

Red Ape in the Red

–

Abundance, Threats and Conservation

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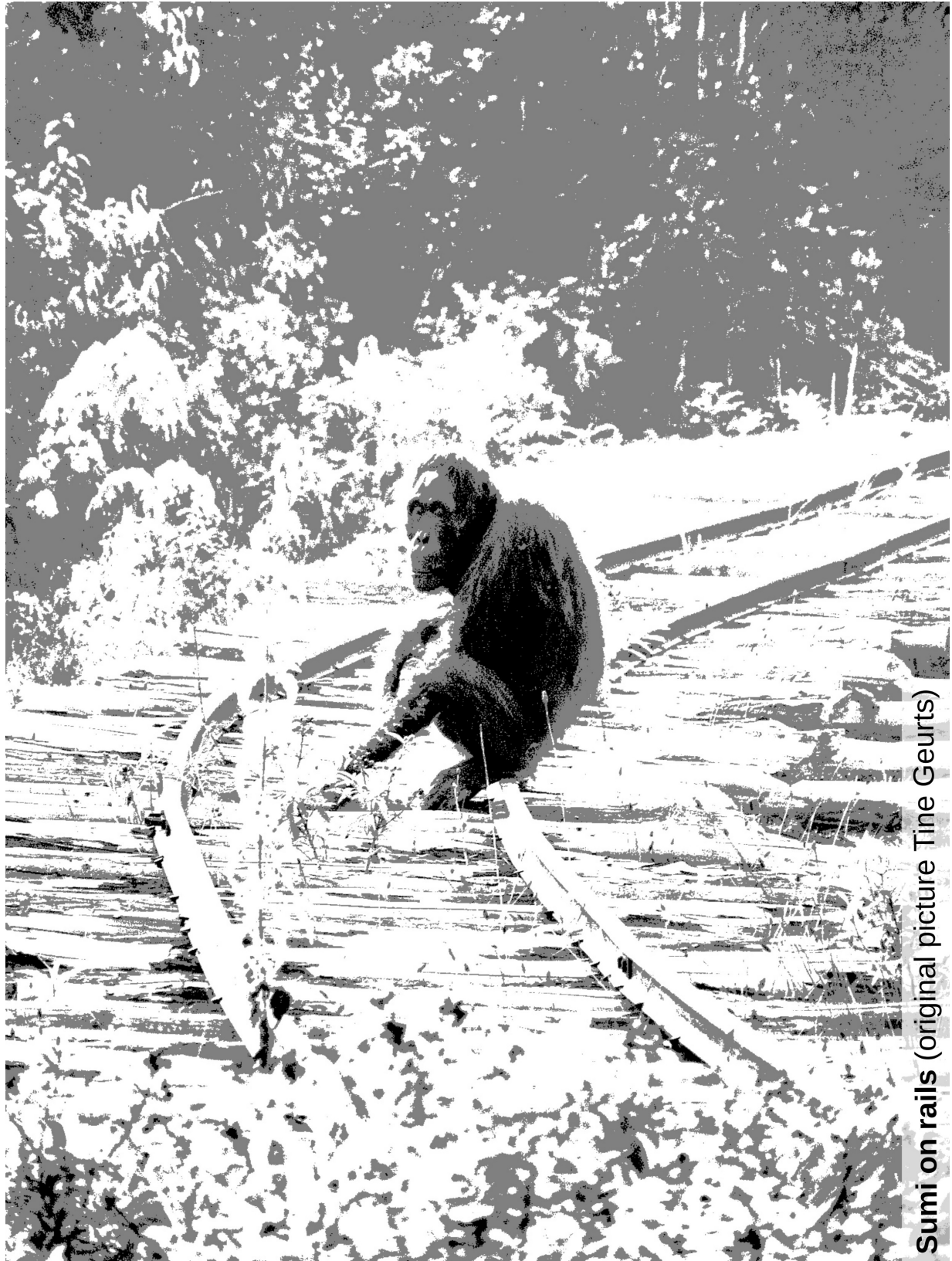
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Sumi on rails (original picture Tine Geurts)

To Mom, Dad and Robert for everything!

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Table of Contents

SUMMARY	1
CHAPTER 1	3
INTRODUCTION	3
Biodiversity changes in the tropics.....	3
Why are orangutans special?.....	3
Orangutans on Borneo – past and present distribution.....	4
Drivers of orangutan decline.....	5
Orangutan conservation and impediments.....	6
Objectives of the thesis.....	7
CHAPTER 2	15
GLOBAL DEMAND FOR NATURAL RESOURCES ELIMINATED MORE THAN 100,000 BORNEAN ORANGUTANS	15
Summary.....	18
RESULTS	19
Bornean Orangutan Field Survey Data.....	19
Estimating Change in Bornean Orangutan Density Distribution.....	19
Linking Remotely Sensed Resource Use and Density Distribution.....	22
DISCUSSION	24
STAR METHODS	33
KEY RESOURCES TABLE	33
METHOD DETAILS	34
Study area and orangutan data.....	34
Predictor variables of orangutan abundance.....	35
Future orangutan abundance.....	37
QUANTIFICATION AND STATISTICAL ANALYSIS	37
Calculating model offset.....	37
Effective strip width.....	37
Estimation of nest decay rate and extrapolation.....	38
Model structure and multi-model inference.....	39
Parametric bootstrapping to estimate confidence limits.....	40
Spatial overlap of orangutan density distribution and resource use.....	40
CHAPTER 3	43
DEFORESTATION PROJECTIONS IMPLY RANGE-WIDE POPULATION DECLINE FOR CRITICALLY ENDANGERED BORNEAN ORANGUTANS	43
INTRODUCTION	45
MATERIAL AND METHODS	47
Identifying main deforestation drivers on Borneo.....	47
Deforestation model framework.....	47
Simulations.....	48

Validation and analysis.....	48
Priority areas for orangutan conservation based on deforestation projections....	48
RESULTS.....	49
Deforestation model for Borneo.....	49
Validation.....	49
Spatial deforestation projections.....	49
Probability of deforestation projections on Borneo over time.....	51
Projected threat to orangutan populations within states.....	52
Projected threat to orangutan populations within land-use and management categories.....	53
DISCUSSION.....	55
Drivers of deforestation on Borneo.....	55
Observed and projected deforestation.....	55
Projected deforestation and orangutans in PAs and logging concessions.....	56
Projected deforestation and orangutans in plantations and other non-protected areas.....	57
Considering regrowth of forests.....	58
Potential to expand the modeling approach to other species.....	58
Killing as an additional driver of orangutan loss.....	58
Implications for biodiversity conservation.....	59
CHAPTER 4	67
ORANGUTAN POPULATIONS ARE CERTAINLY NOT INCREASING IN THE WILD	67
CHAPTER 5	73
CHALLENGES AND OPPORTUNITIES FOR MONITORING A CHARISMATIC SPECIES IN THE TROPICS –	
INTEGRATING DATA AND STAKEHOLDERS	73
INTRODUCTION.....	75
BORNEAN ORANGUTANS - STATUS, TREND AND THREATS.....	77
Population status and trend.....	77
Threats to orangutan populations.....	77
MONITORING.....	78
Variables of interest and methods of observation.....	78
Sampling design.....	80
MODELS FOR SPECIES MONITORING.....	82
Species distribution models.....	82
Integrated population models.....	83
Models to improve monitoring.....	84
REPORTING.....	84
Monitoring data for use.....	84
Taxa-specific databases.....	85
Tools for reporting.....	86
Integration of stakeholders.....	87
CONCLUSION.....	89
CHAPTER 6	97
SYNTHESIS	97
Estimating the density distribution of species.....	97
Importance of communication and integration.....	98
Conservation and global socio-political climate.....	99
Is there still hope?.....	100

APPENDIX

I

<i>Appendix – Chapter 2</i>	<i>i</i>
<i>Appendix – Chapter 3</i>	<i>vi</i>
APPENDIX S1.....	<i>vi</i>
Further description of source data and deforestation model for Borneo.....	<i>vi</i>
Spatial layers of deforestation drivers.....	<i>vi</i>
Deforestation model and calibration.....	<i>vii</i>
Simulations.....	<i>viii</i>
<i>Appendix – Chapter 5</i>	<i>xvii</i>
APPENDIX S1:.....	<i>xvii</i>
Further description of monitoring methods.....	<i>xvii</i>
Observation methods.....	<i>xvii</i>
Observing nests on transects.....	<i>xvii</i>
Camera traps.....	<i>xviii</i>
Interview surveys.....	<i>xviii</i>
Citizen science.....	<i>xix</i>
Digitization of observations.....	<i>xix</i>
Observations of additional process variables.....	<i>xix</i>
Direct and indirect observations of drivers and threats.....	<i>xx</i>
<i>Curriculum Vitae</i>	<i>xxv</i>
<i>List of publications and conference participations</i>	<i>xxix</i>
<i>Authors' contribution</i>	<i>xxxi</i>
<i>Acknowledgements</i>	<i>xxxiii</i>
<i>Eigenständigkeitserklärung</i>	<i>xxxvii</i>

Summary

Although orangutans captivate people around the world, their numbers and the extent of their habitat have steeply declined in recent decades. This thesis substantially contributes to the evidence base for Bornean orangutan conservation by quantifying orangutan loss in response to past and future drivers and reviewing points of action to overcome existing impediments and improve species monitoring.

In **chapter 2** I used a compilation of a unique set of observation and predictor data to estimate the abundance of Bornean orangutan populations. I found that overall abundance had dramatically declined by 148,500 individuals (95% CI: 48,100 – 252,300) in the 16 years between 1999 and 2016. The availability of spatio-temporal patterns of orangutan density allowed me to quantify the effects of land-use and land-cover change on rate and total loss of abundance over the study period. My analysis enabled me to gauge the pervasiveness of human impact on orangutan populations and indicated that half of the orangutan population was affected by logging, deforestation or conversion to industrial plantations. While the highest rates of decline were linked with land clearance, it accounted for only a small proportion of the total loss. The majority of orangutans were lost from selectively logged and primary forests, which harbored larger parts of the whole population. This suggests that other drivers, independent of forest loss or conversion, have contributed to orangutan loss. This finding supports previous studies that identified orangutan killing as a major cause for orangutan decline.

To determine the potential deforestation impacts on orangutans, I adapted a spatially-explicit deforestation model to project future tree cover loss on Borneo in **chapter 3**. Along with killing, habitat loss is the main driver of orangutan decline. Our projections until 2031 point to continued deforestation in all states on the island, which could lead to habitat loss directly affecting up to 10,400 orangutans. Coupling Bornean orangutan density distribution with future projections of deforestation helped to understand where and under which land-use or management orangutan strongholds will be threatened and where they will be effectively protected in the near future. Populations that currently persist in industrial plantation concessions and other unprotected forests are expected to account for the majority of projected orangutan losses. The information generated in chapter 3 is especially relevant for optimally allocating the scarce resources for orangutan protection and improving existing land-use plans by anticipating future risk from habitat loss. The deforestation projections can

also provide crucial support for the spatial conservation planning of other forest-dependent species.

In spite of the findings published in chapter 2 and a number of other recent studies on the status and trend of the three orangutan species, in mid-2018 the Indonesian government reported an increase in orangutan numbers across official sampling sites. Together with my co-authors, I raised attention to this contradiction in **chapter 4**, and questioned the validity of these numbers presented by the Indonesian government. These were based on limited and biased sampling coverage predominantly situated within protected areas or release sites and are contrary to known parameters of orangutan reproductive biology and unabated habitat loss. We furthermore challenged the feasibility of the targeted increase of orangutan populations by 2% annually, suggested improvements to official monitoring strategies and proposed an increase in efforts to integrate the research community and stakeholders involved in orangutan conservation.

To follow up on these recommendations, in **chapter 5**, I reviewed the literature to identify challenges in monitoring elusive tropical species, using the orangutan as a case study. I suggest opportunities to improve monitoring effectiveness based on this review. To increase overall sampling coverage in the future, standard methods could be complemented by a range of approaches such as camera trap networks, helicopter transects or drones that would enable monitoring of larger areas with higher frequency. Integrated species distribution and population modeling can combine information about species presence and abundance from different survey techniques by explicitly accounting for the observation processes. However, orangutan monitoring, and ultimately conservation, can only be significantly improved by overcoming additional barriers to success, especially lack of data sharing and lack of integration of stakeholders. I discuss how databases can bridge the gap between data users and producers and help preserve monitoring data. Interactive web-tools can be designed to communicate and visualize customized results in near-real time and support stakeholder engagement and collaboration.

The review in chapter 5 elucidates how integration of novel technologies, different data sources and stakeholders are key elements of successful monitoring, which underpins conservation management. Combined with information on species loss and past and future threats in chapters 2-4, this thesis thus considerably advances the evidence base for species conservation on Borneo. By evaluating potential pathways to achieve successful monitoring, the findings and suggestions can help to steer future priorities for monitoring and conservation and contribute to tackling the unprecedented loss of species in this tropical biodiversity hotspot.

Chapter 1

Introduction

Biodiversity changes in the tropics

Anthropogenic changes are severely degrading the quality and extent of natural ecosystems across the globe. The impacts of these changes are highest in the tropics, where most biodiversity remains (*Dirzo et al., 2014; Gibson et al., 2011; Laurance et al., 2012*). The majority of the global biodiversity hotspots – characterized by the exceptional concentration of endemic species threatened by exceptional levels of habitat losses (Mittermeier et al., 2005) – are in this region. In Southeast Asia, Borneo is a hotspot that has experienced deforestation and habitat degradation at one of the highest rates worldwide, with severe consequences for biodiversity (Gaveau et al., 2016; Margono et al., 2014; Turubanova et al., 2018). Among the large number of species occurring on Borneo, the Bornean orangutan (*Pongo pygmaeus*) is without doubt one of the most emblematic (Cribb et al., 2014; Rijksen and Meijaard, 1999; Spehar et al., 2018).

Why are orangutans special?

As a consequence of their evolutionary proximity to humans, their charismatic nature and their role as keystone species, orangutans, and primate species in general, have received particular attention by research and society (Cribb et al., 2014; Marshall et al., 2016; Marshall and Wich, 2016; Meijaard et al., 2012). Studying and, ultimately, protecting primates allows us to understand human evolution, biology and culture in a broader phylogenetic context (Boyd and Silk, 2012; Marshall and Wich, 2016; Van Schaik et al., 1999).

Orangutans have always fascinated people and fulfill an important function as flagship species for conservation (Clucas et al., 2008; Cribb et al., 2014; Marshall et al., 2016; Meijaard et al., 2012). They draw in considerable funds and promote the protection of the habitat they share with other species. When environmental and economic interests collide,

the plight of great apes can raise critical awareness to the situation (Alamgir et al., 2019; Sloan et al., 2018). However, the features that make orangutans special, are also the features that make them especially vulnerable to environmental threats. Large brains and long juvenile periods result in long generation times, and make orangutans more likely to suffer population declines and less able to recover after disturbances. This making their study particularly timely and relevant (Marshall and Wich, 2016).

Orangutans on Borneo – past and present distribution

Fossil remains indicate that the genus *Pongo* originated 6 to 5 million years ago (Harrison et al., 2006). During the Pleistocene, multiple *Pongo* species occurred across southern China, mainland Southeast Asia, and the Sunda Shelf, the landmass connecting the present-day islands of Sumatra, Java, and Borneo (Spehar et al., 2018). Towards the end of the Pleistocene (126 to 12 thousand years ago) the distribution of orangutan species started to become smaller, and densities decreased most likely as a consequence of human activities, especially hunting (Spehar et al., 2018). At the Pleistocene/Holocene boundary, only three *Pongo* species remained on Borneo and Sumatra, representing approximately 20% of their original range (Harrison et al., 2006; Ibrahim et al., 2013; Louys et al., 2007).

Declines continued until modern times (Bruford et al., 2010; Goossens et al., 2006; Meijaard et al., 2010b). Today the three extant orangutan species on Sumatra (*P. abelii* and *P. tapanuliensis*) and on Borneo (*P. pygmaeus*) are considered critically endangered (IUCN, 2019). Bornean orangutans can further be differentiated into three subspecies (*P. p. wurmbii*, *P. p. morio*, *P. p. pygmaeus*) of which a number of metapopulations prevail in large habitat fragments separated by physical barriers such as roads and rivers (Chapter 2; Wich et al., 2008).

Orangutans are predominantly found in dry lowland and hill forests, alluvial forests and freshwater- and peat swamp forests (Husson et al., 2009). These forests are prime habitat, offering sufficient food resources to support permanent, high-density populations. Yet, orangutans have a relatively wide geographical niche and can also be found in other forest types, albeit at much lower density (Husson et al., 2009).

Although orangutan species have been severely influenced by humans since the late Pleistocene (Spehar et al., 2018), their behavioral flexibility has allowed populations to adapt to a certain degree of alteration to their habitat. Recent studies have shown that orangutans appear to be able to inhabit previously logged forests, depending on the type and intensity of logging (Ancrenaz et al., 2010; Deere et al., 2017; Hardus et al., 2012; Morrogh-Bernard et

al., 2014). Although predominantly arboreal, recent studies have found that orangutans can move on the ground, for example to cross plantations (Ancrenaz et al., 2014). They can also build nests on exotic trees, such as oil palms and can feed on their fruits (Ancrenaz et al., 2015; Campbell-Smith et al., 2011). It seems that, in the absence of killing, orangutans can persist in forest fragments within human-modified landscapes such as timber and oil palm plantations (Ancrenaz et al., 2015; Meijaard et al., 2010a; Spehar and Rayadin, 2017). However, densities have been shown to decrease with distance to forest fragments, and the extent to which these adaptations can guarantee the long-term survival of orangutans in anthropogenic landscapes has yet to be determined (Ancrenaz et al., 2015; Spehar and Rayadin, 2017).

Drivers of orangutan decline

Precipitous declines of Bornean orangutan distribution and numbers are mainly driven by killing of orangutans and habitat degradation or loss. Habitat loss occurred as a consequence of intensive logging, conversion to industrial and smallholder agriculture, El Niño-induced large-scale fires, and infrastructure development (Austin et al., 2019; Betts et al., 2017; Gaveau et al., 2018, 2016; Sloan et al., 2017). Between 2000 and 2017 the area of old-growth forest on Borneo has declined by 14%, while the area converted to industrial oil palm and paper pulp plantations has increased by 170% (Gaveau et al., 2018). Forest loss and conversion have disproportionately affected lowland forests on mineral soils and peat land, both of which are prime habitat and harbor high orangutan densities.

The timing of key human cultural development in the orangutan range since the late Pleistocene, such as hunting innovations and important environmental modifications, coincided with range contraction and density decline of the species, implying a role of humans mainly through hunting (Spehar et al., 2018). Since the colonial period in the 19th century, encounter rates of orangutans on Borneo have dropped further (Meijaard et al., 2010b). In the 2000s, interview surveys with villages in the orangutan range in Kalimantan found that killing of orangutans for food or due to conflicts with humans remained high. Estimated rates amounted to an average of 2,000-3,000 Bornean orangutans killed per year (Ancrenaz et al., 2015; Davis et al., 2013; Marshall et al., 2009; Meijaard et al., 2011). Together with a constant number of cases publicized in the media (e.g., Baskoro, 2018; Gokkon, 2018a, 2018b), these findings demonstrate that orangutan killing continues to exert considerable pressure on current populations.

Conversion to industrial agriculture, infrastructure development and the expanding human population on Borneo also increase the spatial overlap of orangutan habitat and anthropogenic landscapes. Orangutans in human-dominated areas sometimes exploit crops for food, giving rise to conflict situations that result in death or injury of individuals (Davis et al., 2013; Humle, 2015; Meijaard et al., 2011). Live-trade of orphaned baby orangutans is an additional and significant threat to orangutan populations (Freund et al., 2017; Nijman, 2017). As a consequence of their slow reproductive cycle, orangutan populations are especially susceptible to increased mortality. Population models have suggested that offtake rates of more than 1% cannot be sustained by wild populations, while current rates have been estimated to be much higher (Marshall et al., 2009; Meijaard et al., 2011).

Future climate change could also have a considerable impact on Borneo's environment and wildlife (Scriven et al., 2015; Struebig et al., 2015b). Climate changes are threatening to exacerbate projected landcover change, affecting orangutan habitat as suitable conditions shift and habitat is fragmented or lost (Gregory et al., 2012; Struebig et al., 2015a; Wich et al., 2015). Effects will be especially severe in the Southeastern parts of the island (Struebig et al., 2015a; Wich et al., 2015), where climate variability is already leading to degradation during prolonged drought periods, and large-scale fires (Siegert et al., 2001; Sloan et al., 2017).

Orangutan conservation and impediments

Despite the growing evidence base for orangutan distribution change, the lack of information on range-wide abundance and disagreement about the relative importance of drivers and threats has stymied orangutan conservation in large parts of the range (Meijaard et al., 2012; Morgans et al., 2017; but see: Simon et al., 2019). Information about orangutan abundance across the range is essential to identify species' strongholds and to evaluate which conservation strategies are most likely to succeed in stabilizing overall numbers (Ancrenaz et al., 2005).

Traditionally, biodiversity and also orangutan conservation has focused predominantly on designating protected areas and managing species therein (Mace, 2014; Meijaard et al., 2012; Terborgh et al., 2002). Indeed, on Borneo, protected areas seem to retain forest cover better than non-protected areas (Santika et al., 2015; Chapter 3), although they have also experienced at least temporal reduction in cover owing to illegal logging activities and forest fires (Curran et al., 2004; Drake, 2015; Santika et al., 2019). Similarly, orangutan populations within protected areas have exhibited less declines than in other areas (Santika et al., 2017).

Nevertheless, especially in the Indonesian part of Borneo, a large majority of the orangutan range remain unprotected, with more than 75% in areas open for development (Santika et al., 2017; Wich et al., 2012). A number of researchers and conservation organizations have thus emphasized the importance of conservation approaches targeting orangutans beyond formally protected areas alongside the improvement of management, connectivity and the extent of the protected areas network (Meijaard et al., 2012; Spehar et al., 2018). Recognizing the long history of co-existence of orangutans and humans and the adaptability of the species to changing environmental conditions, this landscape approach to conservation strives towards maximizing biodiversity protection and human social and economic objectives within landscapes that are subject to anthropogenic pressures (Sayer et al., 2013). However, as species are not homogeneously distributed throughout their range, knowledge about density distribution is necessary to evaluate the efficacy of such approaches and to achieve more targeted and effective species conservation. In the absence of reliable figures on overall orangutan populations in anthropogenic landscapes, their protection has not been appropriately incorporated in official conservation strategies, such as the national conservation action plan for orangutans (Spehar et al., 2018).

Although killing has been established as an important threat to orangutan populations (Meijaard et al., 2011) it is similarly underappreciated in orangutan conservation, possibly as a result of disagreement of researchers and stakeholders about its overall importance on orangutan populations in the absence of range-wide and authoritative numbers (Meijaard et al., 2012; Morgans et al., 2017). As a consequence, enforcement of existing laws is still weak (Meijaard et al., 2012; Nijman, 2017; but see: Gokkon, 2018c, 2018d). Additional strategies to tackle orangutan killing, such as raising awareness, providing support, and working together with communities and resource managers to develop strategies to avoid conflict without harming the animals are not sufficiently adopted (Spehar et al., 2018).

Objectives of the thesis

This thesis aimed at investigating the current and potential future effects of anthropogenic drivers and threats on Bornean orangutan abundance and reviewing challenges and opportunities to improve the evidence base for orangutan conservation. Given the general interest of society in orangutans and their role as flagships for conservation, these findings could have impact on policies reaching beyond the species itself. This would benefit the exceptional biodiversity on Borneo and supports the relevance of research on this topic.

In **chapter 2** I explore the consequences of land-use change on Bornean orangutans, resulting from global to local resource demand¹. Based on a large compilation of orangutan survey data from across the entire range, I estimate the density distribution of the species. This study is among the first to describe the abundance of a wide-ranging species at this spatial scale and provides the new baseline for orangutan conservation and research. Coupled with spatially- and temporally-explicit information on land-use change, this work improves our understanding of the spatial patterns of orangutan loss and its drivers, and establishes killing as a main threat to orangutan populations. The results of this chapter have been published as Voigt, M., Wich, S.A., Ancrenaz, M., Meijaard, E., Abram, N., Banes, G.L., Campbell-Smith, G., d’Arcy, L.J., Delgado, R.A., Erman, A., Gaveau, D., Goossens, B., Heinicke, S., Houghton, M., Husson, S.J., Leiman, A., Llano Sanchez, K., Makinuddin, N., Marshall, A.J., Meididit, A., Miettinen, J., Mundry, R., Musnanda, Nardiyono, Nurcahyo, A., Odom, K., Panda, A., Prasetyo, D., Priadjati, A., Purnomo, Rafiastanto, A., Russon, A.E., Sihite, J., Spehar, S., Struebig, M.J., Sulbaran-Romero, E., Wilson, K.A., Köhl, H.S., 2018. Global demand for natural resources eliminated more than 100,000 Bornean orangutans. *Current Biology* 28, 761–769.²

In **chapter 3** I implement a novel deforestation model for Borneo to assess projected future patterns of tree cover loss. Coupling the estimates of orangutan density distribution that were generated in chapter 2 with these projections, allows the quantification of potential effects of deforestation on orangutan populations, anticipation of hotspots of future risk and identification of areas where the species is effectively protected. I assess how these areas are distributed among different types of land-use and management and discuss opportunities for conservation. The manuscript of this chapter is currently in preparation for submission to *Global Change Biology* as Voigt, M., Pereira, H. M., Köhl, H. S., Ancrenaz, M., Gaveau, D. L. A., Meijaard, M., Santika, T., Sherman, J., Struebig, M. J., Wich, S. A., Wolf, F., Rosa, I. M. D. Deforestation projections imply range-wide population decline for critically endangered Bornean orangutan.

In **chapter 4**, I raise attention to an official report by the Indonesian government, which presents an increase in orangutan numbers of more than 10% since 2015. Together with my coauthors, I highlight how a population increase of this magnitude is not biologically

¹ Although I did the majority of the work related to chapters 2, 3 and 5, all were produced in collaboration with a number of other researchers. I initiated the work on chapter 4, but it was a joint effort in which the majority of coauthors were equally involved. Thus in this context ‘I’ is used interchangeably with ‘we’. The relative contribution of authors to the work can be found in the [Authors' contribution](#) in the Appendix

² Chapter 2 and 4 are formatted according to the Journal requirements. Chapter 1, 3, 5-6 are formatted with a standard reference style.

possible in such a short time. It also contradicts all scientific evidence about the ongoing loss of orangutans and their habitat, including my findings in chapter 2 and 3. We indicate reasons for the observed discrepancy in findings and offer solutions for improving future orangutan monitoring. Chapter 4 was published as Meijaard, E., Sherman, J., Ancrenaz, M., Wich, S.A., Santika, T., Voigt, M., 2018. Orangutan populations are certainly not increasing in the wild. *Current Biology* 28, R1241–R1242.

In **chapter 5**, I review recent developments and key aspects of species monitoring, using the Bornean orangutan as a case study. I discuss methods of observation and sampling, and how they have been used for orangutan monitoring in the past. I highlight how novel approaches such as integrative species distribution modeling could be used in the future to take advantage of a range of different observation methods, thereby increasing resolution and area covered. Finally, I emphasize the importance of sharing data and discuss impediments to monitoring, which arise from the lack of integration among stakeholders involved in orangutan monitoring and conservation. This chapter is currently in preparation for submission to *Journal of Applied Ecology* as Voigt, M, Pereira, H. M., Ancrenaz, M., Bowler, D., Meijaard, E., Navarro, L. M., Sherman, J., Köhl, H. S., Wich, S. A. Challenges and opportunities for monitoring a charismatic species in the tropics - integrating data and stakeholders.

Chapter 6 is a synthesis of the findings of chapters 2-5 and a discussion of limitations. Here I put results into perspective of the overarching challenges in conservation, investigate how monitoring and conservation has to move forward to be successful, and why there is hope for the future.

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Chapter 2

Global demand for natural resources eliminated more than 100,000 Bornean orangutans

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Highlights

- 50 % of Bornean orangutans were affected by natural resource extraction
- We estimate that over 100,000 Bornean orangutans were lost between 1999 and 2015
- The most severe declines occurred in areas in which habitat was removed
- Most orangutans were lost from forests, implying the importance of hunting

In Brief

Voigt et al. show the negative impact of natural resource use on the density distribution of Bornean orangutans. The habitat of half of the population was affected. Over 16 years, more than 100,000 individuals were lost. Decline rates were highest when habitat was removed. Absolute losses were largest in selectively logged and primary forests.

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].

Video abstract: <https://bit.ly/2Hu5Sij>

Keywords

Pongo pygmaeus, density distribution modeling; decline; resource use; land-use change; industrial agriculture; oil palm; logging; hunting; conflict killing

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 km². 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 S1). Study year, rainfall variability and human population density negatively affected orangutan density (Figure S1, Table S1). 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 S1). 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).

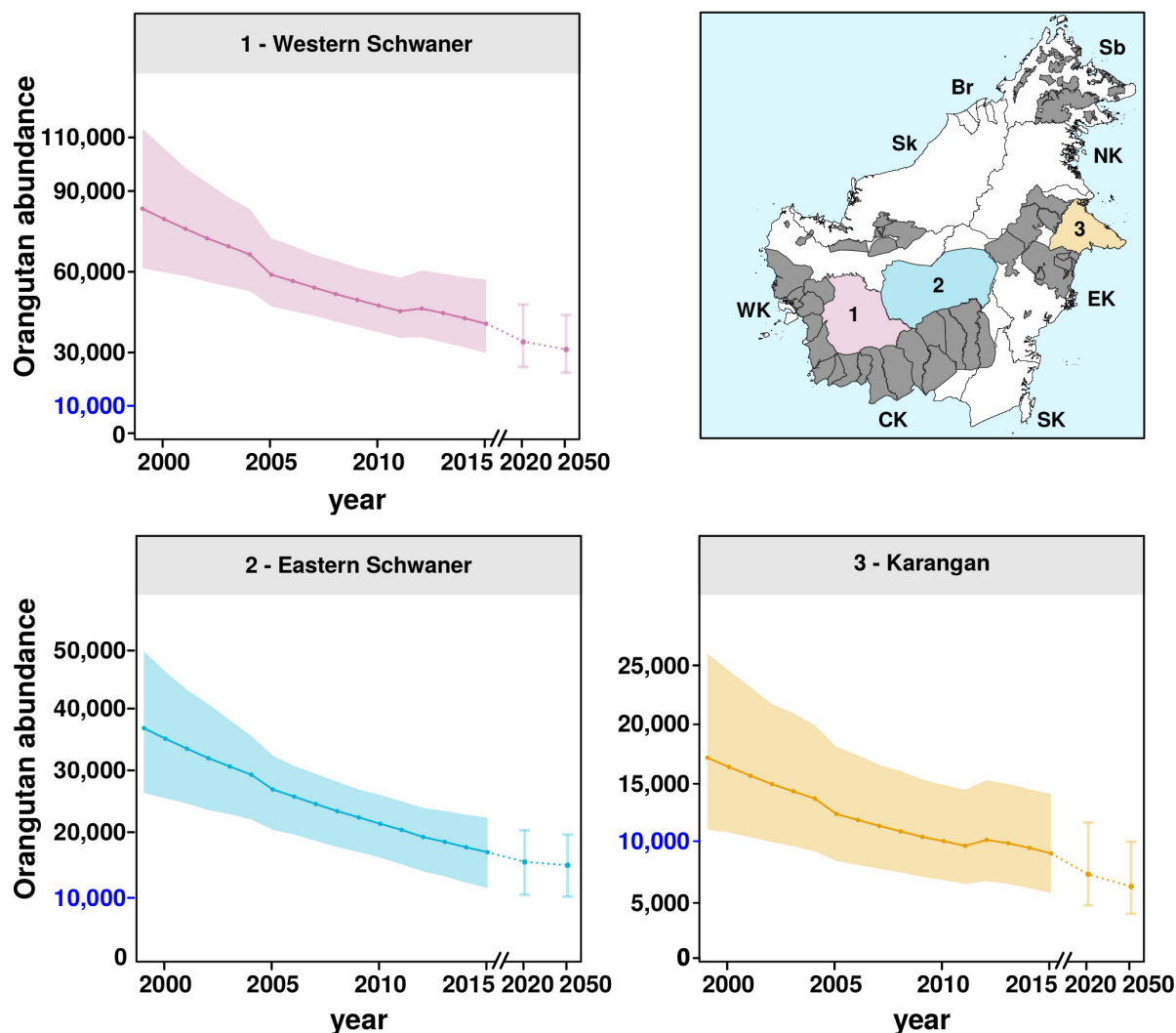


Figure 1: Abundance of the Three Largest Orangutan Metapopulations between 1999 and 2015 and Projected Abundance for 2020 and 2050.

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.

Western Swananer, 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 Swananer, 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).

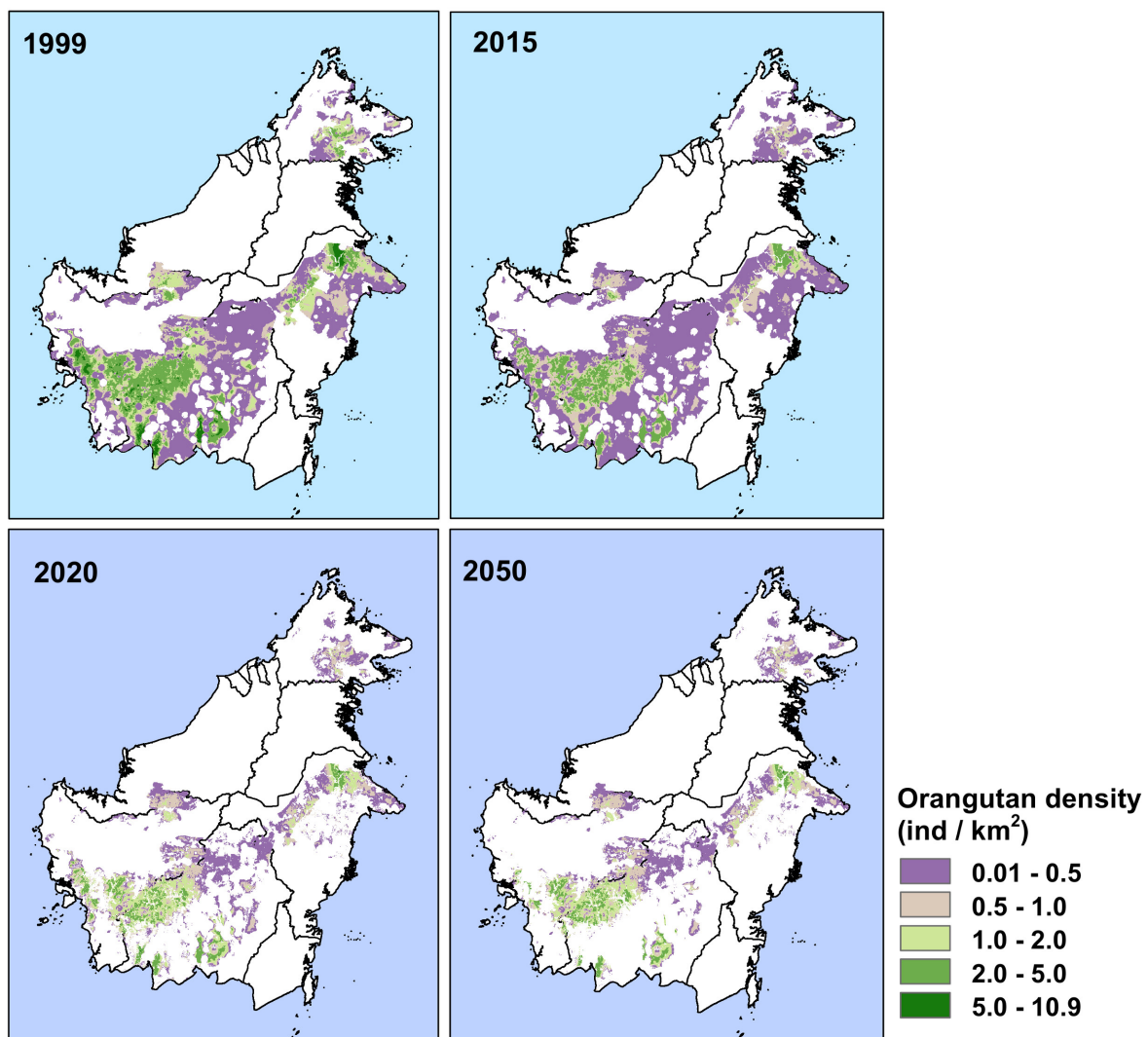


Figure 2: Spatial Distribution of Estimated Orangutan Densities on Borneo for the Year 1999 and 2015, and Projections to 2020 and 2050.

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 in the appendix.

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.

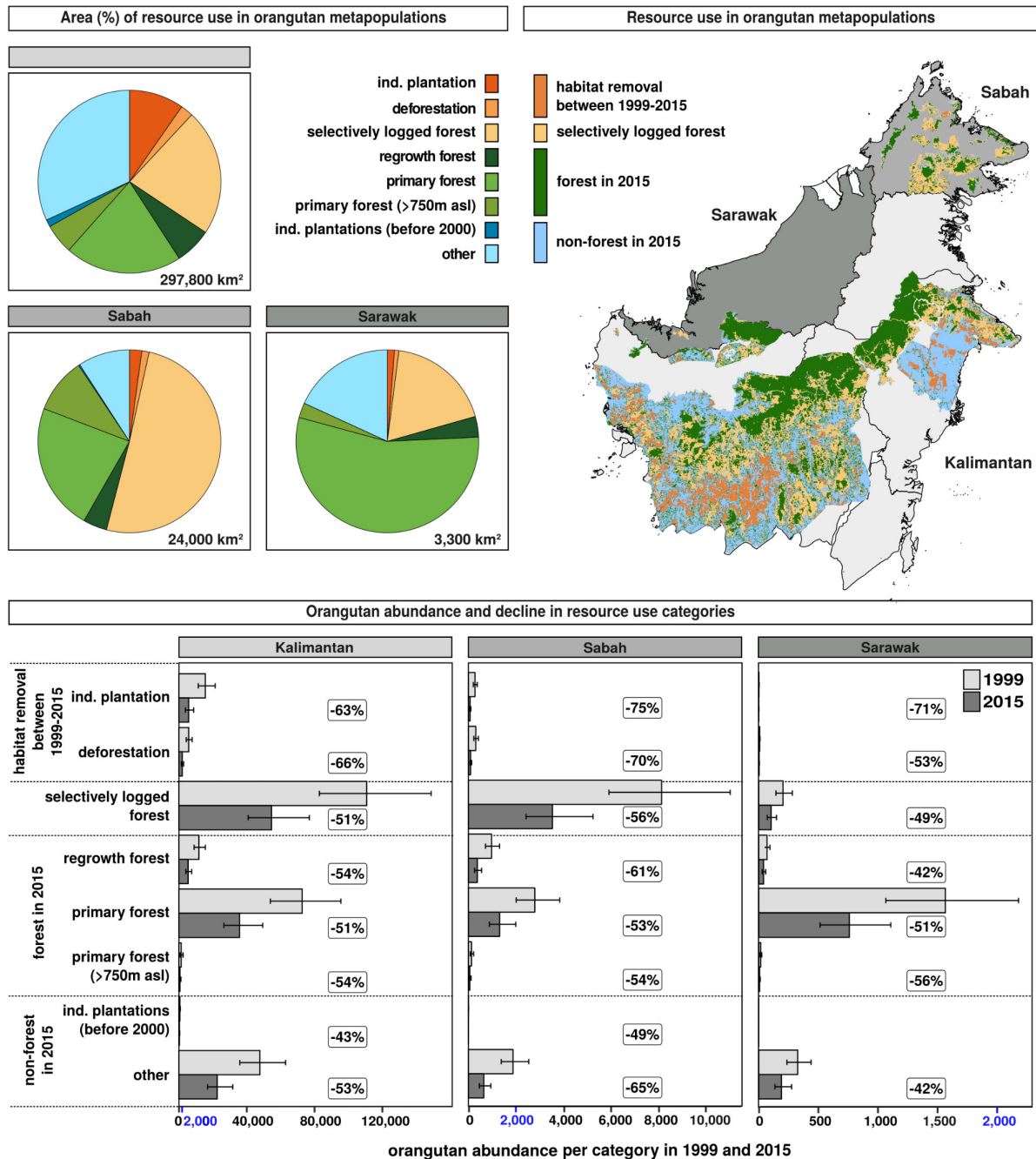


Figure 3: Linking Remotely Sensed Resource Use and Density Distribution.

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 metapopulation areas per province in km² are given in the lower right corner of the pie charts. Areas had 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 “*” indicates the absence of orangutans in the respective category. 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.

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 recog-

nizes 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 contribution

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

Declaration of interest

The authors declare no competing interests.

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STAR ★ METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Orangutan nest surveys	this paper	http://apesportal.eva.mpg.de/database/archiveTable;MYS_IDN_Multiple_sites_1999_01_01_Voigt_Wich et al.
Areas of orangutan absence	Serge Wich [50], this paper	http://apesportal.eva.mpg.de/database/archiveTable;MYS_IDN_Multiple_sites_1999_01_01_Voigt_Wich et al.
Nest decay surveys	this paper	http://apesportal.eva.mpg.de/database/archiveTable;MYS_IDN_Multiple_sites_1999_01_01_Voigt_Wich et al.
Mean daily temperature	[71]	http://www.worldclim.org/bioclim ; BIO1
Yearly variation in rainfall	[71]	http://www.worldclim.org/bioclim ; BIO15
Rainfall in dry months (May to September)	[71]	http://www.worldclim.org/bioclim ; BIO17
Topsoil organic carbon content	[72]	http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/
land-cover (peat swamp, lowland forest, lower montane forest)	Jukka Miettinen [53,54]	https://ornt-crisp.nus.edu.sg/
Deforestation (used in model)	[3]	http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.3.html
Deforestation (used in resource use overlap)	[32]	Forest_area_in_1973.7z
Human population density	[73]	N/A
Orangutan killing estimate in year prior to survey	Nicola Abrams [10]	N/A
Hunting taboo (percent Muslim population)	Truly Santika [11]	N/A
Logged forests	[70]	Forest_area_in_1973.7z
Oil palm and paper pulp plantations	[70]	REGBorneo_OriginOfLandConvertedToITPAndIOPPComplexTrajectory_1973to2016_CIFOR.7z
Forest cover prediction for 2020 and 2050	Matthew Struebig [17,41]	N/A
Experimental Models: Cell Lines		
Bornean Orangutan (<i>Pongo pygmaeus</i>)	N/A	N/A
Software and Algorithms		
R version 3.x	[66]	http://www.r-project.org ; RRID:SCR_001905
R Package Mass	[74]	https://stat.ethz.ch/R-manual/R-devel/library/MASS/html/glm.nb.html
R package car	[67]	https://cran.r-project.org/web/packages/car/index.html
Gdal, version 2.x	[75]	http://www.gdal.org/ ; RRID:SCR_014396
Qgis version 2.14	[76]	http://www.qgis.org/
Python version 2.7.12	[77]	https://www.python.org/ ; RRID:SCR_008394
Other		
Population and Habitat Viability Assessment metapopulation delineation	[16]	N/A

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 χ^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 \sim year + mean temperature + rainfall variability + rainfall in dry months + rainfall in dry months² + 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 S2) 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, as described above, to the null model, only including the intercept and the offset term [65]. 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 S1). The best model was the full-model lacking the orangutan killing estimates and percent population with religious hunting taboos (Table S1 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

We have compiled all original datasets under the ID “MYS_IDN_Multiple_sites_1999_01_01_Voigt_Wich et al.” in the IUCN/SSC APES database, from where they can be requested in adherence to the database policy. The datasets necessary to reproduce analysis and figures can be directly downloaded from a link associated to the database entry. The ID is given in the respective section in the text (as indicated above and in the Key Resource Table). All code used for the described analysis is available at <https://github.com/MariaVoigt/OU-density-distribution-pipeline.git>.

Chapter 3

Deforestation projections imply range-wide population decline for critically endangered Bornean orangutans

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Deforestation projections imply range-wide population decline for critically endangered Bornean orangutan

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Abstract

High rates of deforestation in Borneo are causing deteriorating ecosystems and biodiversity. For endangered species, it is important to understand where the largest numbers of individuals are at risk from future change. Combining tree-cover loss projections with range-wide density distribution models helps anticipate population declines associated with habitat loss, thus significantly improving past assessments based on area estimates alone. Here, we applied a recently developed spatially and temporally-explicit deforestation model to project changes in forest cover and assess the impact on Bornean orangutans for three five-year periods until 2031. Our projections point to continued deforestation in all states on the island, which could lead to the elimination of forest habitat for 10,400 orangutans. Orangutan populations that currently persist in industrial timber and oil palm plantation concessions or forests without officially designated land-use are expected to experience the worst of the losses within the next 15 years, amounting to 6,100 individuals. Unprotected lowland forests in West and Central Kalimantan with high orangutan densities were identified to be under acute threat from deforestation. In contrast, the majority of orangutans remaining in protected areas and logging concessions are found in forests with low levels of projected tree-cover loss. Our results highlight the importance of effective protection and efforts to prevent the degradation or conversion of selectively logged forests. In the context of rapid and extensive forest cover change, quantifying where species are threatened by future habitat loss is an important step in understanding how to halt the exceptional decline of biodiversity on Borneo.

Keywords:

Tree-cover loss, projection, *Pongo pygmaeus*, density distribution, land-use, hotspots

INTRODUCTION

Borneo is a global biodiversity hotspot (Mittermeier et al., 2005) with deforestation rates that are among the highest in the world (Gaveau et al., 2016b; Margono et al., 2014). On the island, high numbers of endemic species are increasingly under threat (Betts et al., 2017; Turubanova et al., 2018). In the past 17 years alone, the area of old-growth forest on Borneo has declined by 14% as a consequence of conversion to industrial plantations, intensive logging, El Niño-induced large-scale fires and infrastructure development (Gaveau et al., 2018, 2016b; Sloan et al., 2017). Deforestation has been highest in forests converted to industrial timber and oil palm plantations. In contrast, low levels of forest loss have been observed in large natural forests allocated to selective timber extraction (hereafter selective

logging concessions) (Gaveau et al., 2018, 2016b; Santika et al., 2015). Although exploited for timber, these areas tend to maintain comparable species numbers to unlogged forest (Deere et al., 2017; Wilcove et al., 2013), and have a significant role to play in island-wide conservation planning alongside protected areas (Struebig et al., 2015b). However, the impacts of forest disturbance and loss are not homogeneously distributed, and so the ultimate implications for species population can vary substantially on the local situation (Deere et al., 2017; Marshall et al., 2006). Parameterizing spatial models with useful local data remains a significant challenge in large-scale biodiversity impact assessments.

With recent improvements in availability of species observation data, computational power and advanced statistical methods, efforts have intensified to model the range-wide density distribution of species (mainly charismatic mammals: Maisels et al., 2013; Strindberg et al., 2018; Voigt et al., 2018; Wich et al., 2016). These new approaches allow to map abundance and offer an improved understanding of species' spatio-temporal patterns. For Borneo, a compilation of data collected for the endemic Bornean orangutan (*Pongo pygmaeus*) has led to estimates of population trends (Santika et al., 2017a) and density distribution (Voigt et al., 2018) across its known range. Orangutans have historically colonized almost the entire island, but are now confined to the remaining lowland and mid-elevation forests (Husson et al., 2009; Rijksen and Meijaard, 1999). Between 2004 and 2014, the species has declined drastically by at least 25% (Santika et al., 2017a; Voigt et al., 2018). While stable populations persist in large protected forests, peatswamp forests and the interior of Kalimantan and Sabah (Mang, 2017; Simon et al., 2019), many orangutan populations occur in forest fragments and have low or decreasing local densities (Voigt et al., 2018). There is growing evidence that orangutans can inhabit forest fragments within plantation landscapes (Ancorenaz et al., 2015; Meijaard et al., 2010; Spehar and Rayadin, 2017). Ultimately, however, the abundance and survival of this species is dependent on halting forest conversion and maintaining a network of forest remnants of sufficient size and connectivity (Ancorenaz et al., 2015; Spehar et al., 2018), while simultaneously addressing other threats such as unsustainable killing (Meijaard et al., 2011a).

Recent advances in spatially-explicit deforestation modeling offer an improved understanding of current and expected future tree-cover loss in the tropics (Gaveau et al., 2009; Gregory et al., 2012; Rosa et al., 2013; Struebig et al., 2015a). In particular, dynamic models allow to project forest cover loss as a sum of local events, influenced by various drivers and historical rates and patterns (Rosa et al., 2013). In these models large-scale deforestation patterns emerge contagiously with increasing rate if adjacent locations are also

affected. Coupled with the availability of tree-cover loss data at high spatio-temporal resolution (Gaveau et al., 2018, 2016a), this approach provides a powerful tool to anticipate future risks and to develop appropriate conservation strategies under rapid land-cover change (Cushman et al., 2017; Gregory et al., 2012; Soares-Filho et al., 2006; Struebig et al., 2015a).

We adapted a deforestation model to project tree-cover loss on Borneo until 2031, and better understand the drivers of this process. We then coupled these findings with results of a new density distribution model applied to the Bornean orangutans in order to estimate the population impacts of this critically endangered flagship species. By combining these models in this way, we were able to quantify where orangutans are the most threatened by or effectively protected from tree-cover loss; vital information for designing better conservation measures for Borneo's highly important levels of biodiversity.

MATERIAL AND METHODS

Identifying main deforestation drivers on Borneo

Deforestation in tropical forests occurs as a consequence of several drivers. These can be grouped into physical and accessibility characteristics (e.g. roads and topography), anthropogenic pressures (e.g. human population density), land-use and protection, such as within strictly protected national parks or extractive reserves (Gaveau et al., 2018, 2014; Geist and Lambin, 2002). As a baseline and predictor of future tree-cover loss in Borneo we used the forest cover data produced by Gaveau, Salim & Arjasakusuma (2016a), which includes deforestation between 2001 and 2016. Then, to reflect a wide range of potential drivers of change, we selected topography, distance to roads and rivers, human population density, occurrence of fire, protected area cover and cover of logging concessions and industrial timber and oil palm plantation concessions as predictor layers. The predictors were selected based on the literature about important drivers for Borneo (Cushman et al., 2017; Gaveau et al., 2013; Struebig et al., 2015a) and their availability across the island for the relevant time period (Appendix S1, Table S1,).

Deforestation model framework

We used a dynamic and spatially-explicit model developed by Rosa et al. (2013) that explicitly considers stochasticity of deforestation events. In the model island-wide forest cover loss rates emerge as the sum of local scale deforestation events, which are more likely to occur in patches surrounding a location of recent tree-cover loss (Appendix S1).

Simulations

After identifying the best statistical model to explain tree-cover loss on Borneo, we used it to project deforestation for the five-year calibration period (2012 – 2016) and for the following three five-year periods (2017-2021, 2022-2026, 2027-2031). Previous studies using the same deforestation model showed that while the selected calibration period had a large influence on the outcome of the model, calibrating with data from the recent past leads to better projections (Rosa et al., 2015). Considering the trade-off between short calibration intervals, potentially reflecting exceptional years, or long intervals, potentially including outdated trends, we calibrated the model with a five-year interval.

Validation and analysis

We validated the model against observed data for the calibration time-period (2012-2016), by calculating the area under the Receiver Operating Characteristic (ROC) curve (AUC value) for the 100 iterations, following Rosa et al. (2013). We also calculated the proportion of match between observed and cumulative tree-cover loss within a certain distance (0, 1, 5 and 10 km) surrounding the pixel, using the function ‘focal’ from the package ‘raster’ in R (Hijmans, 2017).

Priority areas for orangutan conservation based on deforestation projections

We calculated the projected loss of orangutans by excluding deforested pixels until 2017 from the density distribution layer of 2015, to generate a baseline distribution for 2017. We then estimated the number of orangutans affected by tree-cover loss within each deforestation projection ($n = 100$).

We overlaid the projected probability of tree-cover loss from 2012-2031 with a density distribution map of Bornean orangutans (*Pongo pygmaeus*) for the year 2015 (Voigt et al., 2018), to identify areas where populations are likely to be maintained or lost in the future. We grouped tree-cover loss probability into low (0–33%), medium (≥ 33 –67%) and high (≥ 67 –100%) probability and orangutan abundance into low (0.01–0.5 individuals / km²), medium (>0.5–2 individuals / km²) and high (> 2 individuals / km²) local abundance, based on the distribution of pixels within classes. We assigned one of the nine possible combinations of projected tree-cover loss probability and local orangutan abundance to each pixel forested in 2011, the baseline for the model. We then calculated the area and loss of orangutans within administration units, protected areas, logging and industrial plantation concessions, or areas without either concessions or protected areas. As the model was calibrated using layers of land-use and management as a predictor, the resulting projections helped reveal how

differences among them have influenced tree-cover loss in the past, and how this could affect orangutan density in the future if no changes to use and management are enforced.

RESULTS

Deforestation model for Borneo

After testing several combinations, the model that included all variables had the highest test likelihood and was thus used for the simulations of future tree-cover loss until 2031 (Table S2). Past tree-cover loss had the largest effect size, with high past levels being related to high probability of future deforestation (Fig S2). Protected areas and logging concessions were associated with lower probability of tree-cover loss in the future, while industrial timber and oil palm plantation concessions were correlated to higher probabilities (Fig S2).

Validation

The model selection process in which all possible models were screened, yielded a model with good discriminatory power and a mean AUC value of 0.84 (standard deviation, SD = 0.0002). When comparing the spatial match in the calibration period, few pixels that were projected to be lost were in the exact location of pixels with observed loss (0.2%, sd = 0.002, Figure S3). However, 59.5% (sd = 0.451%) of the pixels were in the direct neighborhood (within 1 km), 97.6% within 5 km (sd=0.206%), and 99.5% within 10 km (sd = 0.106%) of a pixel with observed loss.

Spatial deforestation projections

The probability of tree-cover loss resulted in projections that reflected the contagious spread of deforestation. (Fig 1. A, D-G). Given current management regimes and drivers across Borneo, protected and high-elevation areas had a high probability to maintain forest cover until 2031 (Fig 1 B and S4 A). Fragmented lowland forests, forest within industrial timber and oil palm plantations concessions, and forest without protection or concession status, were projected to have increased probabilities of tree-cover loss.

Forest cover varied across administration boundaries (Fig. 2 and Table S3). Central Kalimantan had the largest area covered by forest (76,875 km²) in 2017, representing 50% of the total province area, followed by Sarawak (66,170 km², on 53% of its area), West Kalimantan (59,942 km², 41%), East Kalimantan (59,752 km², 47%), North Kalimantan (59,107 km², 85%) and Sabah (39,427 km², 54%). South Kalimantan had the smallest area covered by forest (7,719 km², 21% of its area).

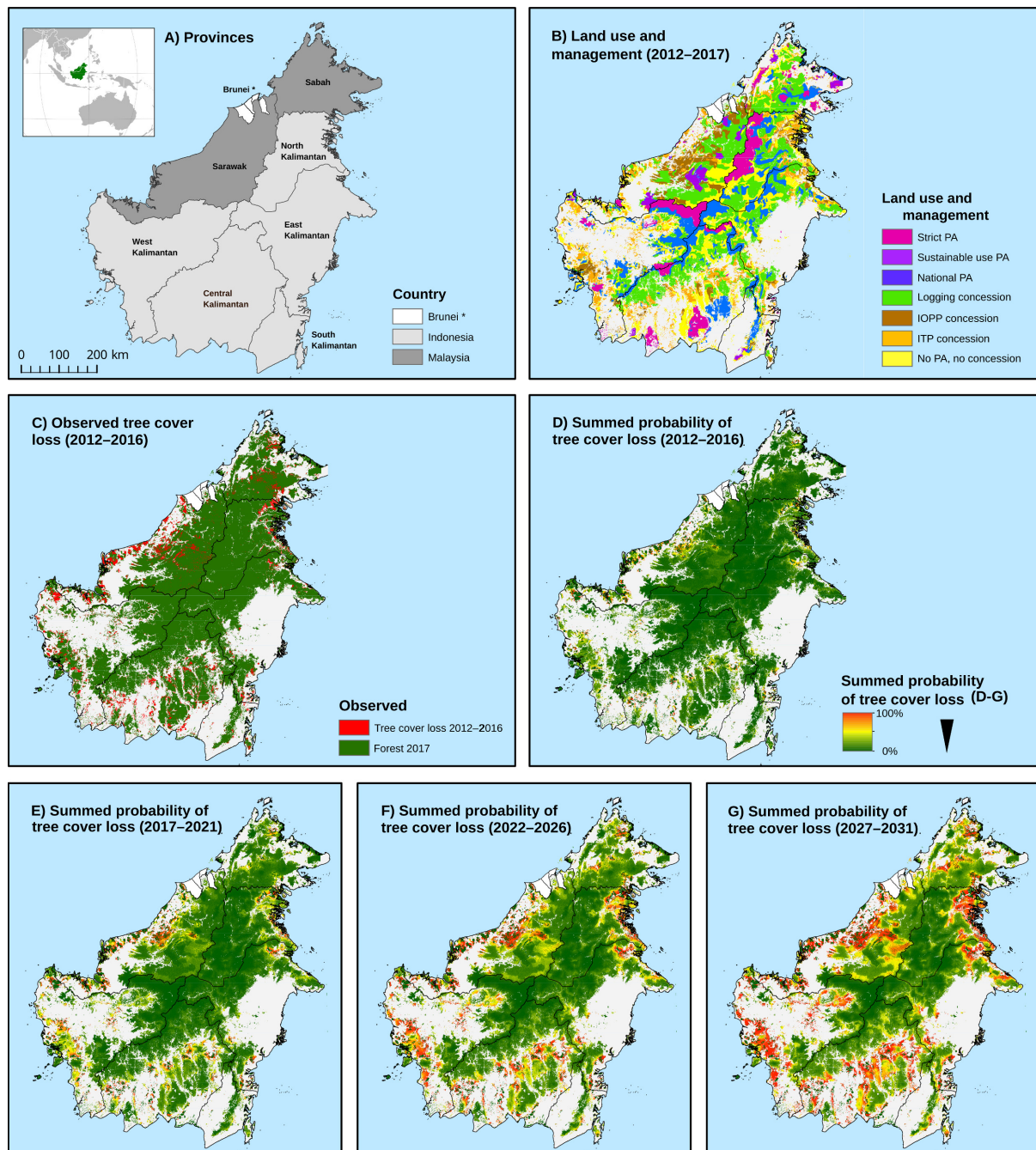


Figure 1: Most important model predictors, administrative boundaries and projected probability of tree-cover loss across Borneo.

Probability of tree-cover loss was projected using variables describing accessibility, human pressure and land-use and management. A) Administrative boundaries of Indonesia, Malaysia and Brunei. Brunei is excluded from the projection in maps B-G as important predictors did not contain sufficient information for this country. The position of Borneo can be seen in inlay. B) Forest land-use and management (PAs - Protected areas, ITP – industrial timber plantation, IOPP – Industrial oil palm plantation). C) Past deforestation, D) – G) Probability of tree-cover loss over time for four five-year intervals from 2012 – 2031. Spatial match between observed tree-cover loss (C) and projected probability of tree-cover loss (D) for calibration period (2012-2016).

In all provinces tree-cover decreased between the start of the observation period in 2000 and 2017, and is projected to decrease further until 2031, ranging from 36% (Sarawak) to 19% (North Kalimantan), relative to the tree-cover in 2017, the end of the observation period (Fig. 2 A and Table S3).

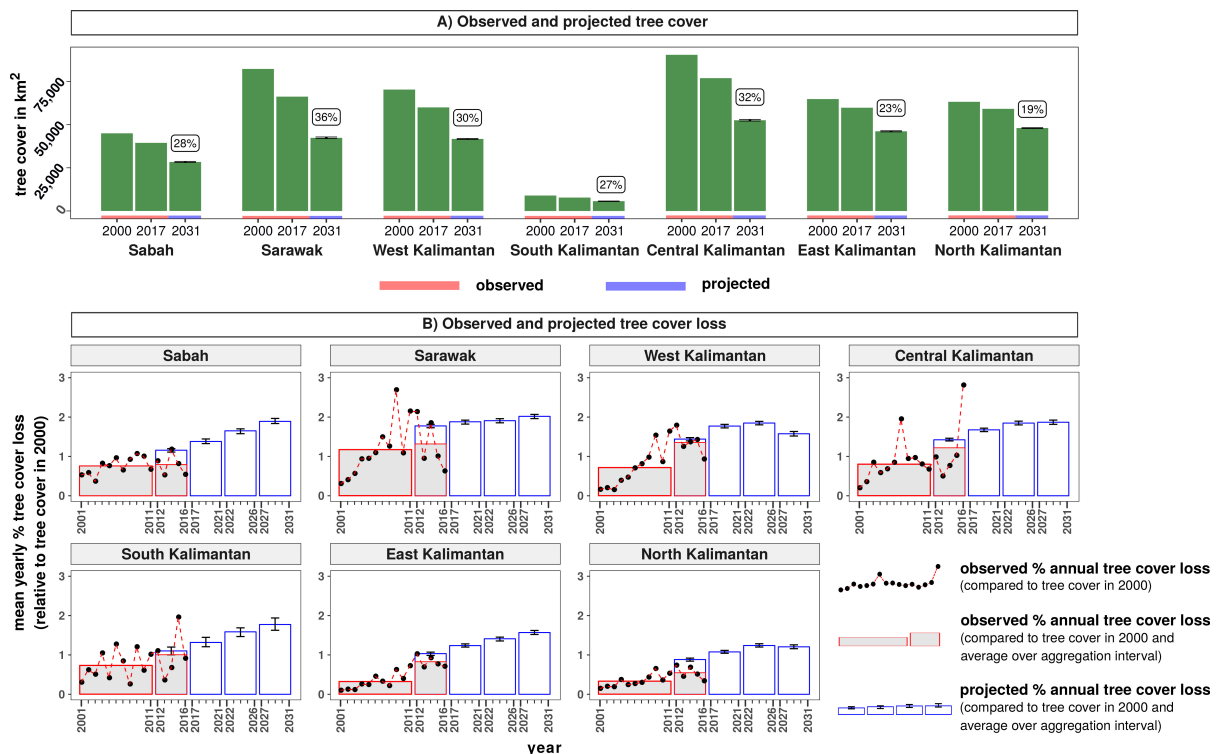


Figure 2: Observed and projected tree-cover area and loss over Borneo from 2000 to 2031.

A) The total observed (red axis) tree-cover (green bars) in the first (2000) and last (2017) year and the median tree-cover in the last five-year period of projection (2027 – 2031) for each administrative unit (red axis), with 95 % confidence interval (error bars). Percent future tree-cover loss from 2017 to 2031 is given above (confidence interval in Table S3). Aggregated average percent tree-cover loss before simulation (2001 – 2011) and in the calibration period (2012 – 2016) (red bars with grey filling). The annual observed tree-cover loss (red line with black dots) was not used for model fitting, but shows interannual variability of tree-cover loss in the states. Deforestation was simulated for four five-year periods from 2012 – 2031 (blue bars, $n = 100$, error bars represent 95% confidence interval). All values in B) given in annual percent loss of the forest cover in 2000, by aggregating over the time-period over which the bar extends and dividing by number of years in interval.

Probability of deforestation projections on Borneo over time

The observed annual tree-cover loss for all provinces and years, relative to the tree-cover at the beginning of the observation period (2000), ranged between 0 – 3%, with high inter-annual fluctuations (Fig. 2B). On average, the rate increased from the first eleven years (‘previous deforestation’) to the calibration period in all provinces, with the exception of Sabah where the deforestation rates were relatively low and consistent (14 km² or 0.03 percent point difference between average annual deforestation). The projected median tree-cover loss ranged between 0.9 – 2%. In the calibration interval the projected loss was larger than the observed rate, with a deviation between 0.1 percent point (West Kalimantan) to 0.5

percent point (Sarawak). However, in all states the projected rate of deforestation was smaller than or within the confidence interval of observed, non-aggregated yearly rates of deforestation.

Over the projection period in the different provinces, the median tree-cover loss increased and then stabilised (Central Kalimantan), decreased in the last time-step (West Kalimantan, and North Kalimantan), or continued to increase (the Malaysian states Sabah and Sarawak, and South and East Kalimantan in Indonesia).

Projected threat to orangutan populations within states

Across Borneo, high probability of future tree-cover loss (2017-2031) coincided with fragmented forests and forests in low elevation areas (Fig. 3 and S4).

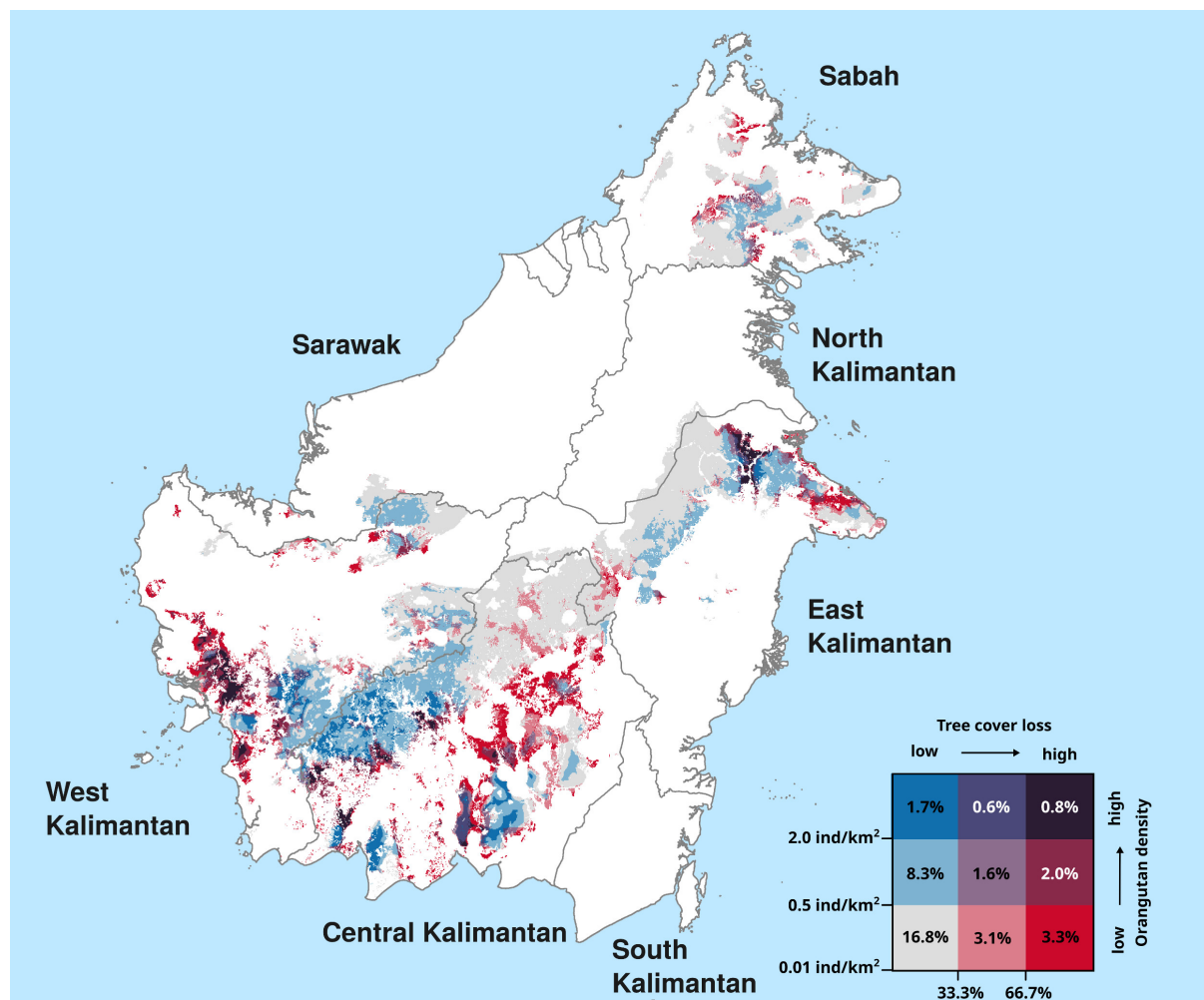


Figure 3: The density distribution of orangutans overlaid with the summed probability of tree-cover loss over Borneo.

Blue shades indicate orangutan density and red shades indicate probability of tree-cover loss, with darker colors conferring higher levels. Purple hues indicate pixels in which both variables are elevated. Percent area within each class is shown in the inset. Only pixels that were forested in 2011 (baseline in the deforestation model) and that have an estimated density of more than 0.01 orangutans/km² are presented.

High local orangutan abundances ($> 2 \text{ ind/km}^2$) in unprotected fragmented lowland and peat swamp forests in West, Central and East Kalimantan, were projected to experience high levels of deforestation (i.e. summed probability of projected deforestation $\geq 67\%$). In contrast, the forests in the central part of West and Central Kalimantan at higher elevations, or in large national parks, harbored medium to high orangutan densities ($> 0.5 \text{ ind/km}^2$) with low probability of tree-cover loss ($< 33\%$ summed probability of projected tree-cover loss).

Although fewer orangutans occurred in Sabah and especially in Sarawak, the majority (74% and 98%, respectively) of them were projected to experience the lowest levels of forest loss (Fig S5). Only 6% (Sabah) and less than 1% (Sarawak) of orangutans occur in areas with high probability of tree-cover loss. In West, Central and East Kalimantan this percentage was larger, with 30%, 16% and 24%, respectively. Orangutans were only present in very low numbers or entirely absent from North and South Kalimantan.

Projected threat to orangutan populations within land-use and management categories

Low probabilities of tree-cover loss were typical of forests within protected areas (PAs) and logging concessions that were occupied by orangutans (Fig 4). Forests in industrial timber (ITP) and oil palm plantations (IOPP) and areas without designated use or management were dominated by high deforestation probabilities.

Overall, forests in protected areas and logging concessions harbored 67% of all orangutans estimated to occur on Borneo in 2017. The majority of these were in areas with low probability of future tree-cover loss (93% of all orangutans within PAs and 90% in logging concessions). In contrast, a large percentage of the orangutans inhabiting forests within areas gazetted for industrial timber and oil palm concessions (66% in industrial timber and 91% in industrial oil palm plantation concessions, together 12% of all orangutans on Borneo), depended on habitat that had a high probability ($\geq 67\%$) of future loss. Areas outside of PAs or concessions included 8% of orangutans, the majority of which was projected to be threatened by habitat loss (43% medium and 40% high probability). Those also included high density areas, notably a large area around the Sabangau peatlands in Central Kalimantan and in the Wehea-Lesan landscape in East Kalimantan.

If current deforestation drivers within protected areas cannot be ameliorated, forest loss is projected to directly affect 1,600 (95% confidence interval (CI): 1,500 – 1,700) orangutans until 2031. In logging concessions loss was projected for the habitat of 2,800 (95% CI: 2,700-2,900) orangutans. Continued deforestation within industrial timber and oil palm plantations could result in the loss of 2,400 orangutans (95% CI: 2,300 – 2,600). The largest

number of orangutans (3,700, 95% CI: 3,500-3,900) threatened by the loss of their habitat until the 2027 – 2031 period occurred in areas without designated land-use or management.

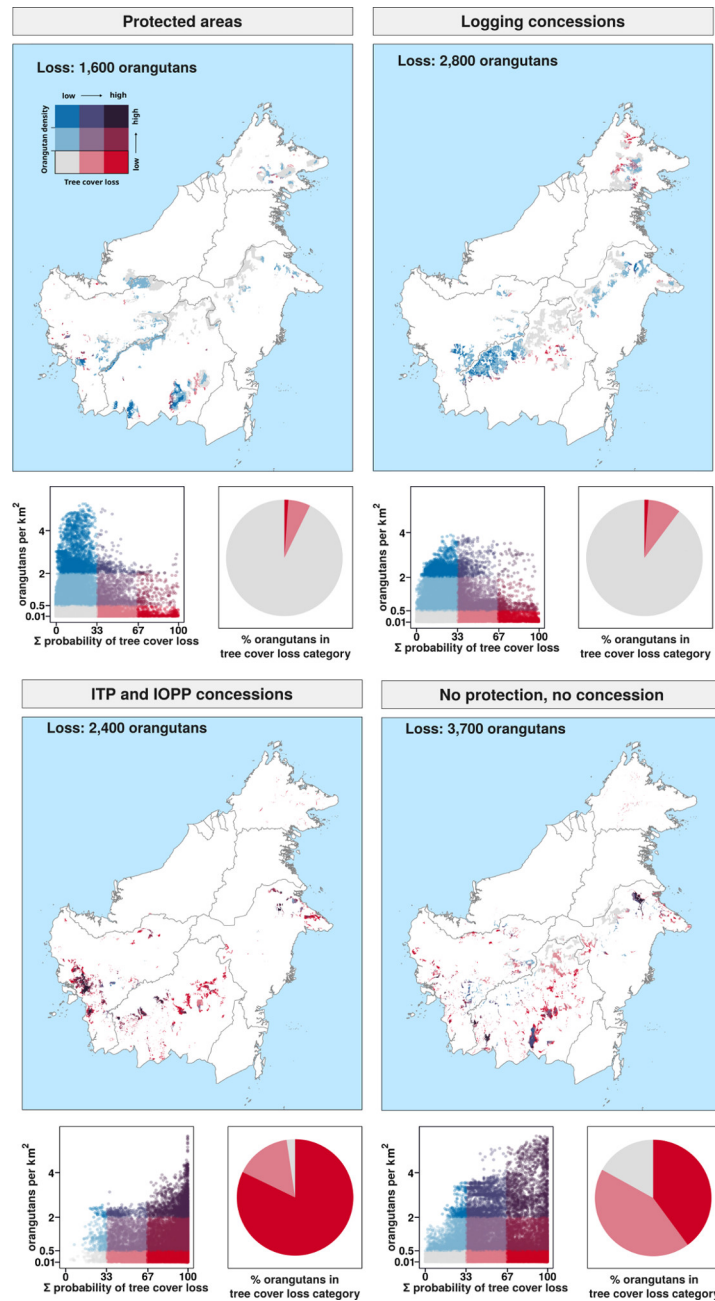


Figure 4: Density distribution of orangutans and summed probability of projected tree-cover loss in land-use and management areas.

Blue shades indicate the density of orangutans and red shades the probability of tree-cover loss. Darker colors identify higher levels. Purple hues represent a mix of elevated levels (maps and scatterplot). Total projected loss of orangutans until 2027 – 2031 per land-use and management category (protected areas (PAs), concessions and areas not designated for either) in each panel rounded to the nearest 100. Industrial timber plantations (ITP) and industrial oil palm plantations (IOPP) concessions were combined to one industrial plantation concession category. Confidence levels are: PA: 1,500 – 1,700 orangutans; Logging concession: 2,700 -2,900 orangutans; industrial plantations: 2,300 – 2,600 orangutans; no PA, no concession: 3,500 – 3,900 orangutans. Strict, sustainable use, and national PAs were aggregated to one category. The distribution of pixels with respect to the orangutan density per square-kilometer and the summed probability of tree-cover loss is shown in the scatterplot. The proportion of orangutans in areas with low, medium or high levels of tree-cover loss (pie charts, red shades only). Only pixels that were forested in 2011 and that have an estimated density of more than 0.01 orangutans/km² were considered.

All orangutan numbers were rounded to the nearest 100. The confidence intervals integrate the variability of tree-cover loss probability.

DISCUSSION

By adopting an innovative deforestation model and combining it with a range-wide density distribution of Bornean orangutans, we expanded previous efforts to project future deforestation on Borneo and understand its effect on this endemic great ape species (Cushman et al., 2017; Gregory et al., 2012; Struebig et al., 2015a; Voigt et al., 2018).

Drivers of deforestation on Borneo

The most important predictor of tree-cover loss was the proportion of pixels within the neighborhood that had already been lost. This has also been found to influence tree-cover loss in other areas in the tropics and over large time-scales (Boakes et al., 2010; Robalino and Pfaff, 2012; Rosa et al., 2013). Levels of deforestation within protected areas and logging concessions on Borneo have been found to be much lower than in forests allocated to industrial plantation concessions (Gaveau et al., 2012, 2019; Santika et al., 2015; but see: Brun et al., 2015). Accordingly, land-use or management category in our model had a large influence on deforestation projections. While stricter protection was linked to lower tree-cover loss, the presence of industrial plantation concessions was related to higher decreases.

Observed and projected deforestation

Over the observation period, total forest area decreased for all administrative units on Borneo, and continued to decrease in the future. Across the island, unprotected lowland forests were projected to disappear, which supports previous estimates for future deforestation (Cushman et al., 2017; Struebig et al., 2015a). The observed average tree-cover loss rate during the calibration interval was driven by years with high deforestation rates. This trend persisted in the projection, resulting in an overestimate of probability of tree-cover loss in the calibration period, which was highest for Sabah, Sarawak and North Kalimantan. The two Malaysian states have a longer history of mechanized logging and conversion to industrial plantation in comparison to Indonesian Borneo (Reynolds et al., 2011). With a focus on intensification instead of expansion, tree-cover loss rates have decreased in the recent past (Varkkey et al., 2018). In Sabah, this could also result from commitments to retain 50% of the state's area under forest cover and the subsequent protection of a large part of remaining forests (Gregory et al., 2012; Varkkey et al., 2018).

A caveat with deforestation models based on historical drivers is that they assume future will mirror the past. This does not need to be the case, and therefore model-based projections

become increasingly uncertain in the future as a consequence of the deep uncertainty associated with socio-ecological processes (Schindler and Hilborn, 2015). Changes in political systems, commodity prices and global climate are very hard to anticipate, but are already driving deforestation patterns on Borneo and might become increasingly important in the future (Gaveau et al., 2018; McAlpine et al., 2018; Sloan et al., 2017). Moreover, a number of infrastructure projects that are currently planned or under development will most likely affect connectivity and integrity in large areas of still intact forests on Borneo (Alamgir et al., 2019). More positively, policies in Sabah on forest protection (Sabah Forestry Department, 2017; Varkkey et al., 2018), and in Kalimantan on fire prevention (Tacconi, 2016), as well as the new forest and peat moratorium in Indonesia (Norwegian Government 2016), could mean that forest loss rates in the future will not be as high as those in the past. Indeed, a recent study indicated that annual forest loss on Borneo in 2017 has been at its lowest in 16 years (Gaveau et al., 2018).

To limit the uncertainty, we restricted the projections to 15 years into the future. Given the sharp decline of orangutans estimated for the 16 years between 1999 and 2015 (Voigt et al., 2018) and rapid changes in land-cover on Borneo (Gaveau et al., 2018, 2014), assessing the loss of tree-cover in the near future is important to evaluate management strategies for the continued survival of the majority of populations. In the future the deforestation model could be coupled with scenarios for management changes, and projections of changing climate or infrastructure development, to better anticipate forest loss over longer time-scales (e.g., Alamgir et al., 2019; Gregory et al., 2012; Runting et al., 2019; Struebig et al., 2015a).

Projected deforestation and orangutans in PAs and logging concessions

We overlaid the orangutan density distribution with the projection of future deforestation to identify orangutan habitat at risk and to assess the proportion of orangutans affected. We found that overall, protected areas and logging concessions were effective in protecting orangutan habitat. These areas also harbored most orangutans (64% of the total number in 2017). Only few small patches within protected areas had elevated levels of threat from tree-cover loss, most notable around Sabangau National park and adjacent areas. Here forest fires caused considerable loss of tree-cover in orangutan habitat in 2015 (Drake, 2015; Mang, 2017; Santika et al., 2019). In logging concessions medium to high probability of tree-cover loss within orangutan habitat were restricted to areas in Central Kalimantan and a number of forest fragments in Sabah. In the latter, most of the forests within logging concessions were harvested, before being designated as protected forests (Reynolds et al., 2011). This last round of logging degraded further the already logged forests and decreased overall cover. But

forests are now regenerating, and future deforestation in these newly protected areas in Sabah is unlikely (Sabah Forestry Department, 2017).

Our findings of low projected habitat loss in protected areas, highlight the relevance of an effective protected area network. Lower deforestation probability in logging concessions also reinforce the need to control degradation within selectively logged forests (Fisher et al., 2011; Gaveau et al., 2014; Struebig et al., 2015b). Policy mechanisms such as REDD+ and certification schemes such as the Forest Stewardship Council (FSC) offer incentives to adopt low impact logging techniques and improved forest management, potentially benefiting forest biodiversity (Bicknell et al., 2015; Deere et al., 2017; Edwards et al., 2014, 2010).

Projected deforestation and orangutans in plantations and other non-protected areas

There have been a number of studies showing that orangutans can also inhabit forest fragments within human-modified landscapes and industrial plantation concessions (Ancorenaz et al., 2015; Meijaard et al., 2016, 2010; Spehar and Rayadin, 2017). We found that within forests in industrial timber and oil palm plantation concessions, the majority of pixels had an elevated probability of tree-cover loss, harboring 82% of the orangutans occurring in forests within these concessions. In particular, the loss of peat swamp forests gazetted for plantations in West and Central Kalimantan, could lead to the destruction of habitat with high orangutan numbers. Based on our projections, and given current drivers of tree-cover loss, 2,400 orangutans could be lost from these and other forests in industrial plantation concessions over the next 15 years. Commitments to prevent these losses are essential to curb the decline of Bornean orangutans. Although their effectiveness is not yet entirely clear, the adherence to sustainable management practices, such as under the Roundtable for Sustainable Palm Oil (RSPO), zero-deforestation commitments, or moratoria to stop conversion of primary and peat swamp forests within plantations, are a step in the right direction (Busch et al., 2015; Carlson et al., 2012; Gaveau et al., 2018; Meijaard et al., 2017).

Our analysis highlights the importance of areas that are not protected or allocated to concessions. Here, the largest number of orangutans (3,700, i.e., 35% of total projected loss) is estimated to disappear in the future on only 20% of the total forest area. By addressing the drivers of deforestation in these areas, considerable losses to orangutan populations, and biodiversity more generally, could be prevented. However, especially in these forests, the situation on the ground can also vary considerably and thus the trajectories of future forest-cover loss. Smallholder plantations, for example, might have played an increasing role in the

expansion of oil palm plantations in recent years (Gaveau et al., 2018; Meijaard et al., 2018). In contrast, where forests are managed by local communities deforestation tends to decrease, at least under some circumstances (Langston et al., 2017; Santika et al., 2017b). It is therefore important to recognize that across Borneo, the tree-cover loss projections could not account for such local variability in drivers and that the resulting layer depicts large-scale patterns, as does the orangutan density distribution (Voigt et al., 2018).

Considering regrowth of forests

Our deforestation model did not account for forest regrowth, and areas without forest in the beginning of 2011 were excluded. We know that degraded or cleared tropical forests can regrow naturally under favorable soil and climatic conditions and that forest is also being actively replanted in some areas (Jong, 2019; Slik et al., 2002). As a consequence, we are currently unable to reliably project deforestation estimates into areas of past regrowth, although we know that orangutans can occur in such areas (Russon et al., 2015), nor can we consider the potential of future regrowth to lower the overall pressure on orangutan populations. Thus, efforts to account for forest regeneration, local-scale drivers, and additionally to close gaps and overlaps in land-use and management layers (Gaveau et al., 2017; Santika et al., 2015) could help to improve the resolution of our analysis in the future.

Potential to expand the modeling approach to other species

Orangutans attract a lot of public interest, and the species has been a focus of research, conservation and welfare efforts (Marshall et al., 2016). The resulting availability of sufficient abundance surveys in space and time allowed us to model density distribution in the past and quantify their loss from projected declines in habitat in this study. However, their long life-history and behavioral flexibility allows them to be more resilient to anthropogenic changes than many other species (Spehar et al., 2018). In the future, the advent of methods to derive abundance estimates over large spatial scales, for example from camera trapping data (Howe et al., 2017), could permit complementary density distribution analyses for other species with more narrow ecological niches than orangutan. This would permit the assessment of more general effects of future tree-cover loss on the fauna of Borneo.

Killing as an additional driver of orangutan loss

Past studies have shown that, besides deforestation, orangutans on Borneo are experiencing major declines also within forested areas as a consequence of hunting, killing in conflict situations and live capture (Abram et al., 2015; Davis et al., 2013; Meijaard et al., 2011b; Spehar et al., 2018, Voigt et al., 2018). This threat is governed by complex socio-economic drivers that remain poorly understood and hinder a rigorous spatial assessment across the

whole island (Davis et al., 2013; Meijaard et al., 2011a). However, conflict killing and the capture of young orangutans as pets have been shown to increase close to recently converted forests (Freund et al., 2017; Meijaard et al., 2011a; Santika et al., 2017a) and effects could thus be spatially related.

Implications for biodiversity conservation

Although deforestation projections did not allow a full description of the future threats faced by Bornean orangutans, the combination of projections with a range-wide density distribution model is a strong tool to quantify the loss of orangutans if historical drivers remain unabated. Our approach allowed us to identify areas of high future risk as well as conservation opportunities and could be applied in future to understand patterns of threats to other species and biodiversity in general. By providing a direction to reduce future Bornean orangutan declines as a result of habitat loss, our findings present a window of opportunity to act, but also highlight the consequences if we fail to do so. In the context of extensive and rapid changes of land-use, land-cover and climate in the current century, increasing efforts to further develop such approaches and to translate them into effective conservation actions is urgently needed to stop the dramatic loss of species in biodiversity hotspots such as Borneo.

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Author Contributions

Conceptualization, M.V., H.M.P., H.S.K., M.A., E.M., J.S., M.J.S., S.A.W., and I.MD.R.; Methodology, M.V., H.M.P., F.W., and I.MD.R.; Software, M.V., F.W., and I.MD.R.; Validation, M.V., I.MD.R.; Formal analysis, M.V.; Resources, D.G., T.S.; Data curation, M.V.; Writing – Original draft, M.V.; Writing - Review & Editing, M.V., H.M.P., H.S.K., M.A., E.M., T.S., J.S., M.J.S., S.A.W., F.W. and I.MD.R.; Supervision, H.M.P, H.S.K., and I.MD.R..

Declaration of Interests

The authors declare no competing interests.

Availability of code

All code used for the described analysis is available at:

https://git.idiv.de/mv39zilo/deforestation_projections_voigt_et.al.git

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Chapter 4

Orangutan populations are certainly not
increasing in the wild

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Orangutan populations are certainly not increasing in the wild

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A recent report, published by the Government of Indonesia with support from the Food and Agricultural Organization and Norway's International Climate and Forest Initiative, states that orangutan populations (*Pongo spp.*) have increased by more than 10% from 2015 to 2017, exceeding the government target for 2019 of an annual 2% population increase [1]. This assessment is in strong contrast with recent publications that showed that the Bornean orangutan (*P. pygmaeus*) lost more than 100,000 individuals in the past 16 years [2] and declined by at least 25% over the last 10 years [3]. Furthermore, recent work has also demonstrated that both Sumatran orangutans (*P. abelii*) and the recently described Tapanuli orangutan (*P. tapanuliensis*) lost more than 60% of their key habitats between 1985 and 2007, and ongoing land-use changes are expected to result in an 11–27% decline in their populations by 2020 [4, 5]. Most scientific data indicate that the survival of these species continues to be seriously threatened by deforestation and killing [4, 6, 7] and thus all three

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are Critically Endangered under the International Union for Conservation of Nature's Red List.

We applaud the Indonesian conservation authorities for providing publicly available documentation on forest management impacts, and for their use of quantitative measures of wildlife conservation progress [1]. Based on the above-mentioned discrepancy, however, we question whether appropriate methods and efforts were employed to assess management impacts on wildlife trends. For orangutan impact monitoring, the Indonesian government reported on nine monitoring sites including national parks for which the 2015 population was established to be 1,153 orangutans [8]. By 2016, the government estimated that these sampled populations had more than doubled to 2,451 individuals [8]. There are three major issues with this reported population trend. First, it is biologically impossible for an orangutan population to double its size in a year [9]. Second, some of the government-sampled sites are used for orangutan introductions or translocations from other sites (for example, Bukit Baka–Butit Raya National Park), implying that any net positive change in the monitored sites was inevitable preceded by at least an equally large negative change in non-monitored populations from which orangutans had been initially removed. Third, the nine government sampling plots and their reported populations represents less than 5% of the Bornean and Sumatran orangutan ranges, and zero percent of the Tapanuli orangutan range. Furthermore, all monitoring sites are within protected areas, whereas the majority of orangutans occur in non-protected lands [4, 6, 7]. It is thus scientifically unjustified to extrapolate population trends from these sampling sites to the total range of all three species.

The apparent mismatch between reported and achievable population growth for orangutans is not limited to this species alone. Indeed, the report states that populations of 19 of the Indonesian government's 25 priority species also grew by more than 10% [1]. This is not possible for some of the listed species, such as the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), given known breeding rates and threat levels. For the past several decades overall Sumatran-rhinoceros birth rates have been exceeded by death rates [10].

We acknowledge the difficulty of accurately estimating population trends for elusive, low-density species such as orangutans. However, we believe that the current Indonesian government methods provide an unrealistically positive and biased picture of orangutan population trends. The direct measurements of orangutan numbers could, for example, be complemented with an assessment of changes in their forest habitat, which would offer a more robust estimate of their current status. Establishing targets such as an increase in the percentage of orangutan habitat that is protected or well managed, including not only forest

management but also the implementation of zero-killing policies, might allow easier verification of progress towards established goals.

We urge the Indonesian government to review its conservation-impact methods since they offer an inaccurate description of the current reality. There is an experienced group of Indonesian and foreign scientists working across disciplines who are willing to help set realistic targets and develop feasible and scientifically robust monitoring methods. Given the Indonesian government's recent successes in implementing policies to reduce fires and restore peatlands [1], there is a timely opportunity to step up urgently needed improvements in species conservation and to demonstrate real success in protecting Indonesia's rich biodiversity and its unique natural heritage. Only effective collaboration between governments, non-governmental organizations, scientists, rural communities and the corporate sector will save the orangutan.

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Author contributions

Conceptualization, E.M., J.S., M.A., S.A.W and M.V.; Writing – Original draft, E.M., J.S., M.A., S.A.W and M.V.

Declaration of Interests

The authors declare no competing interests.

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Chapter 5

Challenges and opportunities for monitoring a charismatic species in the tropics – integrating data and stakeholders

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Challenges and opportunities for monitoring a charismatic species in the tropics - integrating data and stakeholders

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Abstract

Effective species monitoring and conservation is crucial to curb ongoing biodiversity loss. Long-term population monitoring underpins estimations of status and trends in species distribution and population abundances, the identification of underlying drivers and threats and determination of appropriate conservation actions. Especially in the tropics, where high biodiversity coincides with high levels of threats, monitoring programs face a number of challenges, resulting in large spatio-temporal gaps in available data and large confidence

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intervals of resulting estimates. We identify essential components of effective monitoring programs in tropical regions, exemplified by the case of the Bornean orangutan. We discuss existing sampling methods to assess abundance and occurrence, population dynamics, drivers and threats to this critically endangered species. We show that opportunistic observations, data collected by citizen scientists, as well as novel technologies such as drones or camera trap networks can be used to broaden the range of observations, and increase the quality and spatio-temporal resolution of the known species density distribution. We discuss the trade-off between extensive large-scale and intensive small-scale sampling and how recent advances in integrative species distribution modeling can harness the strengths of both approaches. Integrative models can also incorporate population dynamics, significantly improving inferences drawn for conservation. We highlight the importance of mechanisms for data sharing and dissemination of results to inform managers and other stakeholders in accessible language and format, their potential for bridging the gap to global repositories, and their relevance for stakeholder engagement and increased transparency and accountability. Ultimately, an integrative monitoring framework that actively cultivates collaborations and the flow of information between all actors involved in monitoring and conservation, including scientists, decision makers, resource managers and local communities, will be one of the key elements to ensure a future for endangered species, such as the orangutan.

Keywords

Bornean orangutan; *Pongo pygmaeus*; density distribution modeling; data sharing; data-base; tool-kit; species conservation

INTRODUCTION

In face of massive changes of biodiversity and loss of natural habitat, nations have committed to halt species declines and ecosystem degradation through the Aichi Targets of the Convention on Biological Diversity (CBD, 2011; Leadley et al., 2014; Mace et al., 2018; Tittensor et al., 2014). Our capacity to tackle the ongoing biodiversity crisis is, however, very much dependent on our knowledge about states of natural systems in space and time and our ability to coordinate effective conservation actions across all societal levels (Nichols and Williams, 2006; Yoccoz et al., 2001). This has made the monitoring of biodiversity and of drivers of change a cornerstone of conservation programs (Buckland and Johnston, 2017; Navarro et al., 2017; Pereira et al., 2010). Monitoring programs are important to address research questions about system processes and drivers, assess species population status and vulnerability to extinction (Nichols and Williams, 2006; Yoccoz et al., 2001). Among many

other things, monitoring can also help to identify mitigation strategies for development, areas of offsets, ascertain adherence to legal commitments, evaluate management outcomes, and document status of species for certification needs (Lindenmayer et al., 2017; Pickett et al., 2013).

Long-term and large-scale monitoring is necessary to inform policies and conservation action plans that are often decided at a regional or national scale (Buckland and Johnston, 2017; Lindenmayer et al., 2018). In practice, monitoring is, however, often limited to local and short time-scales or not prioritized altogether (Pyhälä et al., 2019; Sheil, 2001) as a result of scarce funding and high costs. Thus, especially in tropical, developing countries, where high species diversity is exposed to high levels of imminent threat, there is a large gap in species observation (Collen et al., 2008; Laurance et al., 2012).

Here, we review challenges and opportunities for species monitoring in the tropics, using the Bornean orangutans (*Pongo pygmaeus*) as a case-study. In comparison to the majority of sympatric species, past survey effort has allowed for estimates of Bornean orangutan (hereafter orangutan, unless indicated otherwise) abundance and its trend over time (Santika et al., 2017; Voigt et al., 2018). However, a number of challenges for orangutan monitoring remain. First, orangutans occur at very low density across their range, are semi-solitary and elusive, making the species very difficult to detect. Second, large parts of the orangutan range, which covers more than 150,000 km² (Gaveau et al., 2014; Wich et al., 2012), are remote and difficult to access, imposing logistic and financial constraints on any monitoring activity. Third, land-cover is changing at one of the highest rates worldwide, mainly as consequence of commodity driven conversion of forest and large-scale fires (Gaveau et al., 2018; Sloan et al., 2017), thus requiring a highly adaptable approach to sampling.

Here we highlight how the development and application of novel approaches in monitoring and species distribution modeling can make a large difference in monitoring efficiency. In recent years, technologies such as aerial surveys, drones or camera trap networks have been increasingly implemented for species monitoring in the tropics (Ancrenaz et al., 2005; Rovero and Ahumada, 2017; Wich and Koh, 2018). In combination with the development of integrative modeling approaches, it is now possible to harness the strengths of a number of data sources (Miller et al., 2019; Navarro et al., 2017). This is promising for significantly improving inferences from monitoring, and resultant higher resolution, larger-scale and more robust population estimates in the near future (Miller et al., 2019; Santika et al., 2017; Zipkin and Saunders, 2018). This improvement has to be matched by active integration of stakeholders to overcome barriers to data sharing and uptake of results, and bridge the space

between research and implementation for effective species conservation (Navarro et al., 2017; Toomey et al., 2017).

BORNEAN ORANGUTANS - STATUS, TREND AND THREATS

Population status and trend

Three sub-species of Bornean orangutans occur in Borneo within the Malaysian states of Sabah and Sarawak, and the provinces of Kalimantan in Indonesia (Wich et al., 2008). A compilation of available surveys across its entire range showed that Bornean orangutans have declined by more than 25% between 2004 and 2014 (Santika et al., 2017) and that at least 100,000 individuals were lost between 1999 and 2015 (Voigt et al., 2018). These estimates are a significant improvement compared to past expert-based calculations, but confidence intervals remain large (Voigt et al., 2018).

Threats to orangutan populations

Although the biggest threats to orangutans, specifically habitat loss and direct killing, have been identified for some time, their relative contribution to overall population decline is not fully understood (Abram et al., 2015; Davis et al., 2013; Gaveau et al., 2018; Meijaard et al., 2012, 2011). Since the spatial and temporal pattern of orangutan killing is not well described, this threat is especially difficult to estimate and tackle (Davis et al., 2013; Meijaard et al., 2011).

Furthermore, orangutans have a long life-span and slow reproductive rates (Marshall et al., 2009) and are resilient to a certain degree of disturbance, for example, by using adjacent areas, free of on-going disturbance (Ancrenaz et al., 2010). As a result, orangutan populations respond slowly to environmental degradation and population collapse can occur with a considerable time lag (Spehar et al., 2018). It is therefore difficult to relate changes in orangutan numbers to drivers and threats when monitoring extends only over short temporal scales (Husson et al., 2009; Marshall et al., 2009; Russon et al., 2015). As a consequence of these challenges, Bornean orangutan conservation has not been effective throughout its entire range and conservation actions need to be better adapted to address causes and threats at a species-wide scale (Meijaard et al., 2012; Spehar et al., 2018; but see: Simon et al., 2019).

MONITORING

Variables of interest and methods of observation

Different variables are of interest to understand the state of Bornean orangutan populations, as well as the necessity, appropriateness and effectiveness of conservation actions (Fig 1). Presence and abundance of a species are the variables at the core of the majority of monitoring programs (Nichols and Williams, 2006). While the information about presence and thus distribution of a species is the most basic variable, abundance and its changes through time is more informative to establish a baseline for conservation of the target species and assess population trends. Both measures are included as essential biodiversity variables (EBVs), proposed by the Group of Earth Observations Biodiversity Observation Network (GEO BON), a globally coordinated biodiversity observation network that aims at improving the acquisition, integration and delivery of biodiversity observation (Navarro et al., 2017, Pereira et al., 2013).

Current orangutan abundance is a function of past abundance, their reproduction, mortality, dispersal, as well as rescue and translocation efforts (Marshall et al., 2009). Human pressures drive these demographic processes and thus eventually impact orangutan numbers. Therefore, monitoring programs that also aim at gaining a mechanistic understanding of population dynamics or their causes of decline, benefit from including the direct observation of these processes, their drivers and threats to the species (Fig 1).

A number of observation methods are available to monitor orangutan numbers, population dynamics, drivers and threats (Appendix S1). The standard approach to assess orangutan abundance employs nest counts along a linear transect following the Distance method (Buckland et al., 2015; Kühl et al., 2008; Schaik et al., 1995) (Fig 1 and 2). By accounting for imperfect detection, this allows estimation of the absolute abundance of individuals within a fixed area (i.e., density). Aerial nest counts allow sampling of larger and more remote areas, but only capture an index of abundance. These approaches are tailored to present-day orangutans being a semi-solitary, elusive species occurring at low density (but see: Spehar et al., 2018). With the exception of Sabah, abundance observations on line transects only comprise a small share of overall available sampling data (Fig 2 C). Primary forest and metapopulation areas further inland and at higher elevations, have notably less survey effort (Fig 2 C and D). New technologies such as drones and camera trap networks to capture observations, and Artificial Intelligence (AI), and citizen scientists to extract and

digitize them, could increase the feasibility and scope of orangutan monitoring schemes at larger spatial scales in the near future (Fig. 1 and 2, appendix S1).

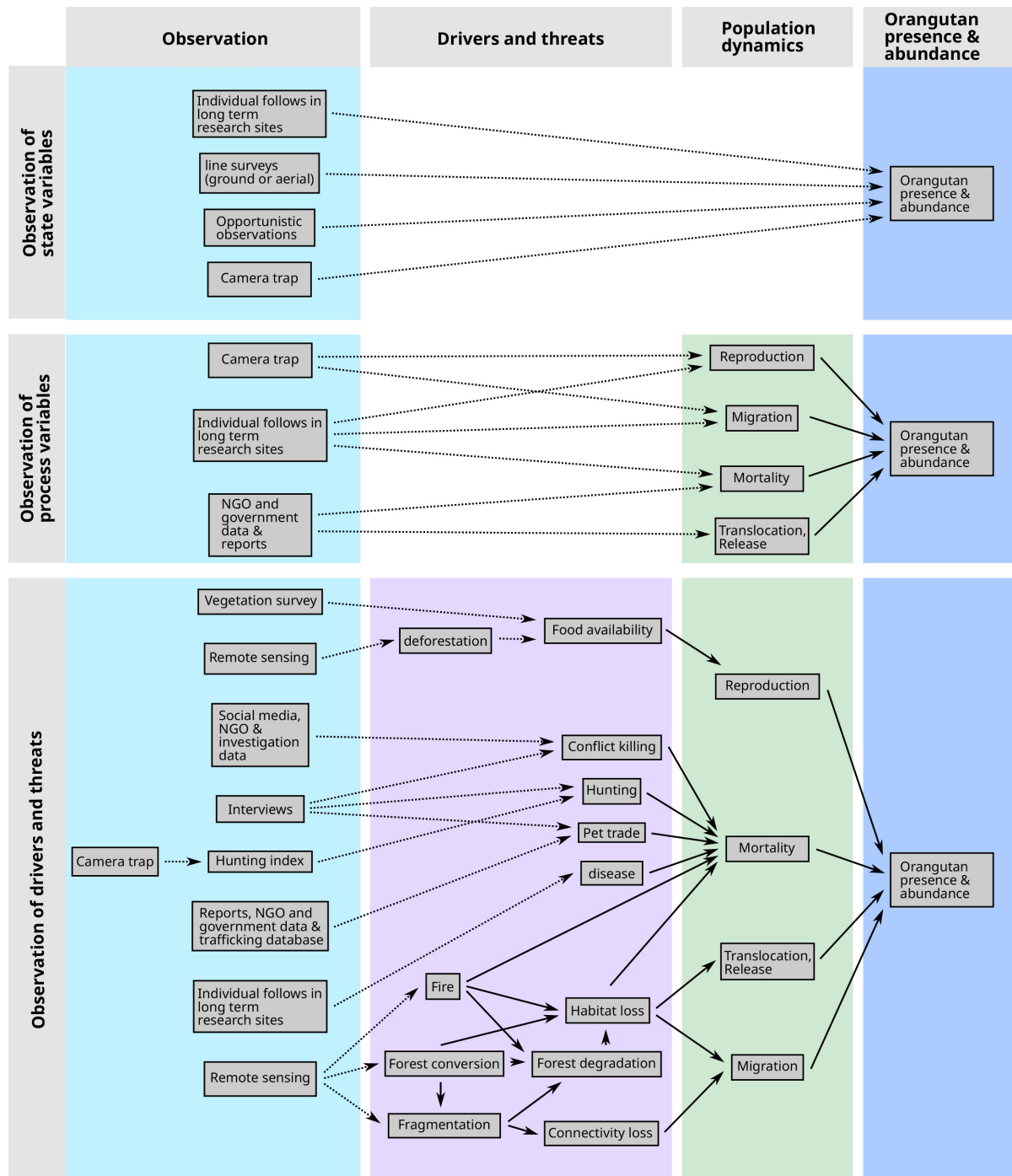


Figure 1: Conceptual model orangutan monitoring.

State variables, process variables and drivers and threats can be directly or indirectly observed through different methods (light blue, left). Drivers (violet) influence population dynamics (green) which result in orangutan presence and abundance (dark blue, right). The observation process is indicated with a dashed arrow, while system processes are indicated by a solid arrow. Individual follows in long term research sites also include, for example, the collection of genetic and hormone data that allows to assess reproduction and mortality. A hunting index derives the hunting pressure from the ration of species with different sensitivity to hunting (Yasuoka et al., 2015). See also Appendix S1.

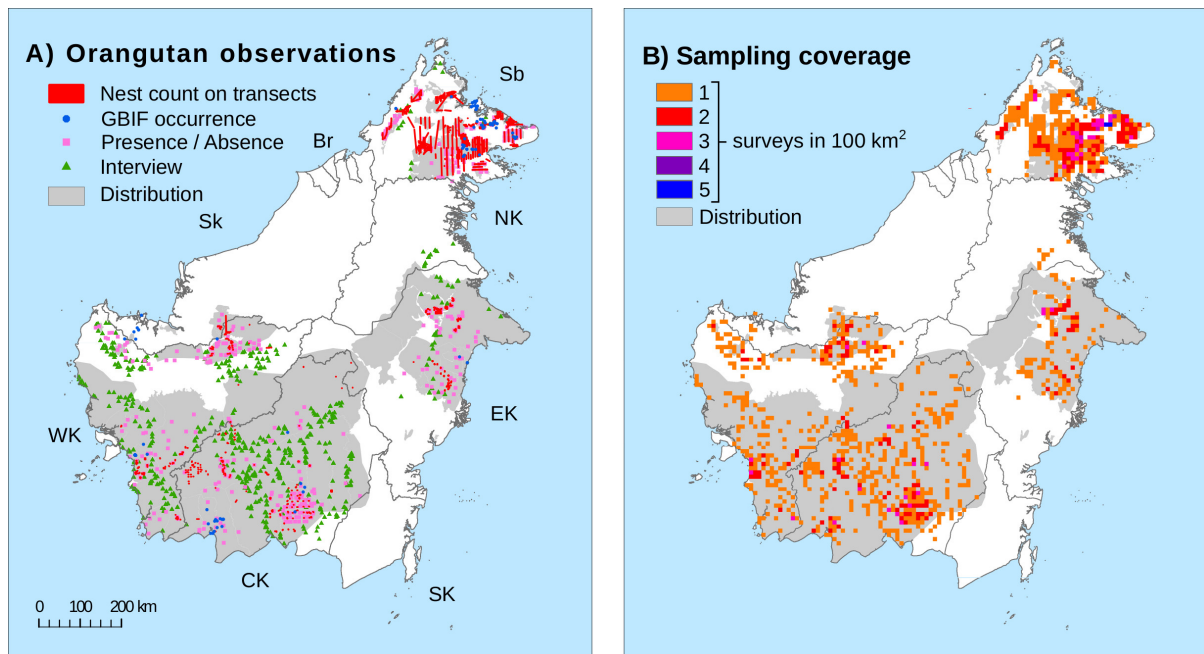


Figure 2: Current monitoring and sampling coverage.

A) Data available for Bornean orangutan monitoring with information on location, year and administrative boundaries. Surveys comprise nest counts on ground and aerial transects, occurrence surveys, interview surveys (excluding locations with low reliability (Meijaard et al., 2011)), global biodiversity information facility (GBIF) occurrences of orangutans within Borneo (excluding points outside of Borneo or from sanctuary/zoo) (GBIF.org, 2019). 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. B) Number of sampling events within 10x10 km cells, considering an effective strip width of ground transects of 16 m and aerial transects of 75 m to either side (Voigt et al., 2018).

Sampling design

A well-designed monitoring program is representative in space and time with a sufficiently large sample size that allows valid inference (Buckland and Johnston, 2017). In general, there is a trade-off between the number of sites, samples over time and variables a monitoring program can measure (Pereira et al., 2017). The ability of monitoring programs to detect and quantify trends can be critically dependent on how sampling effort is allocated between these components (Rhodes and Jonzén, 2011).

Sampling schemes differ in their approach and objective, and can be separated into targeted monitoring, aimed at answering specific *a-priori* questions, or surveillance monitoring, aimed at collecting as much information as possible (Lindenmayer and Likens, 2010; Nichols and Williams, 2006; Wintle et al., 2010). Depending on their spatial scope, monitoring programs can also be differentiated into extensive or intensive (site-based) (Pereira et al., 2017). In extensive sampling schemes, only a few variables are collected at many sites over large areas, often with the participation of citizen scientists (Couvét et al., 2011). Site-based and targeted monitoring, often undertaken in parallel with research aimed at understanding

fundamental ecological mechanisms, is characterized by a high sampling effort in a small area (Nichols and Williams, 2006; Pereira et al., 2017). With this type of monitoring, individual primates and their behavior are, for example, observed over an extended time period. On the other hand, the extensive surveillance approach to monitoring has been criticized for being a waste of scarce resources, as it does not allow hypothesis- and model-driven conclusions (Nichols and Williams, 2006). Others have suggested to make use of these data since they can be valuable for measuring biodiversity change at large spatial scales and thus relevant to policy and decision making (Couvet et al., 2011; Pereira et al., 2017).

Sampling representativeness is achieved by random or stratified random allocation (Buckland and Johnston, 2017). Such a selection of sampling sites was partially employed, for example, to estimate abundance of orangutans on Sumatra (Wich et al., 2016) and to estimate nation-wide chimpanzee densities in Liberia and Guinea Bissau (Murai et al., 2013; Tweh et al., 2014). Often, however, sampling locations cannot be placed systematically due to the high financial, logistic and human resources required. In such cases models can attempt to correct for lack of representativeness and the density or presence is inter- or extrapolated across the whole range (Buckland et al., 2012). Such a model was used, for example, to estimate abundance of Bornean orangutans and gorillas and chimpanzees in Western Equatorial Africa (Strindberg et al., 2018; Voigt et al., 2018).

In the Bornean orangutan range, monitoring efforts have predominantly been site-based. With the exception of Sabah and Sarawak, where all large forest blocks have been systematically surveyed (Ancrenaz et al., 2005; Pandong et al., 2018; Simon et al., 2019), single or repeated surveys cover only a small part of the total known orangutan range on the island (Fig 2 D). Most of the site-based long-term research efforts are located within primary lowland forests that are protected, of easier access and with comparably high orangutan abundance (Husson et al., 2009). As a consequence, throughout the range there are large gaps where no surveys were conducted or for which data were not made available (Fig 2 C and D).

Although the majority of orangutan long-term research and survey sites have suffered disturbances through either logging or forest fires, anthropogenic habitats are underrepresented among sites (Spehar et al., 2018; see also: Hockings et al., 2015). Monitoring in agricultural landscapes such as oil palm or paper pulp plantations require a sound understanding of orangutan ecology in these habitats and potentially different approaches than in natural forests to account for differences in detectability (Ancrenaz et al., 2004). Although a number of studies have specifically assessed presence, number and behavior of orangutans in forest fragments within agricultural or degraded landscapes

(Ancrenaz et al., 2015, 2015; Meijaard et al., 2016, 2010; Russon et al., 2015; Spehar and Rayadin, 2017), repeated assessments are scarce and overall survey effort in these landscapes is much smaller than their relative share of the total orangutan range. Crucially, areas where orangutans have previously been absent or occurring at very low density and areas that are suitable for orangutan colonization, such as regrowth forests, have been largely overlooked by surveys and monitoring. For as long as monitoring is restricted to high density areas, it is much more likely to detect declines than stabilization or increases (Fournier et al., 2019). It is thus important to also monitor suitable habitats with small populations or that are devoid of orangutans, to assess colonization processes and population recovery on a large spatial scale, and the effectiveness of conservation actions and policies.

MODELS FOR SPECIES MONITORING

Species distribution models

In monitoring and conservation management, models play an important role in harmonizing data within and across sites and among different observation methods. Models can be used to improve existing monitoring programs or to design new ones (Honrado et al., 2016; Miller et al., 2019).

Species distribution models (SDMs) have become an important tool to understand the relationship between species presence or abundance and environmental characteristics (Miller et al., 2019). SDMs allow extra- or interpolation of observed distribution or density patterns in space and time, and can also be used to predict species response to disturbance or future changes in climate. Outputs of SDMs thus have an essential role in species conservation and management. Measures of total species abundance and distribution on a national or range-wide scale is needed to report and evaluate adherence to international conservation commitments (e.g., 2020 Aichi Targets of the Convention on Biological Diversity, Red List assessments or species conservation action plans) (CBD, 2011; IUCN, 2019, Leadley et al., 2014).

In the tropics only a few examples of standardized monitoring of primates and other charismatic species exist at a national or range-wide scale, which enables accounting for observational uncertainty and facilitates direct comparison among sampling sites (Ahumada et al., 2011; Karanth, 2011; Murai et al., 2013; Tweh et al., 2014). However, if we look beyond data available from site-based or structured monitoring, a wealth of knowledge on past and present species locations is available from non-standardized datasets such as opportunistic and citizen science observations, museum samples and historical records

(Couvét et al., 2011). Recently developed integrated species distribution models can combine such non-standardized, but extensive and spatially-rich data, with standardized, site-based and temporally-rich data (Dorazio, 2014; Miller et al., 2019; Pacifici et al., 2017; Pagel et al., 2014; Zipkin and Saunders, 2018). Harnessing the strength of different data types, these integrated approaches significantly increase resolution, scale and possible inference from data sets, leading to overall population estimates with greater certainty (Miller et al., 2019). The advances in data integration rest on the premises that species distributions are the aggregated locations of individuals and can be described as a point process. Different data sources are integrated by linking each data source to the common underlying point process and accounting for the differences among data types (Miller et al., 2019). Viewing species' occurrences as a spatial point pattern even enables aligning presence-data with abundance data, as well as aligning data collected at different spatial scales. Using hierarchical models further allows separation of the process generating the distribution of individuals from the process of the observation, so that each dataset can have a tailored detection model.

In the same way in which successful sampling programs are informed by an *a-priori* understanding of the system and research or management questions, integration across data sources needs to be motivated by an understanding of ecological, sampling, and observation processes generating them (Nichols and Williams, 2006; Pacifici et al., 2017). Explicitly modeling sources of error in observation improves integrated species distribution models considerably (Miller et al., 2019).

In the light of increasing use of unstructured data, a number of authors have cautioned that the pragmatism that drives their use should not come at the expense of long-term, high-quality monitoring (Bayraktarov et al., 2019; Buckland and Johnston, 2017; Lindenmayer et al., 2018; Lindenmayer and Likens, 2010). Indeed, the caliber of available datasets will ultimately determine the quality of inference that can be drawn from integrative species distribution modeling (Zipkin et al., 2017).

Integrated population models

Integrative approaches can also be used to include dynamic components to model population processes governed by survival, reproduction and movement (Zipkin et al., 2017).

Understanding these processes is especially relevant for conservation management of populations, to track which demographic parameters have the largest influence on change and to identify interacting drivers of spatial and temporal variation in abundance (Rhodes and Jonzén, 2011; Zipkin et al., 2017). Integrated population models within a Bayesian

framework allow modeling of population-level extinction probabilities, typical components in population viability analysis (Servanty et al., 2014). These metrics are increasingly important for orangutan populations on Borneo, considering that many of them might already be below minimum viable size (Marshall et al., 2009; Voigt et al., 2018). Integrated population models can be extended to be spatially explicit (Chandler and Clark, 2014), thus allowing estimation of species distribution, abundance and vital rates across large spatial scales. For Bornean orangutans, Santika et al., (2017) implemented such a spatially-explicit integrated population model, using ground transect, aerial data, presence data and interviews, to estimate past species trends.

Models to improve monitoring

Coupling integrated models with simulations can help assess the relative value of different data types for inference, explore different sampling designs and the costs associated to gathering or adding new data sources. Simulations are useful to evaluate potential adjustments in the field, and spatio-temporal allocation of samples to optimize parameter accuracy and limit bias (Miller et al., 2019). When resources are limited, simulations can also explore survey designs that maximize results and quality based on the amounts of funding or effort available. A range of methods are available for optimizations of monitoring, such as power analysis, linear programming or graphical solutions (Sanderlin et al., 2014, 2012; White, 2019). Modeling the sampling process can also play a vital role in communicating gains of monitoring with all stakeholders and decision makers involved. Models can increase transparency about potential outcomes, revealing which type of results can be expected and thus avoid unrealistic expectations (Honrado et al., 2016). Finally, modeling, for example using Value of Information theory, can also indicate how to best balance monitoring and conservation actions, to limit the diversion of critical resources from species protection (Bennett et al., 2018; Lindenmayer et al., 2013).

REPORTING

Monitoring data for use

Methodological advances in the integration of different data types are only valuable if data are accessible to scientists and decision makers to use it. A number of databases and portals were designed with the purpose of making species observations available in a standard format. For example, the global biodiversity information facility (GBIF), the largest portal of its kind with over a billion record listed in 2018, collates information on species occurrences

from digitized collections, field surveys, and citizen science initiatives. In order to contribute to the global effort of monitoring biodiversity, management programs should make the reporting of their data to such databases and portals an integral component of their monitoring workflow. Unfortunately, data custodians tend to have high workloads that do not prioritize reporting to external databases, and often lack incentives to share their data (Heinicke et al., 2019). There is also a large resistance in making data openly available, out of fear of losing intellectual property rights, especially for data that were collected under high investment of resources in remote locations and under demanding conditions prevalent in the tropics, and disclosing sensitive species localities (Heinicke et al., 2019; Lindenmayer et al., 2017; Lindenmayer and Scheele, 2017; Lindenmayer and Likens, 2010; Lowe et al., 2017; Meijaard and Nijman, 2014). As a consequence, global information platforms such as GBIF exhibit spatial biases, which are especially apparent in tropical regions. In the case of Bornean orangutan monitoring, the opportunistic data found in GBIF are a very small subset of the survey data that are being collected by monitoring efforts (Fig. 2). It is thus urgent to find adequate mechanisms that would better capture these various data sources and contribute to compiling them in an accessible format.

Taxa-specific databases

Taxa-specific databases could bridge the space between global databases and local efforts. Specifically for great apes, the IUCN/SSC A.P.E.S. database was created to connect data producers and data users, and to collate and archive datasets (Heinicke, 2019). Past efforts to model trend and abundance of Bornean orangutans (Santika et al., 2017; Voigt et al., 2018), based on a large set of data points, were only possible due to a unique effort of a few well-connected individuals and a willingness among orangutan researchers to share their data. In the future, such databases can improve the evidence base for species, actively engage different actors and address the particular challenges of the field. In the case of the A.P.E.S. database, data are made available in accordance to specified user and sharing agreements, maintaining intellectual property as desired by the custodian. Summary statistics from collected data are being fed into national conservation action plans, and reports and assessments for funding organizations (Heinicke et al., 2019). Information from regional or taxa-specific databases could also be used to derive information for global initiatives such as GEO BON (Navarro et al., 2017). Beyond the direct benefit of archiving and providing access to data, a database curated by species specialists can also foster long-term integration among stakeholders and actors in the field by generating trust and collaboration opportunities (Heinicke et al., 2019).

Tools for reporting

Accessibility of monitoring data can also be increased through interactive web-tools that visualize results and summary statistics for conservation managers and decision makers. This has been successfully implemented, for example, to monitor deforestation and fire (globalforestwatch.org and Musinsky et al. (2018)). For Borneo, a web-tool allows tracking of yearly deforestation and land-use change within industrial oil palm concessions (cifor.org/map/atlas/). For species monitoring such a tool could combine a range of data streams on species observation and threats (Fig. 3).

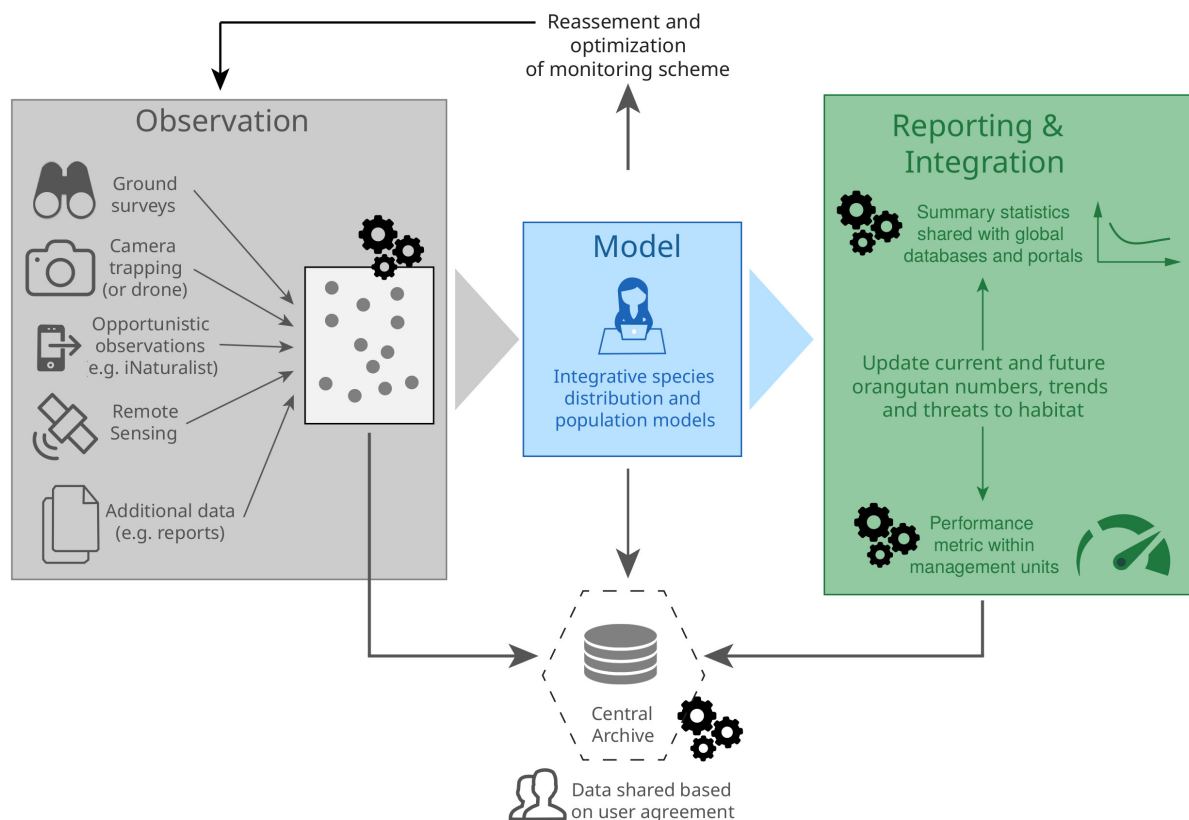


Figure 3: A toolkit for orangutan monitoring.

A toolkit for orangutan monitoring could use different observations (grey) that are digitized or semi-automated and feed into integrative species distribution models (blue). The models help to optimize monitoring and can be used to produce metrics (green) that allow to evaluate performance within management units. Both observations and model output can be archived to a central archive. From models summary statistics for global databases or performance metrics for data managers can be derived. The cogwheel indicates products which stakeholders can assess or interact with via the tool-kit.

Potential data for Bornean orangutan monitoring include digitized and processed observations from ground surveys, camera traps or drone missions that are processed with machine learning or the help of citizen scientists, and opportunistic observations from databases and data portals such as GBIF. These data could be coupled with near-real time alerts on drivers such as deforestation, fire or killing events, as well as static layers of

orangutan predictors, such as climate, habitat and protected area extent (Hansen et al., 2016; Justice et al., 2011). From this information an integrative species distribution model could compute indicators relevant for orangutan conservation, which could be output and visualized within management units (e.g., states, protected areas, and resource use concessions). Metrics of interest include habitat loss, loss of connectivity, and current and near-future orangutan abundance and trend. Facilitating access to updated information on these indicators would be an important tool for resource managers, decision makers and donors to understand local orangutan population trends and drivers and take appropriate actions.

Furthermore, optimization models could be implemented within the tool to plan new and improve ongoing monitoring efforts. Mapping ongoing monitoring effort could help to coordinate activities so that they complement each other in space and time. An expanded tool-kit for orangutan monitoring could also encompass an application for mobile data collection, for example via the Open Data Kit (opendatakit.org). This would facilitate data collection in the field with a standard format. Orangutan observations and other information contributing to the tool could be archived automatically via the IUCN/SSC A.P.E.S. database (Heinicke et al., 2019). Lastly, an interactive user forum, and outreach and capacity building surrounding the tool-kit, could connect data producers, data users and scientists developing the applications and bridge the gap between them.

Integration of stakeholders

The lack of integration among research, government and nongovernmental institutions as well as conservation organizations is one of the main barriers to data accessibility and the success of large-scale monitoring programs in achieving conservation relevance (Bainbridge, 2014; Lindenmayer and Likens, 2010). Organizations differ in their structure, what they aim to achieve with monitoring, their day-to-day activities, and how they are funded or evaluated. They also have different approaches to data sharing and property rights. Conservation challenges do not stop at borders and the Bornean orangutan range falls within the jurisdiction of two Malaysian states and at least three Indonesian provinces (Fig 2).

Monitoring programs that overlook such differences will not be able to construct the network of stakeholders needed for coherent and high-quality monitoring and effective and efficient conservation actions (Lindenmayer and Likens, 2010). Monitoring programs therefore need to explicitly address, varying backgrounds and motivations to monitor, and actively foster exchange and a common language. Integration leads to mutual benefits for all

parties by allowing exchange of knowledge among stakeholders, increasing the range of data that is available, building capacity and supporting the validation of results. While policy makers and conservation organizations know the type of high level information that is needed for management and policy change, scientists may have a better understanding of the underlying primary observations needed to produce this policy-relevant information, and how to design the necessary and robust monitoring schemes that can make use of new statistical and technological developments in the field.

The integration of a range of expertise on the monitoring of the components of systems of interest will facilitate the conceptualization of those systems, processes and thresholds, thus yielding more appropriate sampling schemes, relevant monitoring output and effective species conservation. Crucially, integration can avoid conflicts by clarifying expectations regarding possible outputs, associated cost and providing transparency about the level of confidence achieved for a given effort.

Estimates of total species numbers and distribution have been corrected in the past, when more data and new methods became available (Strindberg et al., 2018; Voigt et al., 2018; Wich et al., 2016). Without appropriate and stakeholder-specific communication about the reasons for these changes, new estimates can alienate conservation managers or policy makers, whose evaluation and financial support may be tied to these metrics. Stakeholders could lose trust in monitoring results, or worse, in the scientific approach that underpins them. This may lead to ignoring broad scientific consensus on species trends, in favor of numbers gained from insufficient sampling (Meijaard et al., 2018).

In a successful example of stakeholder integration in the Malaysian state of Sabah, researchers and nongovernmental organizations were able to work with the government to protect the majority of the Bornean orangutan habitat, following a systematic, state-wide orangutan survey (Ancrenaz et al., 2005; Sabah Forestry Department, 2017). To improve conservation decisions and management for the species, both the knowledge on the distribution of orangutan populations in the state and a functional cooperation between different stakeholders were necessary. Following the baseline data established in the early 2000's, a survey was able to confirm stable populations in a number of the newly protected fragments (Simon et al., 2019). This partnership also involved local people in Kinabatangan, an area with high species diversity and local conservation value, to maintain the habitat for the Bornean orangutans and other sympatric species (Ancrenaz et al., 2007). This example shows that the integration of local communities in monitoring and conservation actions,

including capacity building and co-production of knowledge, can also significantly increase acceptance and success of monitoring schemes (Ancorenaz et al., 2007; Pyhälä et al., 2019).

CONCLUSION

We argue that some of the key challenges that riddle species monitoring in the tropics, exemplified here with the Bornean orangutan, can be tackled by integration, both on the level of data sources and of stakeholder engagement. The employment of novel technologies and integrative modeling techniques maximizes the inference that can be drawn from a range of different data and expertise. Nevertheless, even technically advanced and well executed monitoring programs with integrative models will not be sufficient for species conservation if their output is not made available in a format that is suitable to address the needs of conservation managers and decision makers. Thus, in order to halt the loss of species worldwide, considerations about robust sampling and monitoring must be complemented by consistent data sharing and functional collaborations among different stakeholder groups. For successful conservation and the achievement of international commitment such as the Aichi biodiversity targets of the CBD, such integration has to be recognized and implemented as a key element of monitoring programs.

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Declaration of Interests

The authors declare no competing interests.

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Chapter 6

Synthesis

This thesis substantially contributes to the evidence base for Bornean orangutan conservation in two ways. First, by quantifying and evaluating species loss in response to past and future drivers and threats. Second, by reviewing points of action which can assist in overcoming existing impediments and improving species monitoring.

Estimating the density distribution of species

In the tropics where natural ecosystems are changing at unprecedented rates (Laurance et al., 2012), knowledge about the geographical distribution of species, their density and total numbers are essential to explore the consequences of land-use, land-cover and climate change (chapter 2 and 3 and e.g., Gregory et al., 2012). The range-wide density distribution established in chapter 2, for example, revealed the pervasiveness of human impact on orangutan populations, and how their decline varied across different types of land-use and land-use change. The availability of abundance information also allows the separation of range losses from abundance losses, delineation of species strongholds and their prioritization for conservation (chapter 3). This information is needed to evaluate which conservation interventions are most effective in reducing species and biodiversity decline and to establish baselines for conservation (Stokes et al., 2010; van Schaik et al., 1995).

In the future more research effort is required in marginal orangutan habitat and forest fragments in anthropogenic landscapes (chapter 5; Spehar et al., 2018). Current approaches do also not sufficiently consider the option value of such forests for dispersal or as potential refuge areas outside of the current range. Even though marginal habitats might harbor very low orangutan densities at a given moment in time, they could be relevant for long term

survival and, especially under a changing climate in the future, could gain considerable importance (Husson et al., 2009; Struebig et al., 2015).

Models for orangutan conservation

Robust models, based on good monitoring data, are a powerful tool in advancing our understanding, and an essential component supporting conservation decisions (Honrado et al., 2016). In chapter 2 and 3, models improved our understanding of past and future drivers of orangutan abundance on a range-wide scale, especially for areas with few or no observations. When sampling is difficult and expensive, using models and simulations to evaluate different sampling schemes can maximize efficiency and quality of output (chapter 5; Honrado et al., 2016; Miller et al., 2019). In future, improvement of modeling methods through integrating different data sources are promising to refine current efforts, improving overall resolution and quality of density distribution estimates (chapter 5; Merow et al., 2017).

Model outputs are contingent on a number of decisions and assumptions, including, for example, the selection of datasets and modeling approaches used, as well as the form of visualization. As a consequence, results have to be thoroughly validated and assumptions and limitations have to be transparent and well communicated (chapter 5). Models are often needed to support decisions, but cannot substitute the process of decision-making. Considering these constraints, it is especially crucial to involve stakeholders in the process of conceptualization and validation of modeling results, ensuring a general understanding of the values of models and confidence associated with results (Lindenmayer and Likens, 2010).

Importance of communication and integration

In the past, the lack of collaboration and integration of different stakeholder groups has significantly hampered orangutan research and conservation (chapter 4 and 5; Meijaard et al., 2012). Implemented conservation actions are not able to stop population declines in large parts of the orangutan range (chapter 2), and uptake of scientific evidence in prominent orangutan conservation arenas have been limited (chapter 4). One example is the most recent Orangutan Action Plan (2007 - 2017) that represents official Indonesian government policy for orangutan conservation. Neither killing, a major threat to orangutans (chapter 2; Abram et al., 2015; Davis et al., 2013; Meijaard et al., 2011), nor the protection of orangutans outside of protected areas, where the majority of orangutans occur (chapter 3), were appropriately recognized and addressed.

Similarly, a large number of nongovernmental organizations involved in orangutan conservation focus on orangutan rescue, translocation, rehabilitation and release (Meijaard et al., 2012; Russon, 2009). While from an animal welfare perspective there is a need for such actions and they receive a lot of public attention and funding, they are ineffective in ensuring the survival of the species, and instead merely treat the symptom and not the threat itself (Meijaard et al., 2012; Russon, 2009).

Focus in research is often on the ‘how’, and not on the values and premises of the question, who is involved or affected and how results can be implemented on the ground (Meijaard and Sheil, 2011). However, the active engagement of research and relevant institutions, general public and local communities can promote a diversification of viewpoints and approaches, to overcome the research-implementation gap and ascertain that monitoring and conservation is effective (Bainbridge, 2014; Lindenmayer and Likens, 2010; Meijaard and Sheil, 2011). In the future, such an exchange could identify feasible conservation targets and conservation priorities, and verify that they are in line with what is needed on the ground (chapter 4; chapter 5; Sanderson, 2006).

Conservation and global socio-political climate

While habitat loss and orangutan killing are the main threats to orangutan populations, there are underlying drivers that contribute to why orangutan conservation is falling short of halting species decline. These direct threats are ultimately symptoms of global to local demand for natural resources (chapter 2). Globalization of markets leads to teleconnections of producing and consuming countries and results in developed countries diminishing biodiversity elsewhere (Lenzen et al., 2012; Marques et al., 2019; Wilting et al., 2017). Such effects are expected to escalate as the global population grows and becomes wealthier, increasing the demand for natural resources. Already now 25% of biodiversity impacts are driven by consumption that is based on international trade (Marques et al., 2019). Problems are exacerbated as political agendas are dominated by narratives of economic growth and development, while protection of natural assets is neglected. Future conservation programs and policies need to recognize and address these underlying drivers, for example through global awareness campaigns, international commitments and trade policies (e.g., Greenfield and Veríssimo, 2019; Olmedo et al., 2018; Wiedmann and Lenzen, 2018).

In the context of orangutan and forest conservation, palm oil and the calls for its boycott have been widely advocated (e.g., Meijaard and Sheil, 2011; Rival, 2017). To single out one crop as the problem and offer a fix by excluding it from the production process, however, is

an example of a solution that falls short of acknowledging the complexity of the situation and ignores potential pathways to accomplish sustainable futures for local people and the environment (Rival, 2017). Instead, a range of different approaches, including regulations, disincentives and partnerships with extractive industries, such as oil palm plantation concessions, can be an effective way to achieve best practices and conservation within anthropogenic landscapes (Ancrenaz et al., 2016; Koh and Wilcove, 2007; Meijaard et al., 2016).

As such, there is a geographical divide in the cost and benefits of protecting orangutans (Meijaard and Sheil, 2011). Local communities do not understand why Western conservation projects invest heavily in protecting, rescuing and caring for orangutans, while they subsist in poverty and cannot meet basic needs (Meijaard et al., 2012; Meijaard and Sheil, 2011). At the same time, in Europe and other developed countries agricultural landscapes dominate, and large predators have been driven to extinction and are hardly tolerated upon their return (e.g., Drenthen, 2015; Mech, 2017).

Is there still hope?

There is still hope for orangutans and other wildlife on Borneo. Recent efforts to map land-use in the ‘One Map initiative’ could overcome uncertainties around land tenure and improve conservation planning (Gokkon, 2018a; Mulyani and Jepson, 2017). Policies on fire prevention (Tacconi, 2016), as well as the new forest and peat moratorium in Indonesia (Norwegian Government 2016) and forest protection in Sabah (Sabah Forestry Department, 2017; Varkkey et al., 2018), might already be decreasing habitat loss and could do so even more in the future (Gaveau et al., 2018).

Special attention to orangutans as a flagship species has given rise to a number of research projects and organizations focused on orangutan conservation (Marshall et al., 2016; Meijaard et al., 2012). This attention guarantees that when orangutan populations are threatened, the international community can build momentum and will not allow orangutans to disappear unnoticed (e.g., Gokkon, 2018b; Sloan et al., 2018).

The long history of human and orangutan’s co-existence on Borneo and the adaptability of the species in the face of change, means that, if managed carefully, co-existence in anthropogenic landscapes is possible. Simulations of orangutan population dynamics have shown that they could colonize areas where they have gone extinct previously and slowly bounce back (Marshall et al., 2009), thereby proving wrong our projections of future tree cover loss based on past drivers (chapter 2 and 3).

However, to achieve a future where both people and wildlife on Borneo can thrive, we need to understand the complexity and intricacies of these coupled ecological and socio-economic systems spanning global to local dimensions (Meijaard et al., 2012; Spehar et al., 2018). Although there is a multitude of different approaches to protect orangutans and biodiversity on Borneo, conservation problems tend to be wicked and complex. Solutions need to be tailored to the specific conditions and challenges on the ground (chapter 2; Game et al., 2014; Meijaard and Sheil, 2011). To prevent further decline of the exceptionally rich biodiversity on Borneo and in the tropics, biodiversity conservation must become a guiding principle in the public discourse and in political decision-making processes. Participatory approaches, integrating across all aspects of society, built on effective collaboration between governments, non-governmental organizations, scientists, local communities and the corporate sector will be key to ensure future survival of orangutans and biodiversity in general.

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Appendix

Appendix – Chapter 2

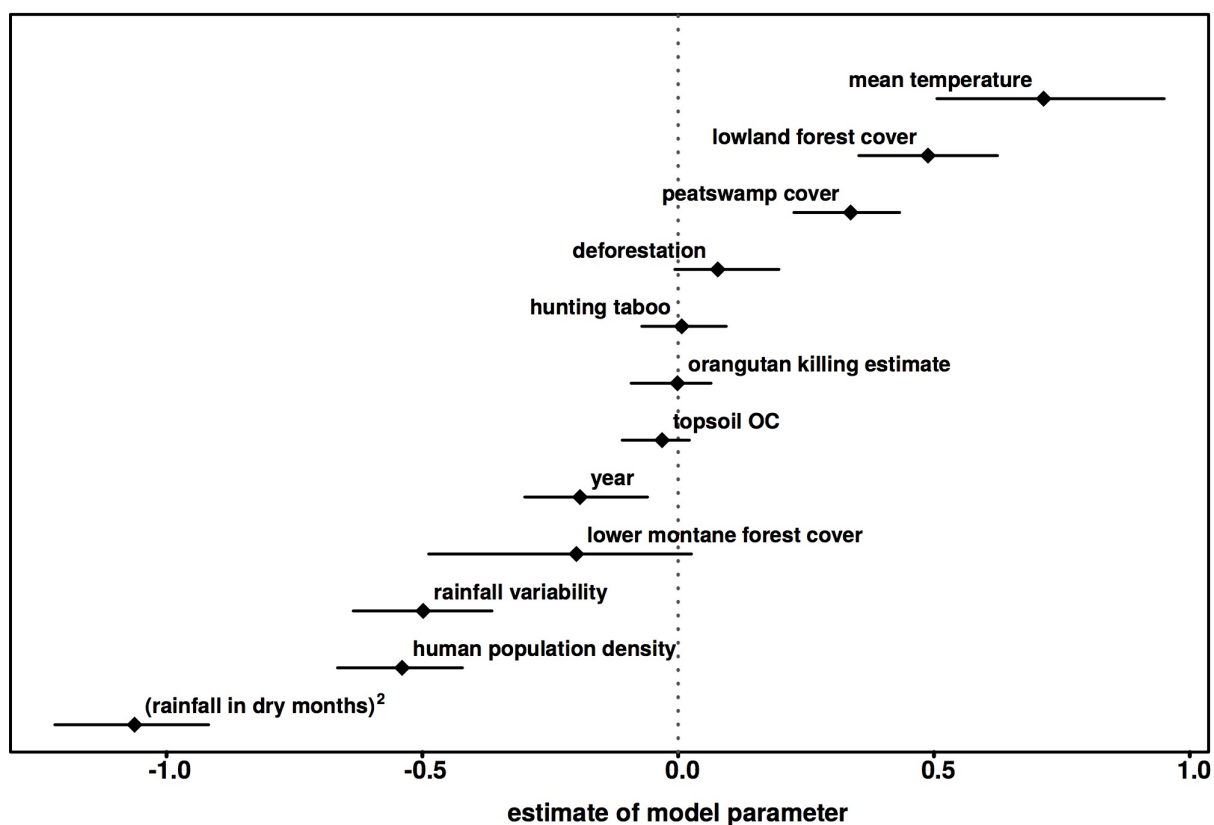


Figure S1: Model-averaged Parameter Estimates, Related to Figure 1 and 2.

Predictors were standardized to a mean of zero and a standard deviation of one to facilitate the comparison. Parameter estimates (diamonds) and 95% confidence intervals (horizontal lines) were model averaged, using the AIC weights. The interpretation of the linear term of rainfall in dry months depends on whether the quadratic term is included in the model. All models which only included the linear (but not the quadratic) term had AIC weights < 0.001. Therefore the coefficient is not shown here.

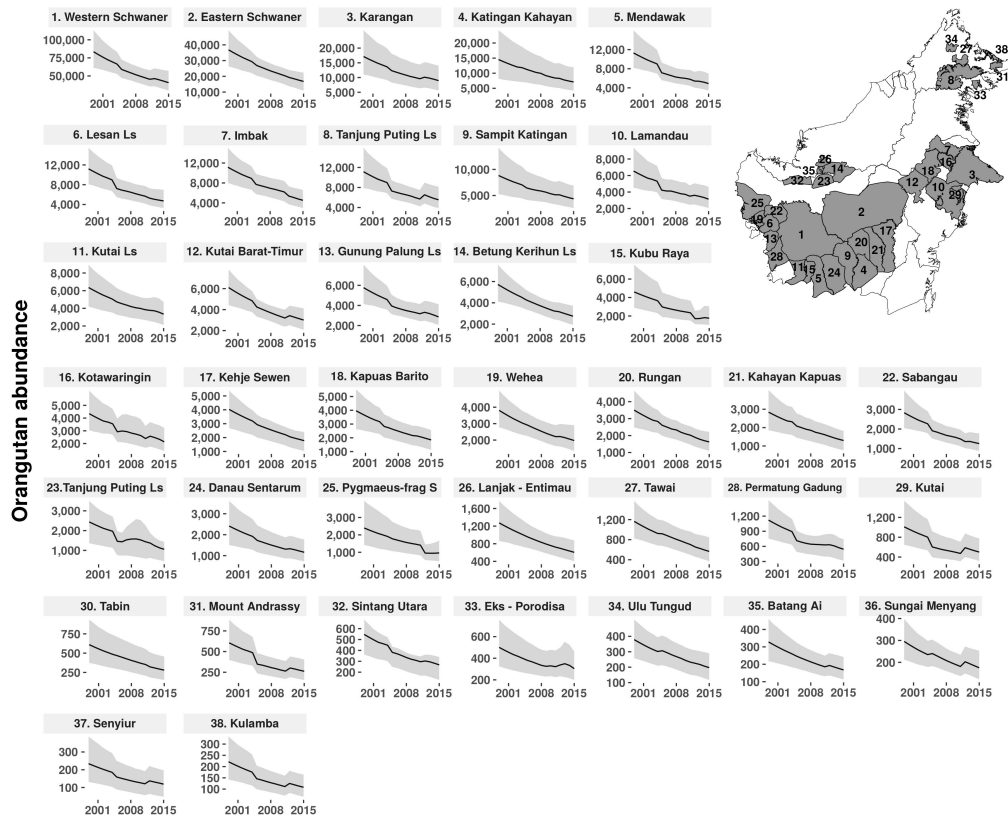


Figure S2: Yearly Abundance of All Viable Orangutan Populations between 1999 and 2015, Related to Figure 1.

Orangutan abundance of all populations with more than 100 individuals in 2015 over the study period from 1999 to 2015 including the 95% confidence intervals (grey). Study years are represented on the x-axes. Map shows the location of the populations. Abbreviations in population names as follows: Ls = Landscape, frag S = fragmented South.

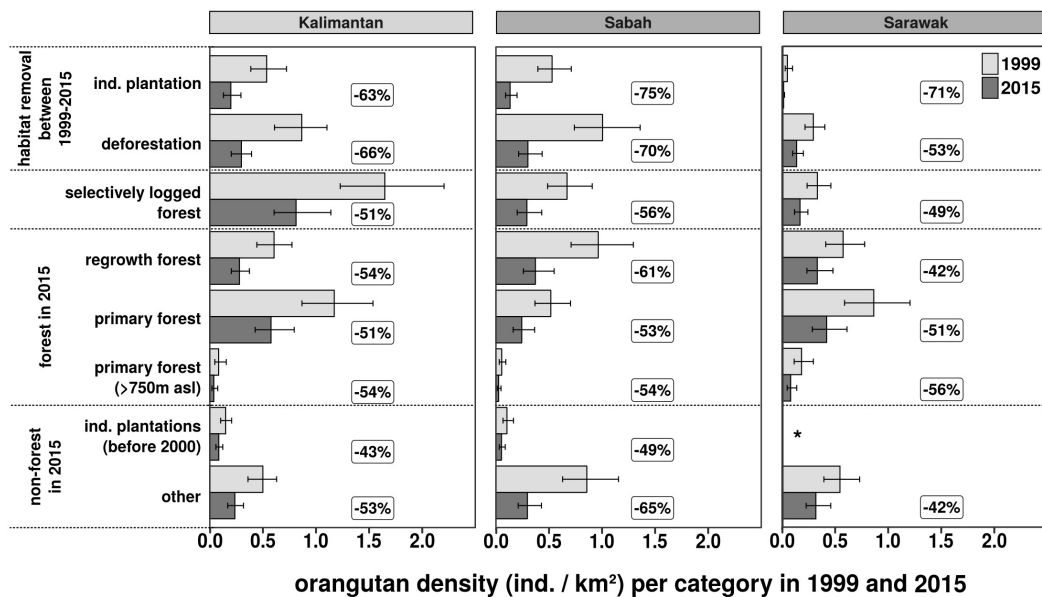


Figure S3: Bornean Orangutan Density and Decline in Resource Use Categories, Related to Figure 3.

Average density and its change between the first study year (1999) and last study year (2015) in areas in which industrial oil palm or paper pulp plantations were established, which were deforested or selectively logged during the study period (1999 – 2015), in areas with forest (regrowth, primary and montane forest) and in areas without forest (areas that were transformed in plantations before 2000 and other areas). The “*” indicates the absence of orangutans in the respective category. The error bars indicate the 95% confidence interval. The percent orangutan density loss in comparison to 1999 is given in rectangles.

Table S1: Model Coefficients from Full and Best Model and Summed AIC Weights, Related to Figure 1 and 2.

Model	AIC weights	Model estimates	
		Full	Best
Intercept	-	-0.56	-0.57
Year	1.00	-0.22	-0.19
Mean temperature	1.00	0.80	0.66
Rainfall variability	1.00	-0.47	-0.49
Rainfall in dry months	1.00	-1.30	-1.31
(Rainfall in dry months) ²	1.00	-1.08	-1.06
Topsoil organic carbon content	0.48	-0.08	-0.06
Peatswamp cover	1.00	0.35	0.35
Lowland forest cover	1.00	0.52	0.47
Lower montane forest cover	0.82	-0.14	-0.27
Deforestation	0.85	0.10	0.09
Human population density	1.00	-0.53	-0.55
Orangutan killing estimate	0.14	0.02	-
Hunting taboo	0.29	0.01	-
AIC		16204.29	16195.93
Model weight		0.0037	0.2455
Model rank (of 6144 models)		25	1

AIC weights of coefficients are calculated by summing the AIC weights of the models in which the coefficient is present. A weight close to 1 indicates an influential predictor. The interpretation of the linear term of rainfall in dry months depends on whether the quadratic term is in the model and should not be averaged over all models. All models which only included the linear term had AIC weights < 0.001. Their influence on the average coefficient value was thus negligible. For the full and the best model the AIC, model weight and model rank are given at the bottom of the table.

Table S2: Correlation Matrix for the Predictors Used in the Density Distribution Model, Related to Figure 1 and 2.

Model predictors	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
(1) Year	1.000										
(2) Mean temperature	0.026	1.000									
(3) Rainfall variability	0.143	0.459	1.000								
(4) Rainfall in dry months	-0.093	-0.406	-0.675	1.000							
(5) Topsoil organic carbon content	0.066	0.241	0.223	-0.118	1.000						
(6) Peatswamp cover	0.153	0.219	0.188	-0.129	0.370	1.000					
(7) Lowland forest cover	-0.194	0.005	-0.291	0.239	-0.204	-0.256	1.000				
(8) Lower montane forest cover	0.004	-0.817	-0.32	0.343	-0.116	-0.109	-0.296	1.000			
(9) Deforestation	0.409	0.265	0.209	-0.241	0.063	-0.002	-0.362	-0.164	1.000		
(10) Human population density	-0.013	0.338	0.484	-0.389	0.161	0.063	-0.468	-0.148	0.120	1.000	
(11) Orangutan killing estimate	0.052	-0.51	-0.254	0.289	-0.098	-0.043	0.075	0.48	-0.188	-0.306	1.000
(12) Hunting taboo	0.026	0.261	0.327	-0.602	0.022	0.029	0.057	-0.285	0.122	-0.041	-0.097

Table S3: Models Included in the 95% Confidence Set, Related to Figure 1 and 2.

Model Nr.	Model coefficients												df	AIC	ΔAIC	AIC weight	
	Y	T	RV	RD	RD ²	OC	PC	LC	MC	DF	PD	KE					HT
1														14	16195.9	0	0.245
2														13	16196.2	0.3	0.209
3														15	16198	2.1	0.086
4														14	16198.1	2.2	0.081
5														14	16198.9	3	0.056
6														12	16199	3.1	0.054
7														13	16199.4	3.5	0.044
8														12	16200.4	4.5	0.026
9														13	16200.4	4.5	0.026
10														14	16201	5.1	0.019
11														15	16201	5.1	0.019
12														13	16201.1	5.2	0.019
13														14	16201.1	5.2	0.018
14														13	16202	6.1	0.012
15														13	16202.3	6.4	0.01
16														12	16202.4	6.5	0.01
17														13	16202.4	6.5	0.01
18														15	16202.8	6.9	0.008

The model rank, the included coefficients, degrees of freedom (df), their AIC, ΔAIC and AIC weights are given. The full model included orangutan nest count on transect ~ year (Y) + mean temperature (T) + rainfall variability (RV) + rainfall in dry months (RD) + rainfall in dry months² (RD²) + topsoil organic carbon content (OC) + peat swamp cover (PC) + lowland forest cover (LC) + lower montane forest cover (MC) + deforestation (DF) + human population density (PD) + orangutan killing estimate (KE) + hunting taboo (HT).

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Appendix – Chapter 3

APPENDIX S1

Further description of source data and deforestation model for Borneo

Spatial layers of deforestation drivers

At a resolution of 30 m, the original forest cover layer (Gaveau et al., 2016a, 2016b) incorporates the change based on global forest loss estimates (Hansen et al., 2013) (Fig 1a). To account for the varying probability of deforestation between different types of protected areas and concessions (Gaveau et al., 2016b), we included a layer of land-use and management as a predictor of tree-cover loss (Fig 1b, (Santika et al., 2017)). This layer characterizes the differences in land-use and management, and includes forests within protected areas, logging concessions and unconverted forests within industrial timber plantation concessions, industrial oil palm plantation concessions, as well as forests outside of protected areas and concessions.

Since the level of protection, management and use of protected areas can differ, we further specified the category according to the World Database on Protected Areas (WDPA) classification (IUCN and UNEP-WCMC, 2017). We only considered areas from the WDPA present in the layer by Santika et al. (2017), as these were derived from national data, assumed to be more representative of the situation on the ground. All areas included in both sources and ranked as category 1-3 in the WDPA were combined in one class ('strict conservation'), which represents the highest protection and areas with little to no active human intervention (Dudley, 2013). Classes 4-6, where sustainable use can be practiced (Dudley, 2013) and areas included as 'not applicable' and 'not reported' were grouped into a 'sustainable use' class. All areas that were included in Santika et al. (2017), but missing in the WDPA (2017) were classified as 'national' protected areas. They constitute, for example, protection forest (*Hutan Lindung*) and wildlife and nature reserves in Indonesia; protection forest reserves and wildlife reserves in Sabah, and protected forests in Sarawak (Santika et al., 2017).

All predictors were clipped with the forest cover remaining at the beginning of the calibration period (2011), since the model does not calculate probability of tree-cover loss for pixels deforested before. The layers were converted to the Asia South Albers Equal Area Conic projection and resampled to the same extent and origin at 1 km cell size, the highest resolution available for all layers, using bilinear for continuous and nearest neighbor resampling for categorical predictors.

We evaluated whether the overall pattern and area of tree-cover loss were maintained during the change in resolution (Fig. S1). Severe selective logging is detectable as tree-cover loss at a 30 m-resolution. When increasing the spatial grain, the contextual information of local tree loss events is degraded and can be misinterpreted as clear cut deforestation, even when the aggregated area of forest loss is maintained (but see: Amoroso et al., 2018). Thus, when using the terms ‘tree-cover loss’ or deforestation, we acknowledge that we cannot differentiate severe forest degradation over a larger area, for example through intensive logging, from clear-cutting of forest.

Tree-cover loss on Borneo was analyzed within geopolitical units. Province (for Indonesia), state (for Malaysia) and country borders (for Brunei) were downloaded from the Global Administrative Areas database (GADM, 2012), and combined within the extent of the island.

All spatial manipulations were performed in Python (Python Software Foundation, 2016), using gdal (GDAL Development Team, 2017) and numpy (Oliphant, 2016) packages, and aggregated, analyzed and visualized in R (R Core Team, 2017) and ArcGIS (ESRI, 2014).

Deforestation model and calibration

The model of tree-cover loss was adapted from Rosa et al. (2013) and is based on $P_{trloss,x,t}$, the probability that trees in a cell x are lost in a time interval t . The probability of loss is defined as a logistic function:

$$Ptrloss_{x,t} = \frac{1}{1 + \exp^{-k_{x,t}}} \quad (1)$$

in which $k_{x,t}$ can range from minus to plus infinity and $P_{trloss,x,t}$ from 0 to 1. We then used linear models to describe $k_{x,t}$ as a function of the predictor variables that affect tree-cover loss at location x and time t .

Using a forward stepwise regression, a total of 34 models were fitted to the observed tree-cover loss data (2012 – 2016). Each model differed in the combination of predictor variables that define $k_{x,t}$. The models were fitted using ‘Filzbach’, a freely available library (<https://github.com/predictionmachines/Filzbach>), which uses a Markov Chain Monte Carlo (MCMC) sampling method to return a posterior probability distribution for each parameter.

From this distribution, given a specific parameter combination Θ , the posterior mean and credible interval was extracted. To estimate the parameters, the log-likelihood, a measure of the goodness of fit between the observations and the model predictions, is defined for a particular combination of variables:

$$L(X|s, \Theta) = \sum_{x,t} \log(Z_{x,t} \text{Ptrloss}_{x,t} + (1 - Z_{x,t})(1 - \text{Ptrloss}_{x,t})) \quad (2)$$

in which $Z_{x,t}$ is the observed tree-cover loss at location x and time t , and s one of the 34 models considered.

To assess the predictive power gained by adding variables to the model, a cross-validation technique was used. This checked how accurately the model predictions compared to a randomly selected subset of 50% of the data that was not used to train the model. This cross-validation is necessary to find models that only comprise predictors with evident predictive ability. After successively adding the variable that resulted in the highest likelihood model, the overall best model (i.e. the one with the maximum test likelihood) was selected from the whole set of models.

Simulations

The simulation was based on recalculating equation (1) for each time-step, while using a slightly different set of parameter values at each iteration, thereby incorporating parameter uncertainty. These values were drawn from a Gaussian distribution resulting from the MCMC fitting, using the estimated mean and standard deviation for each parameter. As a result we received an updated $P_{trloss,x,t}$ for each individual cell (x) in each individual time period (t). We subsequently evaluated whether or not the respective pixel was lost, by drawing a random number from a uniform distribution between 0 and 1. We classified the pixel as lost, if the number was less than the probability of tree loss $P_{trloss,x,t}$. This procedure was repeated for all four time-steps and run multiple times ($n = 100$ iterations) to gauge the uncertainty in model predictions over time. The different iterations were aggregated into the summed probability of tree loss and represent the fraction of simulation runs in which the tree-cover in a pixel in location x was lost.

Initial models suggested that the inclusion of a predictor representing the type of soil (mineral or peat), did not significantly improve model predictions, and so soil types were not included. All predictor variables, except for tree-cover loss, were static, i.e., only one time-step was considered. Tree-cover loss in the neighborhood of a cell was dynamically updated by the model in each time-step.

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Table S1: Predictor layers used to calibrate the model for the period 2012-2016, including name, short description of the layer, source and reference year.

Name	Description	Source	Year
Tree-cover loss	Tree-cover loss previous to calibration period (2001-2011) and in calibration period (2012-2016)	(Gaveau et al., 2016b)	2001-2011, 2012-2016
Topography	Elevation in meters derived from digital elevation model	(Jarvis et al., 2008)	2000
Distance to roads	Distance to primary and logging roads	(CIESIN & ITOS 2013; Gaveau et al., 2014)	1973-2010, 2013
Distance to rivers	Distance to major rivers with a minimum of 200 km ² drainage area	(Abram et al., 2015)	2010
Active fire incidence	Aggregated number of active fires (MODIS and VIIRS)	(MODIS Collection 6 NRT, 2018; VIIRS 375m NRT, 2018)	2000/2002-2017
Human population density	Number of humans within 1 km ²	(Bright et al., 2012)	2012
Land-use and management	Including protected areas (PAs), logging concessions, industrial timber plantation (ITP) concessions, industrial oil palm plantation (IOPP) concessions, areas outside concessions and PAs (as reference areas)	(IUCN and UNEP-WCMC, 2017; Santika et al., 2017a)	2012, 2017

Tree-cover loss previous to calibration period was used to inform the projection for the calibration period, while tree-cover loss in the calibration period was used to inform projections in the future. Areas outside of protected areas or concessions were included in land-use and management as a reference area, i.e., it was coded as level 0.

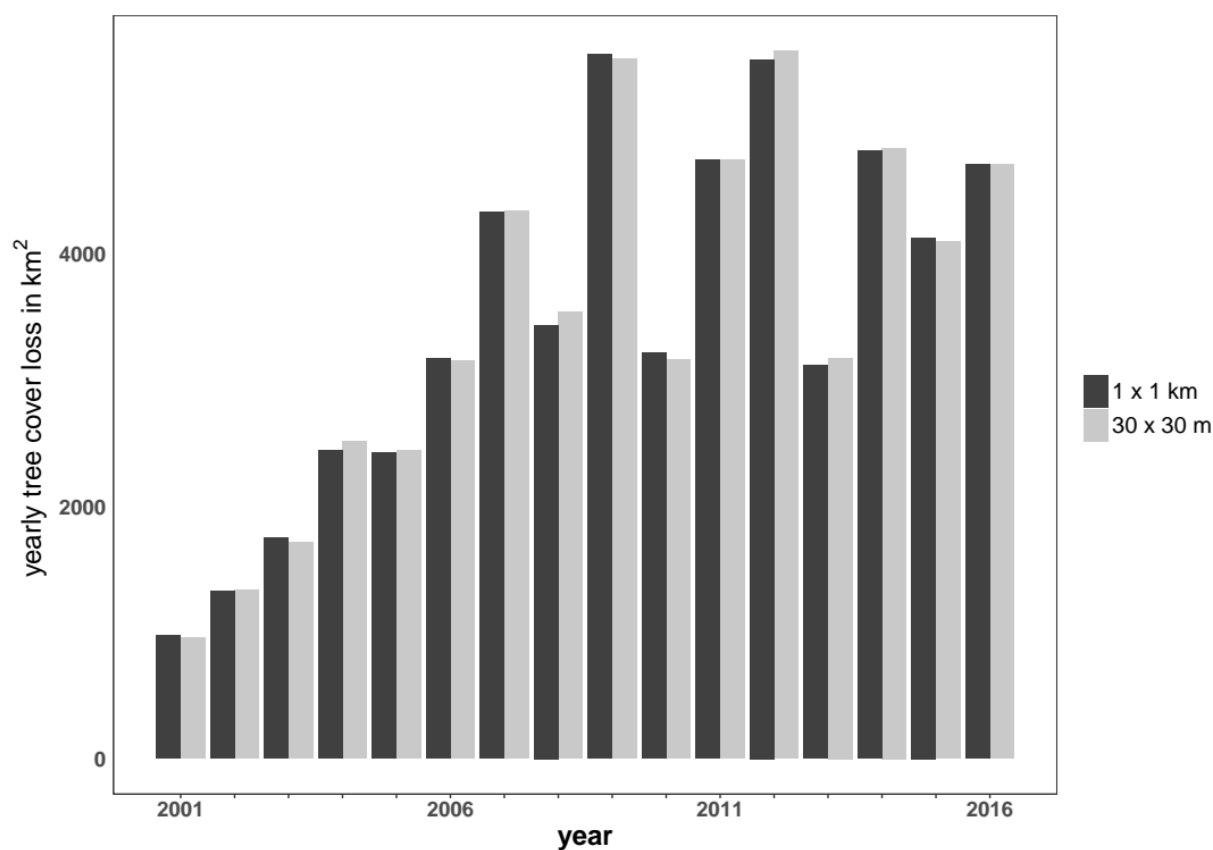
Table S2: All possible models ranked by their test likelihood, predictors and whether they were included in a given model (grey) or not (white).

Model	testlikelihood	Intercept	Previous tree loss	Distance to road	Distance to river	Population density	Topography	Fire incidence	LU and Mngmt
34	-35293.56								
32	-35294.24								
31	-35297.63								
27	-35297.72								
30	-35298.77								
33	-35301.74								
26	-35310.43								
28	-35311.03								
24	-35312.96								
29	-35328.69								
22	-35371.73								
25	-35377.56								
23	-35378.44								
21	-35378.93								
16	-35379.26								
19	-35772.4								
17	-35826.03								
20	-35840.23								
15	-35842.82								
14	-35842.93								
18	-35842.97								
9	-36609.28								
12	-37130.69								
10	-37253.68								
13	-37294.98								
11	-37295.68								
1	-37295.81								
8	-37297.55								
7	-38878.06								
2	-41040.7								
5	-42076.44								
3	-42459.64								
6	-42509.68								
4	-42509.93								
0	-42511.46								

Table S3: Province area, forest area and proportion.

province	Forest in 2000			Forest in 2017		Forest area in 2027 – 2031 in km ²			Tree-cover loss 2017 to 2027 – 2031 in %		
	Name	Area in km ²	Area in km ²	%	Area in km ²	%	<i>M</i>	<i>CI_l</i>	<i>CI_u</i>	<i>M</i>	<i>CI_l</i>
Sabah	73,541	44,952	61	39,427	54	28,358	28,069	28,680	28	27	29
Sarawak	123,797	82,202	66	66,170	53	42,308	41,910	42,854	36	35	37
West Kalimantan	146,981	70,251	48	59,942	41	41,684	41,442	41,956	30	30	31
South Kalimantan	36,620	8,883	24	7,719	21	5,630	5,525	5,742	27	26	29
Central Kalimantan	153,568	90,379	59	76,875	50	52,504	52,087	52,977	32	31	32
East Kalimantan	126,783	64,745	51	59,752	47	46,095	45,827	46,436	23	22	23
North Kalimantan	69,840	63,159	90	59,107	85	47,988	47,780	48,202	19	18	19

Province area, forest area and proportion in beginning of observation period (2000) and at end of calibration period (2017), projected forest area (2027-2031) and projected loss of tree-cover (2017 to 2017-2031).
 %–Proportion , *M*–median, *CI_l*–lower 95% confidence interval, *CI_u*–upper 95% confidence interval.

**Figure S1: Tree-cover lost per year aggregated for a resolution of 1 x 1 km and 30 x 30 m**

Tree-cover lost per year aggregated for a resolution of 1 x 1 km (final layer used) compared to a resolution of 30 x 30 m (original layer). The largest difference in aggregated area between the two resolutions is 2.9%, considered to be negligible.

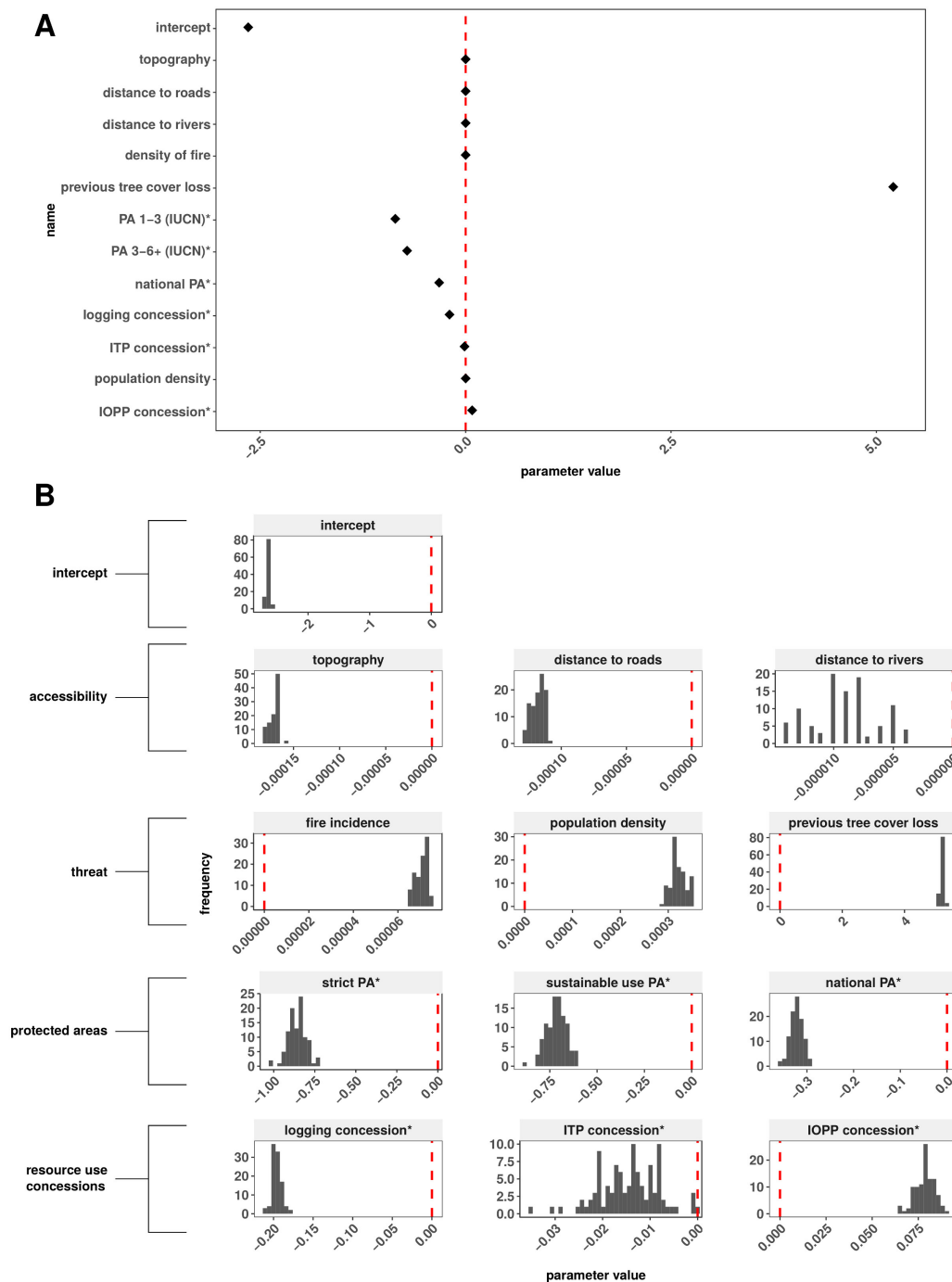


Figure S2: Effect sizes of predictors of tree-cover loss (A) and the distribution of their coefficients (B) over 100 simulation iterations.

Parameter values were drawn from a Gaussian distribution, using the estimated mean and standard deviation for each. The red dashed line indicates zero. Predictors with a coefficient smaller than zero decrease tree-cover loss, while predictors with a coefficient larger than zero increase tree-cover loss. Coefficients close to zero have a low or no influence on tree-cover loss. The effect of the protected areas and concessions (marked by an asterisk) is relative to the effect of no protection or designation as concession. Points in A are sorted by continuous and categorical (*) variables and their effect size. In A the 95% confidence interval is not shown, as it falls within the points.

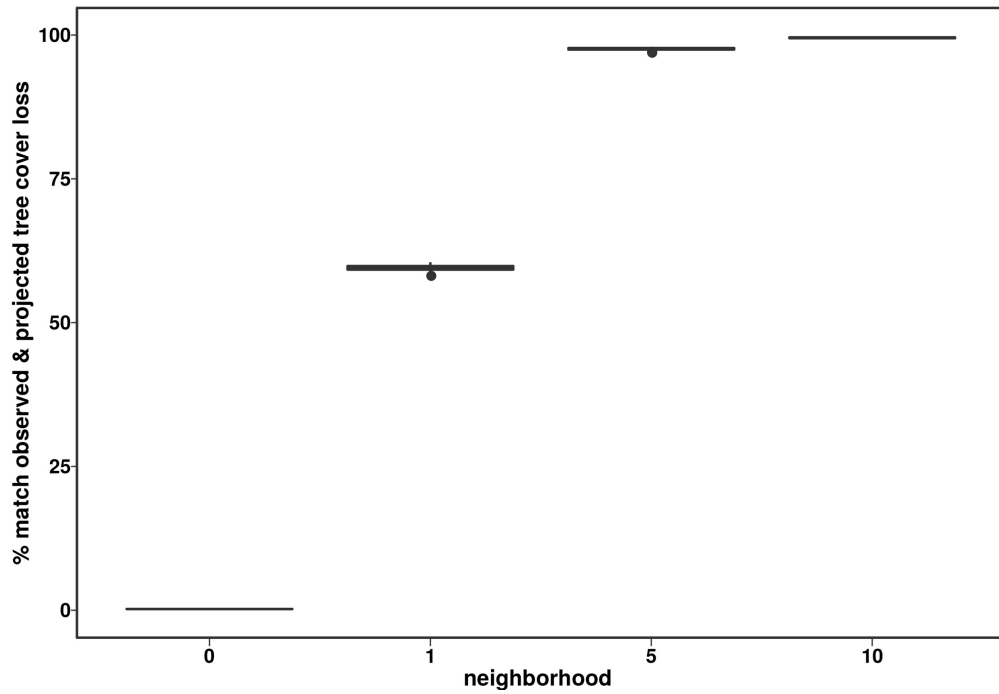


Figure S3: Proportion of match between observed and cumulative tree-cover loss within the neighborhood of a pixel for all simulations.

Boxplot shows the median across simulations ($n=100$). From the hinge (25th and 75th percentile, not visible) upper and lower whisker extend no further than $1.5 * \text{inter-quartile range}$. Values beyond are plotted individually.

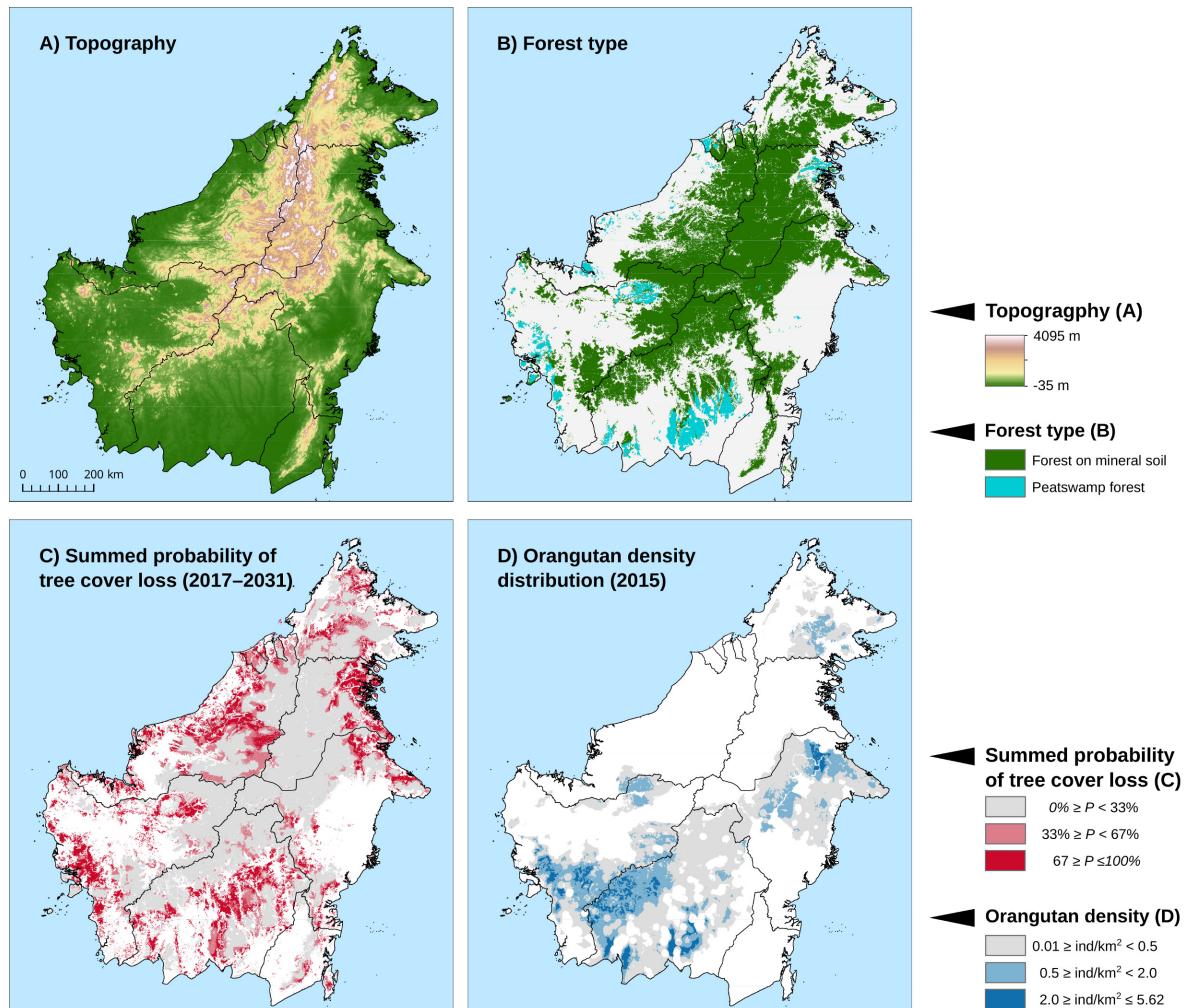


Figure S4: Topography, forest type, summed probability of tree-cover loss and orangutan density across Borneo.

Maps A and B provide context for the interpretation of the probability of tree-cover loss (Figures 1, 3 and 4). The distribution of projected probability of tree-cover loss and the density distribution of Bornean orangutans in maps C and D. Topography (A) was derived from a digital elevation model by Jarvis et al. (2008). Forest type (B) was derived from Miettinen et al. (2016) by combining lowland, lower montane and upper montane evergreen forests to represent forests on mineral soils. Summed probability of tree-cover loss (C) in three classes for all pixels forested in 2011. Orangutan density distribution (D) in three classes for all pixels with a density higher than 0.01 ind/km².

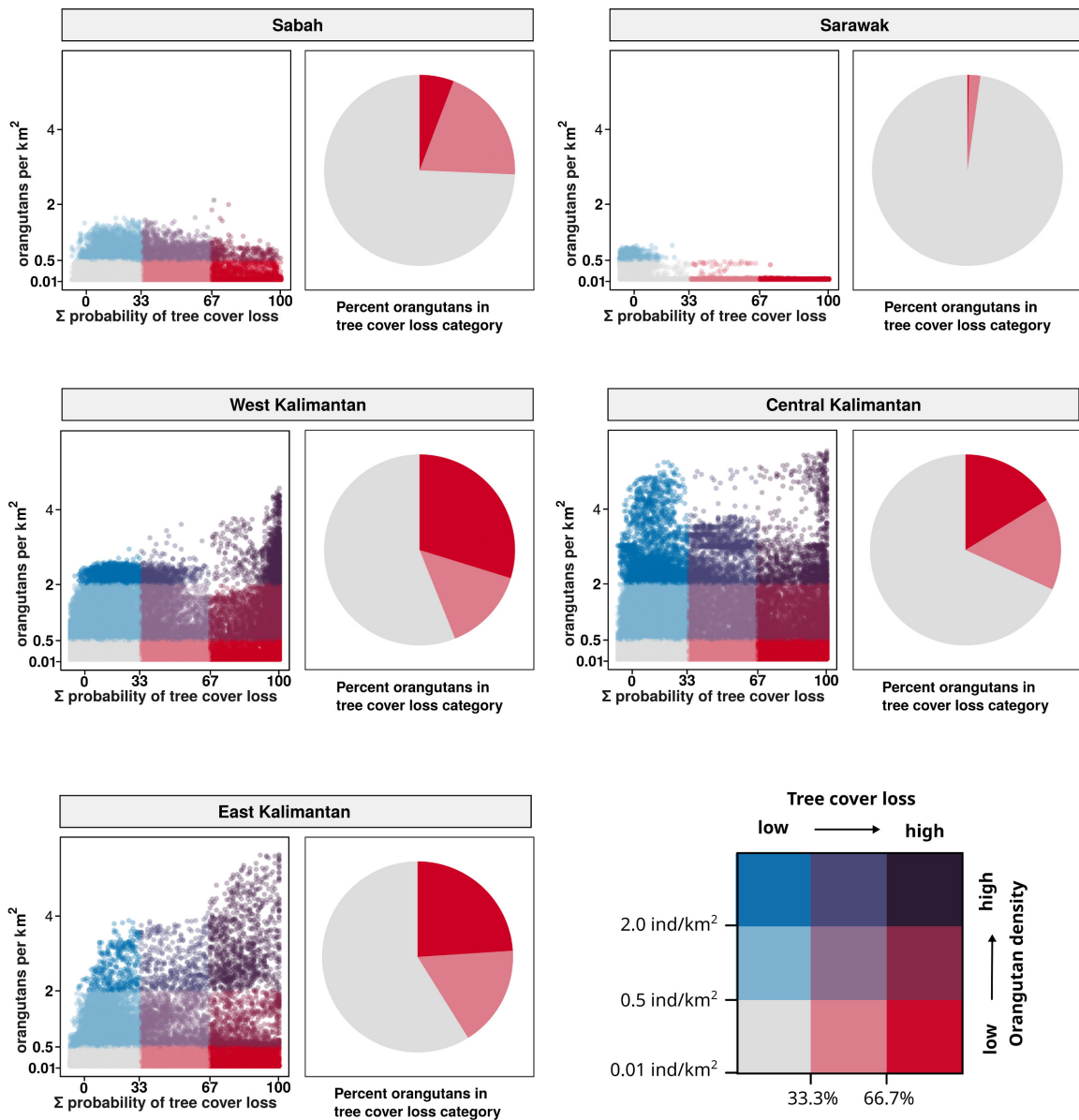


Figure S5: Density of orangutans and summed probability of tree-cover loss in provinces. Density of orangutans (blue) and summed probability of tree-cover loss (red). Blue and red shades indicate either factor, intensity corresponding to values, purple hues represent a mix of elevated levels (in maps and scatterplot). The distribution of pixels with respect to the orangutan density per square-kilometer and the summed (Σ) probability of tree-cover loss in scatterplot. The proportion of orangutans in areas with low, medium or high levels of tree-cover loss in pie charts, red shades only. North and South Kalimantan are not shown, as low number of orangutans (<100 individuals) occurred there.

Appendix – Chapter 5

APPENDIX S1:

Further description of monitoring methods

Observation methods

Orangutan monitoring is rarely focused on observing or counting the individuals directly, as the species is elusive and occurs at low densities. Exceptions are areas with habituated individuals, where the majority of individuals within an area are known and behavioral studies are conducted as well (Husson et al., 2009).

Observing nests on transects

Most commonly for great apes, resting platforms or nests are surveyed systematically along linear transects. These are then used to indirectly infer their presence or abundance (Kühl et al., 2008; Schaik et al., 1995). By measuring the perpendicular distance from the transect to the nest, the distance sampling method allows to account for detectability (Buckland, 2004; Kühl et al., 2008). Nests accumulate in the environment as a function of their rate of production, proportion of individuals within a population that produces these nests and the rate at which they decay. These factors must be known to convert the number of nests into number of individuals.

However, nest duration in particular varies depending on rainfall, wood density, complexity of nest architecture, and other factors that are not fully understood or mapped in space (Ancrenaz et al., 2004; Mathewson et al., 2008; van Schaik et al., 1995). Consequently, the extrapolation of nest decay rates across the range is difficult. As the measurement of nest decay for each survey site and period is very time consuming, often estimates from other sites are used and the conversion of nest to orangutan abundance thus introduces considerable uncertainty into abundance estimates from nest surveys (Marshall and Meijaard, 2009; Mathewson et al., 2008).

The Marked Nest Count method has been suggested as an alternative (Kühl et al., 2008). It avoids the conversion using nest decay by only counting nests that were built between two subsequent surveys. However, this can severely restrict sample size, due to low number of newly built nests. Further comparative studies are needed to establish whether this method is indeed superior in accuracy and effort than standard nest counts (Pandong et al., 2018; Spehar et al., 2010).

In the state of Sabah, systematic orangutan nests surveys were conducted with a helicopter (Ancrenaz et al., 2005). This method enables an increase in total survey area per unit time, as well as coverage of remote and inaccessible areas (Ancrenaz et al., 2005; Simon et al., 2019). With this methodology, all major forest blocks in the state were sampled repeatedly. Aerial surveys still require calibration with number of nests counted from the ground to account for detectability and the differences in nests observed from above and below the canopy (Ancrenaz et al., 2010, 2005; Wich et al., 2015). Although the detection process can be accounted for by measuring the distance to the nest observed, as for example done in marine mammal observations from ships (Kinzey et al., 2000). Sampling with drone technology has potential to provide a feasible alternative to helicopters or planes, although to date their reach is still small (Wich et al., 2015; Wich and Koh, 2018). Novel developments to fit drones with thermal sensors also open the possibility to capture orangutan numbers directly (Kays et al., 2019).

Camera traps

On Borneo camera traps have been used to assess orangutan occupancy in multi-species surveys (Cheyne et al., 2016; Deere et al., 2017) and to study orangutan behavior such as terrestriality (Ancrenaz et al., 2014). Spehar et al. (2015) have successfully tested camera traps with spatial capture-recapture modeling as a method to assess orangutan abundance directly. A recently developed method allows estimation of abundance from camera traps without the need to identify individuals by combining it with distance methods (Cappelle et al., 2019; Howe et al., 2017).

Interview surveys

Interview surveys can be a rapid and cheap way to obtain information about perceived absence or presence of apes over large areas and a good preliminary step before a survey (Kühl et al., 2008; Meijaard et al., 2011b). However in general, interviews are more reliable when confirming absence as opposed to presence. It is also difficult to assess reliability of respondents and accurately link information to specific locations and times (Kühl et al.,

2008). In the orangutan range, interviews have been used to assess relative presence and encounter rates of orangutans (Abram et al., 2015; Meijaard et al., 2011b).

Citizen science

The involvement of citizen scientists or skilled volunteers in monitoring programs have allowed researchers to greatly expand the scope of large-scale monitoring surveys (Chandler et al., 2017). Mostly in developed countries, these surveys were either executed in a structured design or are a collection of opportunistic observations that are contributed via platforms such as iNaturalist or eBird (Pereira et al., 2017). There are a number of challenges associated with using such data, but method exists to evaluate and account for potential biases or errors (Guillera-Arroita et al., 2015). In Borneo, where a large part of the orangutan range is remote and sparsely populated, involvement of volunteers or the usefulness of opportunistic observation from citizen scientists is more limited (Fig 2, in main text).

Digitization of observations

Through the continuous development of methods such as camera traps and drone surveys it is possible to generate a large amount of observations in a short period of time. To be useful for research or conservation, relevant information has to be extracted from these raw observations. Via online platforms, citizen scientists from around the world can help to identify species or signs such as nests from images, which has been implemented successfully for primates (Arandjelovic et al., 2016), and also exists for orangutan nest monitoring from images acquired by drones (www.zooniverse.org/projects/sol-dot-milne/orangutan-nest-watch). Approaches using Artificial Intelligence (AI) are further facilitating the fast interpretation of images taken in monitoring missions that yield high output of unprocessed observations.

Observations of additional process variables

Additional variables such as reproductive success, mortality, migration and nutritional status are relevant to species survival. They can also be monitored, depending on the aim of the survey. Throughout Borneo there are efforts to rescue, rehabilitate and translocate orangutans that inhabit areas of ongoing development and were injured, orphaned, kept as pets or causing conflicts with local communities. These activities can have considerable impact on the numbers of orangutan populations. Thus, monitoring of orangutan abundances needs to take these activities into account as well.

Table S1.: Main methods to monitor Bornean orangutans (adapted from Kühl et al., 2008).

Method	Observed sign	Variable measured	Correcting for detectability	Pro /Con	Examples for orangutans
Ground survey	Nests, rarely also orangutans	Presence, distribution, abundance	Distance, Marked Nest Count	Nest count is standard method; Conversion from nest to orangutan numbers, requires nest decay and introduces uncertainty	(Husson et al., 2009; Johnson et al., 2005; Pandong et al., 2018)
Aerial survey (helicopter or drone)	Nest, (orangutans with thermal camera)	Presence, distribution, abundance	Calibration with ground surveys	Increased area sampled; Access to remote areas; Lower effort, high cost; Groundtruthing necessary	(Ancrenaz et al., 2005; Simon et al., 2019; Wich et al., 2015)
Camera traps	Orangutans	Presence, distribution abundance, population structure	Occupancy modeling, Distance	Detection of behavior, habitat use and population dynamics; Will also detect other species; Location of deployment (canopy vs ground) has to be considered	(Ancrenaz et al., 2014; Cappelle et al., 2019; Spehar et al., 2015)
Genetic data	Feces, shed hair	(Minimum) abundance, population structure	Capture-recapture models	Useful to assess population dynamics, past changes in abundance and dispersal; Expensive and small sample sizes	(Banes et al., 2016; Goossens et al., 2006)
Point count or opportunistic data	Nests, orangutan feeding remains, tools	Presence	Occupancy modeling	Rapid assessment of orangutan presence; Can be contributed by citizen scientists; Can include historic records;	(Meijaard et al., 2010; Rijksen and Meijaard, 1999)
Interviews, questionnaire	Account of orangutans	Presence, values and attitude towards orangutans	Time in forest; Ability to distinguish orangutan from other primate species	Useful as preliminary survey or to supplement field studies; Difficult to confirm presence, location and timing; Limited acceptance	(Meijaard et al., 2011b)
Literature review of expeditions	Orangutan encountered or killed	Index of abundance	Size of party and duration of expedition	Unique historic data, Difficult to confirm location, area covered and timing	(Meijaard et al., 2010)

Direct and indirect observations of drivers and threats

Monitoring programs that aim at understanding or managing abundance changes need to include the monitoring of drivers and threats. A range of drivers related to habitat loss, such as deforestation, forest conversion, infrastructure development and other landcover change, can be monitored via remote sensing with high spatio-temporal resolution (Gaveau et al., 2018, 2014; Hansen et al., 2016). Human population density, a proxy for anthropogenic pressures, can be inferred from remote sensing of night-time light (Tan et al., 2018).

Killing for conflict, hunting and live-capture of infants for the pet trade is one of the major threats to orangutan populations. Interviews were crucial to quantify the importance and extent of this threat across Kalimantan (Abram et al., 2015; Davis et al., 2013; Meijaard et al., 2011a). They can also play a vital role in directly assessing socio-economic factors, values and belief systems that drive human behavior influencing species abundance (Meijaard et al., 2011b; Struebig et al., 2018). However, to better understand the prevalence of this threat and to design appropriate conservation actions, additional efforts to improve spatio-temporal resolution are needed. Authorities and conservation organizations are often reluctant to share data on killing, rescue, translocation and release operations. If they do, the quality of the data with regards to location or time often precludes further analysis. In the future, a combination of repeated interview surveys, mining of social media and web pages, as done for the illegal trade of wildlife (e.g., Di Minin et al., 2019), and the collaboration with local conservation organizations and authorities could improve the assessment of spatio-temporal patterns of orangutan killing and live-capture.

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- Wich, S.A., Koh, L.P., 2018. *Conservation drones: Mapping and monitoring biodiversity*. Oxford University Press.

Curriculum Vitae

PERSONAL DATA

Name: Maria Voigt
Nationality: German, Brazilian, US American
Place and date of birth: San Diego, 7th September 1988
Gender: Female
Address: c/o Max Planck Institute for evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig
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EDUCATION AND RESEARCH EXPERIENCE

- 2014-present PhD in Conservation Biology and Primatology** at the Max Planck Institute for evolutionary Anthropology and the German Centre for Integrative Biodiversity Research (iDiv), Halle – Jena – Leipzig, thesis awarded from Martin-Luther-University Halle-Wittenberg, Germany.
Supervisors: Dr. Hjalmar S. Kühl, Prof. Henrique M. Pereira
PhD advisory committee: Prof. Serge A. Wich, Prof. Erik Meijaard, Dr. Marc Ancrenaz, Dr. Isabel M.D. Rosa.
Thesis topic since August 2015 (changed from original topic): Bornean orangutan abundance, drivers of loss, projected habitat loss and monitoring opportunities.
Graduate program: yDiv (12 of 12 credit points completed)
- 2011-2014:** Master's degree (2nd cycle Bologna) in Environmental Management (taught in English), Kiel University
Grade: 1.0 (excellent)
Master Thesis title: "Comparison of tree density estimation methods with a virtual ecologist approach" in collaboration with the Université Libre de Bruxelles, the Vrije Universiteit Brussels, and the Dresden University of Technology, including a 6 month stay in Brussels, Belgium.
Supervisor: Prof. Farid Dadouh-Guebas
- 2013:** Promos-semester in the interuniversity Master program 'Oceans & Lakes', Vrije Universiteit Brussel, University of Ghent and University of Antwerp, Belgium.
Grade: 18 of 20 (excellent)
- 2007-2011:** Bachelor's degree (1st cycle Bologna) in Biology, Dresden University of Technology
Grade: 1.7 (good)
Bachelor Thesis title: "Assessment of natural resource use and socio-economic aspects in a marine reserve in Northeast Brazil", in collaboration with the Leibniz Center for Tropical Marine Ecology and Pará State University, including 3 months of fieldwork in Bragança – Pará, Brazil.
- 2007-2011:** Studies in Regional Sciences of Latin America (Accompanying studies in Portuguese, translation and Brazilian and Hispanic American Studies), Dresden University of Technology, Germany.
Grade: 1.2 (excellent)

January-July 2010: Studies in Biology, University of Brasilia, Brazil.

Grade: 9-10 of 10 (excellent)

August-December 2009: Studies in Ecology, University of São Paulo (UNESP) – Rio Claro, Brazil.

Grade: 73% (good)

OUTREACH AND MEDIA COVERAGE OF RESEARCH

OUTREACH

- **Voigt, M., Wich, S., Kühl, H., et al. (2019).** Roter Affe in den roten Zahlen. Talk at FORUM Unibund 2019 at the Leipzig Book Fair, in Leipzig, Germany.
- **Voigt, M., Wich, S., Kühl, H., et al. (2018).** Roter Affe in den roten Zahlen. Invited talk at an information event of the Borneo Orangutan Survival Foundation in Zürich, Switzerland.
- **Voigt, M., Meijaard E., Wich, S. (2018).** We surveyed Borneo's orangutans and found 100,000 had 'disappeared'. The conversation. <https://theconversation.com/we-surveyed-borneos-orangutans-and-found-100-000-had-disappeared-91944>.

MEDIA COVERAGE

- **Meijaard et al. (2018):** Altmetric score of 240, in the top 5 % of all research outputs scored, with >25 news stories (<https://www.altmetric.com/details/50782472/news>)
Highlights: Interviews with dpa (German press agency) and Deutschlandfunk (German public radio station).
- **Voigt et al. (2018):** Altmetric score of 1966, in the top 5% of all research outputs scored with >225 news stories (<https://altmetric.com/details/3324933/news>).
Highlights: Interviews with newspapers for articles including the Guardian, Reuters, dpa, National Geographics; radio interviews including BBC, American National Public Radio (NPR), Deutschlandfunk; and interviews for television, including 3Sat (German television network), ORF (Austrian national public service broadcaster) and Al Jazeera International (live).

SCHOLARSHIPS AND AWARDS

- **December 2018:** iDiv Science communication award 2018 for public outreach (1,000 €).
- **July 2018:** Conference travel grant awarded by the German Academic Exchange Service (DAAD) for presenting at the atbc conference in Kuching, Malaysia (1,245 €).
- **June 2018:** Career grant for female scientists at iDiv for visiting Prof. Kerrie Wilson's group at University of Queensland (1,207 €).
- **December 2017:** iDiv Shadowing grant for science-policy exchange - visiting the Center for International Forestry Research (CIFOR) in Bogor, Indonesia, Dr. David Gaveau in Bali, Indonesia, and HUTAN-KOCP and Dr. Marc Ancrenaz in Sukau, Malaysia (2,000 €).
- **February – July 2013:** PROMOS scholarship awarded by the German Academic Exchange Service (DAAD) for studies in Belgium, 6 months.
- **March – August 2010:** Scholarship holder in the 'Programa de Iniciação Científica' of the Brazilian National Council of Technological and Scientific Development (CNPq) at the University of Brasilia (Brazil), 6 months.

OTHER ACADEMIC ACTIVITIES

INTERNATIONAL MEETINGS AND WORKSHOPS

- **May 2016:** Orangutan Population and Habitat Viability Assessment in Bogor, Indonesia with scientists, NGOs and industry stakeholders (including talk about Bornean orangutan density distribution, work on habitat models and contribution to report).
- **November 2015** ‘Exploring the earth system data cube’-workshop at Max Planck Institute for Biogeochemistry in Jena, Germany.

GIS SUPPORT

- **2018-2019:** GIS analysis of forest and Bornean orangutan loss within different orangutan meta-populations, provinces and management units for the evaluation of the Bornean orangutan action plan 2007-2017, in collaboration with Julie Sherman, Erik Meijaard and Marc Ancrenaz.
- **May 2016:** GIS analysis of habitat extent and deforestation within different populations for Orangutan Population and Habitat Viability Assessment 2018.

TEACHING AND SUPERVISION

- **October 2015 – March 2016** Supervision of technical assistant to digitize, clean and archive orangutan survey data.
- **October 2012 – February 2013:** Teaching assistant in practical course ‘Plant ecology’ at Kiel University.

ACADEMIC LEADERSHIP

- **2015 – 2017** Student representative in the yDiv board (Graduate school at iDiv), involved in the development of ideas, concepts and strategies of the graduate school.
- **2012 – 2013** Member of the Student government of the master program at Kiel University.
- **2011-2012** Organization of a student run seminar about current topics of environmental research at the ecology center of Kiel University.

Skills


INFORMATICS

- **Remote sensing and GIS:** ArcGIS, QGIS, gdal/ogr2ogr
- **Programming languages:** R, Python, Netlogo, bash, C++ (basic)
- **Databases:** PostgreSQL + PostGIS (basic)
- **Other:** LaTeX, Knitr, git, Microsoft and Libre Office, Inkscape

LANGUAGES

- **German:** Mother tongue
- **English:** Proficient in spoken and written English
- **Portuguese:** Proficient in spoken and independent in written language
- **French:** Basic knowledge

Leipzig, 22.03.2018



Maria Voigt

List of publications and conference participations

Publications of the dissertation

- **Voigt, M.**, Pereira, H. M., Ancrenaz, M., Bowler, D., Meijaard, E., Navarro, L. M., Sherman, J., Kühl, H. S., Wich, S. A. *in preparation for Journal of Applied Ecology*. Challenges and opportunities for monitoring a charismatic species in the tropics - integrating data and stakeholders.
- **Voigt, M.**, Pereira, H. M., Kühl, H. S., Ancrenaz, M., Gaveau, D. L. A., Meijaard, M., Santika, T., Sherman, J., Struebig, M. J., Wich, S. A., Wolf, F., Rosa, I. M. D. *in preparation for Global Change Biology*. Deforestation projections imply range-wide population decline for critically endangered Bornean orangutan
- Meijaard, E., Sherman, J., Ancrenaz, M., Wich, S.A., Santika, T., **Voigt, M.**, 2018. Orangutan populations are certainly not increasing in the wild. *Current Biology* 28, R1241–R1242.
- **Voigt, M.**, Wich, S.A., Ancrenaz, M., Meijaard, E., Abram, N., Banes, G.L., Campbell-Smith, G., d’Arcy, L.J., Delgado, R.A., Erman, A., Gaveau, D., Goossens, B., Heinicke, S., Houghton, M., Husson, S.J., Leiman, A., Llano Sanchez, K., Makinuddin, N., Marshall, A.J., Meididit, A., Miettinen, J., Mundry, R., Musnanda, Nardiyono, Nurcahyo, A., Odom, K., Panda, A., Prasetyo, D., Priadjati, A., Purnomo, Rafiastanto, A., Russon, A.E., Sihite, J., Spehar, S., Struebig, M.J., Sulbaran-Romero, E., Wilson, K.A., Kühl, H.S., 2018. Global demand for natural resources eliminated more than 100,000 Bornean orangutans. *Current Biology* 28, 761–769.

Peer-reviewed publications

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- **Voigt, M., Wich, S., Kühl, H., et al. (2018)**. Roter Affe in den roten Zahlen, was wir über den Rückgang der Borneo Orang-Utans wissen. Lecture in a series on applied nature conservation at the University of Würzburg, Germany.
- **Voigt, M., Wich, S., Kühl, H., et al. (2018)**. The red ape in the red. Annual meeting of the association for tropical biology and conservation (atbc) in Kuching, Malaysia.
- **Voigt, M., Wich, S., Kühl, H., et al. (2017)**. Consumption, conservation and orangutans. iDiv Annual conference, Leipzig, Germany.
- **Voigt, M., Heinicke, S., Wich, S., Kühl, H., et al. (2015)**. Determining the influence of socio-economic conditions on the range-wide density distribution of two African and Asian ape taxa. iDiv Annual conference, Leipzig, Germany.
- **Voigt, M., Dahdouh-Guebas, F., Grütters, U., et al. (2014)**. Comparison of density estimators in coastal populations using a modelling approach. (Poster) VLIZ Young Marine Scientists' Day 2014, Bruges, Belgium.

Authors' contribution

Chapter 2: Voigt, M., Wich, S.A., Ancrenaz, M., Meijaard, E., Abram, N., Banes, G.L., Campbell-Smith, G., d'Arcy, L.J., Delgado, R.A., Erman, A., Gaveau, D., Goossens, B., Heinicke, S., Houghton, M., Husson, S.J., Leiman, A., Llano Sanchez, K., Makinuddin, N., Marshall, A.J., Meididit, A., Miettinen, J., Mundry, R., Musnanda, Nardiyono, Nurcahyo, A., Odom, K., Panda, A., Prasetyo, D., Priadjati, A., Purnomo, Rafiastanto, A., Russon, A.E., Sihite, J., Spehar, S., Struebig, M.J., Sulbaran-Romero, E., Wilson, K.A., Kühl, H.S., 2018. Global demand for natural resources eliminated more than 100,000 Bornean orangutans. *Current Biology* 28, 761–769.

Data compilation, cleaning and curation: Voigt, M. (60%), Wich, S.A. (25%), Ancrenaz, M. (1%), Meijaard, E. (1%), Abram, N., Banes, G.L., Campbell-Smith, G., d'Arcy, L.J., Delgado, R.A., Erman, A., Gaveau, D., Goossens, B., Houghton, M., Husson, S.J., Leiman, A., Llano Sanchez, K., Makinuddin, N., Marshall, A.J., Meididit, A., Miettinen, J., Musnanda, Nardiyono, Nurcahyo, A., Odom, K., Panda, A., Prasetyo, D., Priadjati, A., Purnomo, Rafiastanto, A., Russon, A.E., Sihite, J., Spehar, S., Struebig, M.J., Sulbaran-Romero (10%), K.A., Kühl, H.S. (3%)

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Writing: Voigt, M. (75%), Wich, S.A. (5%), Ancrenaz, M. (3%), Meijaard (3%), E., Abram (corrections), N., Banes (corrections), G.L., Goossens, B. (corrections), Heinicke, S. (3%), Houghton S.H. (corrections), Marshall, A.J. (corrections), Miettinen, J. (corrections), Mundry, R. (3%), Russon, A.E. (corrections), Struebig, M.J. (3%), Sulbaran-Romero, E. (corrections), Wilson, K.A. (corrections), Kühl, H.S. (5%)

Chapter 3: Voigt, M., Pereira, H. M., Kühl, H. S., Ancrenaz, M., Gaveau, D. L. A., Meijaard, M., Santika, T., Sherman, J., Struebig, M. J., Wich, S. A., Wolf, F., Rosa, I. M. D. Deforestation projections imply range-wide population decline for critically endangered Bornean orangutan

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Chapter 4: Meijaard, E., Sherman, J., Ancrenaz, M., Wich, S.A., Santika, T., **Voigt, M.**, 2018. Orangutan populations are certainly not increasing in the wild. *Current Biology* 28, R1241–R1242.

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Chapter 5: **Voigt, M.**, Pereira, H. M., Ancrenaz, M., Bowler, D., Meijaard, E., Navarro, L. M., Sherman, J., Kühl, H. S., Wich, S. A. Challenges and opportunities for monitoring a charismatic species in the tropics - integrating data and stakeholders.

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Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „Red ape in the red–abundance, threats and conservation“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Leipzig, den 22.03.2019



Maria Voigt

The End

