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Summary

Unsustainable exploitation of natural resources is increasingly affecting the highly biodiverse tropics [1,2]. Although rapid developments in remote sensing technology have permitted more 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, 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 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 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 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 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 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 political and societal sectors, such as in land-use planning, resource exploitation, infrastructure development, and education, and by increasing long-term sustainability [12].

Results

Bornean orangutan field survey data

To model Bornean orangutan density distribution and derive metapopulation abundances we 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 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 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^2. During the 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-transformed mean nest encounter rate per year as response, weighted by the number of transects per year and the year as predictor).

Estimating change in Bornean orangutan density distribution

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 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 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 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, 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 more montane forest cover, the cover of deforested areas around transects was slightly positively correlated, but its confidence limits included zero.

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 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 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 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 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 have experienced a strong decline over the studied 16-year period (Figure 1).

Western Schwaner, the largest metapopulation, lost an estimated 42,700 individuals (95% 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 Schwaner, lost 20,100 individuals (95% 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 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).

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 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 Schwaner metapopulation area, 14,700 individuals (95% CI: 9,600 – 19,600) in Eastern Schwaner and 6,100 individuals (95% CI: 3,800 – 10,000) in Karangan by 2050. The total future loss for all 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 orangutan killing for food and in conflict and is therefore most likely an underestimate. All estimates are rounded to the nearest hundred.

Linking remotely sensed resource use and density distribution

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 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 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 primary forest, regrowth forests, industrial plantations established prior to the study period and ‘other’, comprising non-forest areas.

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 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, 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 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 deforestation contributed 7% (Kalimantan), 2% (Sabah), and less than 1% (Sarawak) to the overall estimated loss of orangutans in each of the three regions.

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 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 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) and 83% of the total loss in Sarawak (900 individuals, 95% CI: 250 – 1,600).

Discussion

The unsustainable use of natural resources has caused a dramatic decline of Bornean orangutans. 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 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 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 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 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 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 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 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 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.

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 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 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 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 of the study period. However, we found no indication of this, and so do not consider this to be a limitation of our study.

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 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 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 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 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 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 removal (deforestation and conversion to industrial plantations). This shows that the predictive density distribution model has indirectly captured the deleterious effects of deforestation on 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 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 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 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].

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 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 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].

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 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 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 incentivize these partnerships, by enabling consumers to favor responsible natural resource management [42].

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 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 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 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 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 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 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 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 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 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 the near future.

Knowledge about the density distribution of key species is essential to explore the consequences of 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 decline and loss of biodiversity.

In essence, natural resources are being exploited at unsustainably high rates across tropical 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 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 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 decision-making processes.

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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.; 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., 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.; Writing – Original_draft, M.V.; Writing - Review & Editing, M.V., S.A.W., M.A., E.M., N.A.,

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Declaration of Interests

The authors declare no competing interests.

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Figure Legends

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

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

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

Bornean orangutan density per 1 km² in the beginning and the end of the study period and for 2020 and 2050. Between 1999 and 2015 high density areas (dark green) disappeared, while medium 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 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 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 S3.

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

Percent area affected by resource use in orangutan metapopulations during the study period, forest 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 areas per province in km² 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 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 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 show the scale differences between the three areas. See also Figure S3.

STAR methods

CONTACT FOR REAGENT AND RESOURCE SHARING

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

METHOD DETAILS

Study area and orangutan data

For this study we compiled three types of data: 1) line transect nest count data; 2) nest decay time data; and 3) polygons representing areas inhabited by orangutan metapopulations. Bornean orangutan (*Pongo pygmaeus*) nest count line transect data were compiled from surveys undertaken 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 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 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 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 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 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. 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 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% 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%: 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 years).

We compiled nest decay information from four sites. For two locations (Sabangau in Central 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 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 Palung, West Kalimantan) we used information about nest decay time, estimated by Ancrenaz et al. and by Johnson et al. [25,51].

At the PHVA for Bornean orangutans held between the 24th and 27th of May 2016 in Bogor, Indonesia, 41 orangutan experts mapped 64 Bornean orangutan metapopulations [16]. The resulting metapopulation polygons covered areas between 6 and 58,157 km², amounting to a total area of 333,250 km². Predictions were extrapolated to this area, and although only a small proportion was 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.

Predictor variables of orangutan abundance

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 [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 carbon content, peatswamp, lowland and lower montane forest cover), and anthropogenic pressures on orangutans (deforestation, human population density, orangutan killing estimates, and percent 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. [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 inhabited by a majority of Muslims [9,52].

Before extraction, we reprojected all predictor layers to the Asia South Albers Equal Area Conic, to 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 categorical predictors.

We extracted climate and habitat variables within a radius of 1 km around each transect, resulting in an area of at least 3.14 km², 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 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 influence is most likely (E. Meijaard, unpublished observation).

Information about habitat cover was available for three time points (2000, 2010 and 2015 [53,54]). 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 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 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 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.

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 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 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 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 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 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 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 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 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].

Future orangutan abundance

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 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 occurring in cells that were predicted to lose forest cover by 2020 and 2050, respectively.

QUANTIFICATION AND STATISTICAL ANALYSIS

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 distribution model for Bornean orangutans as proposed by Hedley et al. [59].

Calculating model offset

In the predictive density distribution model, we used an offset term [60] to convert the number of 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 number of orangutans. The area that was sampled is described by the length of each transect (l) multiplied by twice the ESW.

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 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 of the most current nest life-history parameters for Bornean orangutan populations (see below how t was determined).

Effective strip width

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 grouping for different habitat categories, using various key functions and adjustment terms. The model fit was tested with χ^2 statistics for which we set distance intervals under the “diagnostics” 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 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 $\chi 2$ statistics, was one with a half-normal key function and a simple polynomial adjustment of order 4.

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 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. 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].

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 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 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 3.904%, n = 16 years).

Estimation of nest decay rate and extrapolation

We updated the nest decay rate for two sites in the Bornean orangutan range (Sabangau in Central 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 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, 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 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: 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 times and determined the 95% confidence interval by model-averaging the 2.5% and 97.5% lower and upper confidence limits.

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 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 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 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 peatswamp forest nest decay, 399 days [51], for peatswamp forests in West Kalimantan and Sarawak; (f) Kinabatangan nest decay, 202 days [25], for Sabah.

Model structure and multi-model inference

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 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 ~ year + mean temperature + rainfall variability + rainfall in dry months + rainfall in dry months^2 + topsoil organic carbon content + peatswamp cover + lowland forest cover + lower montane forest cover + deforestation + 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 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 rainfall.

We tested for collinearity, which was not an issue (largest Variance Inflation Factor = 4.429, see 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). 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 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 the R package car [67].

To minimize model uncertainty in spatial model prediction, we applied multi-model inference and 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 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 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 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 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 and land-use category of interest to retrieve total abundance per metapopulation or category [16].

Parametric bootstrapping to estimate confidence limits

The 95% confidence limits of the model predictions were estimated using parametric bootstrapping (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 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 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 bootstrapped estimates.

We fit the models with the bootstrapped response, resulting in bootstrapped model estimates and 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 of cells or groups of cells were determined using the percentile method [69].

Spatial overlap of orangutan density distribution and resource use

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 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 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 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 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.

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 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)), 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 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 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 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

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 under https://portal.idiv.de/owncloud/index.php/s/gU6BXYGoEWWdkyg. The code was deposited under https://git.idiv.de/mv39zilo/manuscript_code.git.