predictor space to which estimates were extrapolated. The  
exceptions were the predictors deforestation (63% cover of sampled predictor range), mean  
430 temperature (50 % cover) and human population density (> 1% cover). For the predictor mean  
temperature the low values were not included. These occur in high elevation areas, which were  
432 sampled less as they are difficult to access and harbor fewer orangutans [28]. The surveys also did  
not include areas with high human population density. As the density of orangutans decreases to  
434 zero in high elevation areas and areas with high human population density, the extrapolation error  
cannot become large. Thus, we did not consider the low coverage for these predictors to be a  
436 limitation. The cover of predictor values was at most 3% lower, when excluding the absence  
transects, except for rainfall variability. For this predictor, the absence transects increased the cover  
438 of predictor values by 19%. Finally, all predictors were standardized to a mean of zero and a  
standard deviation of one to facilitate the comparison of model parameters [56].

440

## Future orangutan abundance

442 We used information about remaining forest cover on Borneo projected for 2020 and 2050 from  
Struebig et al. [17,41] together with the orangutan density distribution estimated for 2015 and  
444 predicted orangutan distribution 5 and 35 years after the last study year. Assuming that orangutans

will not be able to survive in the long-term in areas that are not forested, we excluded all individuals  
446 occurring in cells that were predicted to lose forest cover by 2020 and 2050, respectively.

448

## QUANTIFICATION AND STATISTICAL ANALYSIS

450 As an analytical approach, we used a combination of negative binomial regression models [57] and  
design-based inference [15,58] to estimate the parameters necessary for building a spatial density  
452 distribution model for Bornean orangutans as proposed by Hedley et al. [59].

### 454 Calculating model offset

In the predictive density distribution model, we used an offset term [60] to convert the number of  
456 orangutan nests per transect, into the number of individuals per square kilometer. It included the  
product of the area that was effectively sampled and the relationship between number of nests and  
458 number of orangutans. The area that was sampled is described by the length of each transect ( $l$ )  
multiplied by twice the ESW.

460 The number of orangutans per observed nest was estimated using the proportion of nest builders in  
a population ( $p$ ), the daily production rate of nests ( $r$ ), and the nest decay rate ( $t$ ), which represents  
462 the number of days for which a nest remains visible in the forest [13,14]. For these parameters we  
used  $p = 0.88$  and  $r = 1.12$  nests/day/individual from Spehar et al. [61], representing a combination  
464 of the most current nest life-history parameters for Bornean orangutan populations (see below how  $t$   
was determined).

466

### Effective strip width

468 For the ground transects, the effective strip width (ESW) was estimated using Distance 6.0 [49]. We  
used a truncation distance of 27 m. The models were fitted to the observed data with and without  
470 grouping for different habitat categories, using various key functions and adjustment terms. The  
model fit was tested with  $\chi^2$  statistics for which we set distance intervals under the “diagnostics”  
472 tab. The fit of the model using habitat specific detection functions was not better than the fit of the  
model that used a single detection function across habitats, as established by Akaike Information  
474 Criterion (AIC). As a consequence, we applied a global detection function and resulting effective  
strip width (ESW) to all ground transects. The model with the best fit, based on the lowest AIC and  
476  $\chi^2$  statistics, was one with a half-normal key function and a simple polynomial adjustment of order  
4. 478  
Nests with a ppd larger than the truncation distance were excluded from the dataset. We assumed  
that nests without ppd were distributed at similar distances along transects as the nests for which  
480 ppds were reported. Therefore, we truncated them by randomly excluding the same proportion of  
nests that were excluded from transects with known distances, leaving 34,415 nests in the dataset.  
482 The estimated ESW was 15.95 m, and nest detection probabilities for ground transects was 0.59.  
This is in line with reported detection probability for other ape surveys [55].  
484 Helicopter surveys did not contain information about the ppds from the transects to the nests. Thus,  
the ESW for those surveys was set to 75m, which corresponds to half of the maximum visibility  
486 from the helicopter to the sides of the survey line [62]. Yearly abundance estimates were tested for  
sensitivity to the assumed aerial ESW, but did not vary significantly (abundance estimate with aerial  
488 ESW = 100 m in comparison to 75 m: correlation coefficient > 0.99, maximum difference 2.127%,  
aerial ESW = 50 m in comparison to 75 m: correlation coefficient = 1, maximum difference  
490 3.904%, n = 16 years).

## 492 Estimation of nest decay rate and extrapolation

We updated the nest decay rate for two sites in the Bornean orangutan range (Sabangau in Central  
494 Kalimantan and Lesan in East Kalimantan), using the modification of the approach from Laing et  
al. [57], used in Wich et al. [55]. Additionally, we used site-specific decay rates available from the  
496 literature for Kinabatangan, Sabah [25] and Gunung Palung, West Kalimantan [51]. For the  
calculation of the nest decay time we used logistic models (left-truncated with normalized intercept,  
498 log-transformed and reciprocal) [57] and nest age as the only predictor. The product of the daily  
decay probability and time since nest construction was summed over 2000 days to calculate mean  
500 decay time. The model estimates from the three approaches were model-averaged using their AIC  
weights. The time until nest decay for Sabangau was found to be 496.3 days (n = 423, 95% CI:  
502 453.1 to 542.9 days) and 582.5 days (n = 88, 95% CI: 461.2 to 753.1) for Lesan, which is similar to  
the nest decay rate estimated in Spehar et al. [61] for this area. We bootstrapped the data 1,000  
504 times and determined the 95% confidence interval by model-averaging the 2.5% and 97.5% lower  
and upper confidence limits.

506 The sites, for which we had nest decay values, experience different environmental conditions. The  
respective values were thus used for different parts of the Bornean orangutan range, based on the  
508 location of transects within provinces and forest types: (a) Sabangau nest decay, 496.3 days (this  
publication), for peatswamp forests in Central Kalimantan; (b) Lesan nest decay, 583 days (this  
510 publication), for East and South Kalimantan; (c) Average of Gunung Palung lowland forest, lowland  
hill and mid-elevation nest decay, 276 days [51], for lowland forests in Sarawak, West and Central  
512 Kalimantan; (d) Gunung Palung montane forest nest decay, 321.3 days [51], for montane forests (>  
800 m above sea level (asl)) in Sarawak, West and Central Kalimantan; (e) Gunung Palung  
514 peatswamp forest nest decay, 399 days [51], for peatswamp forests in West Kalimantan and  
Sarawak; (f) Kinabatangan nest decay, 202 days [25], for Sabah.

516

## Model structure and multi-model inference

518 We used a Generalized Linear Model with a negative binomial error structure and log link function  
[60] to assess the effect of climate, habitat and anthropogenic pressures on orangutans and predict  
520 the density distribution across the range. The full model, including all predictor variables and the  
offset term, had the following structure: orangutan nest count on transect  $\sim$  year + mean temperature  
522 + rainfall variability + rainfall in dry months + rainfall in dry months<sup>2</sup> + topsoil organic carbon  
content + peat swamp cover + lowland forest cover + lower montane forest cover + deforestation +  
524 human population density + orangutan killing estimates + percent population with religious hunting  
taboos + offset + dispersion parameter. It had been shown that higher orangutan densities occur in  
526 areas of intermediate levels of rainfall in dry months [11], therefore we included the squared rainfall  
in dry months. A negative coefficient indicates highest orangutan densities at intermediate values of  
528 rainfall.

We tested for collinearity, which was not an issue (largest Variance Inflation Factor = 4.429, see  
530 also Table S1) and leverage values as well as DFBeta values did not indicate obviously influential  
cases [63,64]. The model was not strongly overdispersed (dispersion parameter: 1.675).

532 As a test of the significance of the predictors, we compared the fit of the full model [65], as  
described above, to the null model, only including the intercept and the offset term. The comparison  
534 was based on a likelihood ratio test. We fitted the models in R (version 3.x, [66]) using the function  
glm.nb of the R package MASS and determined Variance Inflation Factors using the function vif of  
536 the R package car [67].

To minimize model uncertainty in spatial model prediction, we applied multi-model inference and  
538 assessed all possible combinations of covariates included in the full model ( $n = 6,144$ ) [see also 55].  
Out of all possible models, only 18 models were in the confidence set, combining 95% of the AIC

540 weight (Table S2). The best model was the full-model lacking the orangutan killing estimates and  
percent population with religious hunting taboos (Table S2 and S3). Predictions of all models were  
542 averaged, after weighting by the models' AIC weight [68] and used to predict the orangutan density  
for all 1x1 km cells across the range. We model averaged in link space and only after that  
544 exponentiated the averaged predictions to get the abundance estimate per grid cell.

In the output of the density distribution models, all pixels outside the previously defined  
546 metapopulations were excluded to avoid overestimating Bornean orangutan density, assuming that  
all larger populations are known to date. Density estimates were summed for each metapopulation  
548 and land-use category of interest to retrieve total abundance per metapopulation or category [16].

## 550 Parametric bootstrapping to estimate confidence limits

The 95% confidence limits of the model predictions were estimated using parametric bootstrapping  
552 (n=1,000). The model-averaged fitted estimates and their standard errors (SE), as well as estimate  
and SE for the dispersion parameter, theta, were used to generate 1,000 new instances of model  
554 estimates by sampling from normal distributions with means and standard deviations being the  
model estimates and their standard errors, respectively. These bootstrapped estimates were then  
556 used, together with the model offset and the predictors, to sample an instance of the response from a  
negative binomial distribution with a mean and dispersion parameter determined by the  
558 bootstrapped estimates.

We fit the models with the bootstrapped response, resulting in bootstrapped model estimates and  
560 AIC-values for each model. Using the bootstrapped model-estimates, a prediction was made for  
each grid cell and study year and from these, the confidence limits of the mean and total abundance  
562 of cells or groups of cells were determined using the percentile method [69].

## Spatial overlap of orangutan density distribution and resource use

566 With the aim of assessing the differences in the orangutan abundance and change in response to  
resource use during the survey period, we compared the orangutan density distribution from the first  
568 and last year of the survey period with maps for land-cover classes and area converted into  
industrial agriculture (oil palm and paper pulp plantations) [32,70]. The lack of repeat sampling  
570 through time in areas of land-cover change made it necessary to approach this study in two steps.  
First, we fitted the model using habitat cover and threat predictors and second, overlaid the  
572 estimated densities with independent maps of land-cover change to infer about patterns of  
orangutan loss. However, as these maps represent related information, we cannot entirely exclude  
574 potential circularity in the approach taken. The only approach that completely allows to avoid this  
problem is to systematically sample across gradients of land-use change through time.

576 From the land-use layers we extracted three classes representing changes of orangutan habitat due  
to resource use (establishment of industrial oil palm and paper pulp plantations, deforestation, and  
578 selective logging) that occurred during the study period (1999 – 2015), three classes representing  
forested areas in 2015 (regrowth forest, primary forest, and primary montane forests (> 750 m asl)),  
580 and two classes depicting non-forested areas in 2015 (industrial plantations established before 2000  
and ‘other’). Regrowth forests were areas that were non-forest in 1973, but had forest cover in  
582 2015. The category ‘other’ included scrublands, urban, agricultural and non-forest areas that were  
not contained in the other categories. It was possible that during the study period an area was first  
584 selectively logged or deforested, and then industrial plantations were established. In our analysis,  
we counted these areas only as industrial plantations, as this was the final stage of the land-use  
586 transition. We then pooled the average abundance and density in each land-use class or resource use  
category and calculated the 95% confidence interval.



## **DATA AND SOFTWARE AVAILABILITY**

590 All raw datasets used in this study can be requested from the IUCN SSC. A.P.E.S database  
(<http://apesportal.eva.mpg.de/>). The processed data and data underlying the figures were deposited  
592 under <https://portal.idiv.de/owncloud/index.php/s/gU6BXYGoEWWdkyg>. The code was deposited  
under [https://git.idiv.de/mv39zilo/manuscript\\_code.git](https://git.idiv.de/mv39zilo/manuscript_code.git).