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BIODIVERSITY RESEARCH

Mapping perceptions of species' threats and population trends to inform conservation efforts: the Bornean orangutan case study

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ABSTRACT

Aim We demonstrate a robust approach for predicting and mapping threats and population trends of wildlife species, invaluable for understanding where to target conservation resources. We used the endangered Bornean orangutan (*Pongo pygmaeus*) as our case study to facilitate and strengthen conservation efforts by the Indonesian government to stabilize populations by 2017.

Location Kalimantan, Indonesian Borneo.

Methods Local knowledge of threats to orangutan populations was gathered through questionnaire interviews in 531 villages (512 in Kalimantan) within known orangutan range. These data were integrated with 39 environmental/socio-economic spatial variables using boosted regression tree modelling to predict threat levels and population trends across Kalimantan and to identify key combinations of threats and trends that can help to direct appropriate conservation actions.

Results Nineteen percentage of villages surveyed in Kalimantan reported human–orangutan conflicts. High-predicted conflict likelihood was extensive, strongly associated with road density (very low or high) and temperature seasonality. Recent orangutan killings were reported in 23% of villages. High killing risk was highly associated with greater surrounding orangutan habitat and for villages more than 60 km from oil palm plantations. Killings by respondents were reported in 20% of villages with higher likelihoods associated with greater range in rainfall and temperature, and higher proportion of Christian believers. Orangutan populations were predicted to decline/become locally extinct across the majority of their range in Kalimantan over the next decade, with few regions predicted to support stable populations.

Main conclusions Human–orangutan conflicts and killings occur extensively in Kalimantan, with many populations at risk of decline or localized extinctions. Effective conservation actions are therefore urgently needed. Our approach better informs conservation managers in understanding the extent, spatial patterns and drivers of threats to endangered species such as the orangutan. This is essential to better design management strategies that can minimize or avert the species' decline.

Keywords

Boosted regression tree modelling, conservation planning, Indonesian Borneo, mapping human–wildlife conflict and hunting, mapping population trends, questionnaire surveys.

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INTRODUCTION

Human-induced wildlife mortality is one of the main threats to biodiversity conservation (Rowcliffe *et al.*, 2005; Hoffmann *et al.*, 2010). The International Union for Conservation of Nature (IUCN) lists 26% (17,106) of all known species as globally threatened through unsustainable 'use' (IUCN, 2012). Overexploitation drives the decline of populations and without effective management can result in local or global extinctions. Policies that aim to prevent or limit exploitation can be challenging to implement and enforce, especially if wildlife is killed illegally by communities in rural areas (Natusch & Lyons, 2012). Understanding localities and intensity/extent of such threats to wildlife could help reduce mortality rates by targeting conservation efforts to priority areas.

However, mapping patterns of threats across a species range is complicated, especially for protected species and if trying to obtain information on illegal behaviours (Tourangeau & Yan, 2007). It can also be costly and logistically challenging, for example, to implement ecological monitoring programmes over large spatial scales. Moreover, determining threats such as killing rates is difficult as assessments are usually scale dependent, and understanding spatial variation in such rates requires significant field work (Levi *et al.*, 2011). Several methods exist for spatial modelling of threats. However, generally they require the analysis of proxies such as road and market access for bushmeat (Clayton *et al.*, 1997), landscape features within hunting catchments (Mockrin *et al.*, 2011), and the distribution and density of snares or use of biodemographic applications (Levi *et al.*, 2011). These proxies are rarely well quantified for large areas, thereby resulting in localized information only. Nevertheless, conservation planning for threatened species requires spatially explicit information on threats and population trends throughout the species' range – at sufficiently fine scales – to better promote conservation effectiveness.

In this study, we introduce a robust method using spatially explicit modelling for mapping threats and population trends for threatened species. We employ the Bornean orangutan (*Pongo pygmaeus*) as our case study species. Orangutans exemplify the challenges faced by wildlife authorities and conservation practitioners in attempting to reduce threats from direct harm and habitat losses. The Bornean orangutan, found in Indonesia and Malaysia on Borneo, is fully protected by law, yet is persecuted throughout its range at differing levels of severity, driving population declines and local extinctions (Meijaard *et al.*, 2011b; Wich *et al.*, 2012a). Recent studies have provided insights into: villagers' perceptions of human–orangutan interactions (Meijaard *et al.*, 2011a); estimates of the frequency of killings (Meijaard *et al.*, 2011b); and reasons for conflict and killings at individual and village levels (Davis *et al.*, 2013). Population viability analyses for orangutans indicate that extrinsic mortality rates of > 1% per year will result in population extinction (Marshall *et al.*, 2009). Yet surveys suggest these rates are exceeded in many parts of the orangutans' range (Meijaard *et al.*, 2011b). Indonesia has announced a goal of stabilizing all wild orangutan populations by 2017 (Soehartono *et al.*, 2007). To achieve this will require reducing illegal killings concurrently with reducing habitat loss. Therefore, understanding the social and environmental predictors of conflicts and killings across the species' range, along with indications of population stability/declines, is vital for informing conservation efforts and targeting finite resources.

This study contributes to our understanding of these questions by analysing local people's perceptions on the frequency of seeing orangutans, human–orangutan conflicts, orangutan killings and orangutan population trends across the Bornean orangutan range in Kalimantan (Indonesian Borneo). We integrate this information with interdisciplinary spatial data to generate predictive maps of threats and population trends across the ranges of the three subspecies of Bornean orangutan and interpret the emergent combinations of threats and population trends. These outputs aim to enhance our knowledge and understanding of spatial patterns and trends that lead to orangutan population decline across the landscape and to facilitate targeting conservation efforts, fulfilling a knowledge gap for orangutans (Soehartono *et al.*, 2007). Additionally, this study aims to advance methodological approaches used for mapping and understanding human-induced threats to wildlife and population dynamics.

METHODS

Ethics statement

We conducted questionnaire-based interviews with villagers to collect data on perceptions of human–orangutan interactions. Surveys were led by The Nature Conservancy (TNC), and methods and questionnaires were reviewed and approved by their social scientists. Overall, 21 non-governmental organizations (NGOs) were involved in conducting the surveys, 20 in Kalimantan and one in Sabah (Malaysia). Prior and informed consent was obtained for all respondents, after the project goal had been explained and confidentiality assured. Permission to conduct this research was granted by the Indonesian Directorate General of Forest Protection and Nature Conservation, and the Director of the Sabah Wildlife Department.

Sampling regime

Questionnaire surveys were undertaken in villages within or close to forest with known breeding populations of all three orangutan subspecies: *P. p. morio* in East Kalimantan and Sabah; *P. p. wurmbi* in Central Kalimantan; and *P. p. pygmaeus* in West Kalimantan and Sarawak (Fig. 1). The number of interviews per village ranged from 7 to 11, to enable sampling of hundreds of villages over a wide geographical area.

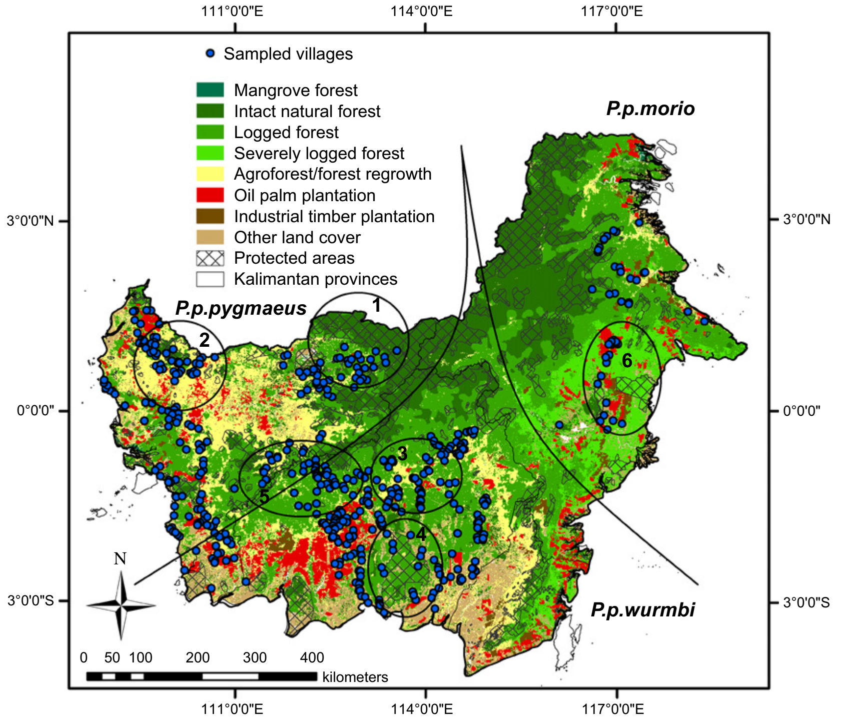

Figure 1 Location of the 512 sampled villages (blue circles) in Kalimantan conducted in 2008, 2009 and 2012, shown on a base map of 2010 land cover with protected areas (cross-hatched) and the four provinces (West, Central, South and East). Circled areas relate to numbered regions, and black lines dissecting the landscape indicate the range of the three subspecies of the Bornean orangutan (*Pongo p. pygmaeus*; *P. p. morio*; *P. p. wurmbi*) in Kalimantan, Indonesian Borneo.

Further details of sample design for village and respondent selection are given in Meijaard *et al.* (2011b).

Surveys were conducted in two waves: from April 2008 to September 2009 (6983 respondents in 687 Kalimantan villages and 145 respondents in 15 villages in Sabah) and the second in 2012 (236 respondents in 23 new villages in Kalimantan and 56 respondents in six villages in Sabah). The dataset was screened for reliability, and interviews from teams that recorded brief or possibly replicated responses were excluded. We also excluded respondents who were unable to identify an orangutan (Meijaard *et al.*, 2011b, 2013). This was assessed by asking respondents to identify nine mammal species from photographs that included the Bornean orangutan and two other primate species, the red langur (*Presbytis rubicunda*), a species similar in colour, and the Bornean gibbon (*Hylobates muelleri*). We used data from reliable respondents, that is those who correctly identified orangutans from all other species and accurately identified either the red langur or Bornean gibbon, or both. Respondent reliability was also cross-validated with responses from other questions; respondents who gave incompatible responses were excluded.

The dataset for generating predictive models included all reliable respondents (n = 4839) in 531 villages (512 villages in Kalimantan and 19 in Sabah). We present results with a focus on Kalimantan (i.e. descriptive statistics based on 512 villages in Kalimantan and predictive mapping for Kalimantan generated from modelling of the full dataset of 531 villages) with a view to inform the Indonesian orangutan action plan 2007–2017 within Kalimantan (Soehartono *et al.*, 2007).

Survey data and response variables

In the questionnaire, forty questions/subquestions addressed interactions with orangutans close to the village (for questionnaire see Meijaard *et al.*, 2011a). These questions related to the respondent's encounters with orangutans; number of orangutans seen in the previous year and location of sightings; knowledge of orangutans entering respondents' gardens; crop raiding frequency; and respondents' reactions to encounters. Questions were asked about orangutans killed in the area over differing time periods, number of orangutans the respondents had killed and reasons for killing. Respondents were asked about their perceptions of past and future changes in orangutan populations and their knowledge of national and customary laws relating to orangutans. Questions were coded into continuous response variables originally at the respondent level then condensed to village level as averages to match the spatial scale of predictor variables.

Within these response variables, there were two potential sources of zero or 'absence' responses: (a) absence of conflict/killings where orangutans are present and (b) absence of conflict/killings potentially due to the absence of orangutans within the local vicinity. Our principal models assume the former (that orangutans are potentially present), because only villages within the known range of the Bornean orangutan were surveyed, and because it is possible that orangutans are present even if not encountered by the village respondents. However, to account for the possibility of (b), we also modelled conflict and killings for a subset of the data, consisting of villages where orangutan(s) had been seen in the year prior to the survey (Figure S2 in Supporting

Information). Models based on this subset were developed for two response variables (likelihood of human–orangutan conflict and orangutan killings around villages within the last year, described below).

Orangutan sightings and conflict

To determine the frequency and location of orangutan sightings, respondents were asked to indicate the number and location (in forest, garden/farm or on the road) of orangutans seen in the past year.

The human–orangutan conflict index was based on the frequency of orangutans entering people's gardens and crop raiding their fruit trees. Four options were provided for the respondents to choose from the following: every week/every month (coded as 2) and once a year/rarely (coded as 1). To gauge respondents' reactions to encounters with orangutans, responses were provided and coded according to the severity of reaction ranging from the following: killing the animal (coded as 2); scaring or chasing the animal (coded as 1); and other or unknown (coded as 0). Recoded values were summed to create an index, and this was '0' if respondent's sum of represents no conflict; ≤ 3 low conflict (orangutans enter gardens infrequently and respondents scare/chase them away); and ≥ 4 high conflict (high frequency of orangutans entering gardens and/or reported reaction of respondents is to kill the orangutans).

Orangutan killings

To understand the prevalence and spatio-temporal patterns of orangutan killings, respondents were asked by whom and when orangutan killings had occurred. The first question focused on when the last orangutan killings took place: in the last week/in the last month (coded as 4); in the last year (coded as 3); in the last 5 years (coded as 2); more than 5 years ago (coded as 1); or don't know (coded as 0). Respondents were also asked to provide the number of orangutans killed in the region of their village within the last year. To gain insight into whether the respondent had themselves killed any orangutans, they were asked to report the number of orangutans they had killed in their lifetime. Respondents may have been reluctant to disclose this information (although assurances were given of confidentiality and absence of repercussions). If such biases occurred, this would presumably underestimate true numbers, and so we regarded these responses as minimum estimates.

Orangutan population trends

To gain insights into temporal trends of local orangutan populations, the respondents were asked to indicate the current number of orangutans in the region compared to 10 years ago and their anticipated trends for the coming 10 years. Respondents were asked to choose from four answers comparing population numbers for the past and future time periods: 'more than now' (coded as 1); 'same as now'(coded as 2); 'fewer than now'(coded as 3); 'locally extinct'(coded as 4); and 'never seen orangutans here' or people say there are no orangutans (coded as 5) (i.e. the respondent does not know or the respondent thinks the species is locally extinct), and 'other or unknown' responses were coded as 0.

Environmental and socio-economic spatial predictor variables

We developed a spatial data framework for our analysis of 39 predictor variables (at continuous, 1 km^2 grid cell resolution) that were regarded as potentially important environmental or human predictors, based on previous analyses of the interview surveys (Davis *et al.*, 2013; Meijaard *et al.*, 2013). Spatial predictor variables fell into the broad categories of the following: (1) orangutan habitat; (2) land use and land cover; (Gaveau *et al.*, 2014) (3) climate and topographical variables; (4) accessibility; and (5) socio-economic factors. For brief descriptions and codes of these, see Table 1. Details of all predictor variables are provided in Appendix S1 and Table S1. Correlations between the 39 predictor variables were calculated, using the full spatial dataset (n = 85,759 pixels).

Predictive modelling

Response variables for spatial modelling consisted of the following: (1) frequency of orangutan sightings; (2) human–orangutan conflict index; (3) reported killings of orangutans; and (4) perceptions of orangutan populations. Village coordinates, taken with a global positioning system (GPS) at the centre of each surveyed settlement, were imported into a geographic information system (GIS) along with the 39 spatial predictor variables. Values for each of the 39 variables were extracted for each settlement, using the 'sample' tool in ArcGIS 10, and used within the statistical modelling. Respondent's values were averaged at the village level and were treated as continuous response variables in the statistical analyses. Correlations were calculated between each pair of the six response variables at the village level.

Boosted regression trees (BRT) were used to develop predictive models, as this method enables sophisticated regression analyses of complex responses, allowing for high predictive performance (Elith *et al.*, 2006, 2008). BRTs fit multiple regression tree models, enabling the selection of important variables based on their contributions over the full ensemble of models. Additionally, BRTs can handle continuous and other variable types, correlated variables, can fit complex interactions between variables, employ cross-validation to optimize bias–variance trade-offs and, through boosting, can overcome issues of model instability and lack of accuracy (Friedman & Meulman, 2003). The BRT models were fitted in R version 2.15.0 (R Core Team, 2013) using the functions 'gbm' and 'gbm.step' in the 'dismo' package (Hijmans *et al.*, 2013). The following specifications were used: a continuous response variable with a Laplace

Table 1 Summary of the 39 spatial predictor variables (layers) used in the boosted regression tree models, used to predict conflict, killing and population trends of the Bornean orangutan (*Pongo pygmaeus*), with each layer's abbreviations and general category.

Category	Spatial predictor layers	Abbreviations
Land cover/Land use	Distance to mangrove	mangrove_m
	Summed cover of mangroves in neighbouring grid cells	mangrove_s
	Distance to intact natural forest	intact_m
	Summed cover of intact natural forest in neighbouring grid cells	intact_s
	Distance to logged forest	logged_m
	Summed cover of logged forest in neighbouring grid cells	logged_s
	Distance to severely degraded logged forest	svlogged_m
	Summed cover of severely degraded logged forest in neighbouring grid cells	svlogged_s
	Distance to agroforests/forest regrowth	agroregr_m
	Summed cover of agroforest/forest regrowth in neighbouring grid cells	agroregr_s
	Distance to industrial timber plantation	indtim_m
	Summed cover of industrial timber plantation in neighbouring grid cells	indtim_s
	Distance to oil palm plantations	oilpalm_m
	Summed cover of oil palm plantations in neighbouring grid cells	oilpalm_s
	Distance to other land cover	otherlc_m
	Summed cover of other land cover in neighbouring grid cells	otherlc_s
	Distance to protected area	pa_m
	Summed cover of protected areas in neighbouring grid cells	pa_s
Carbon	Summed cover of carbon in neighbouring grid cells	carbon_s
Orangutan range	Distance to orangutan range	ou_m
	Summed cover of orangutan range in neighbouring grid cells	ou_s
Topography	Elevation	elevation
	Ruggedness	ruggedness
	Distance to rivers	rivers_m
	River density	river_d
Climate	Temperature seasonality	temp_seaso
	Temperature annual range	temp_annra
	Precipitation seasonality	prec_seaso
	Annual precipitation	prec_annra
Infrastructure	Impermeable surface area (%)	impervious
	Road density	road_d
	Settlement density	settlemt_d
Accessibility	Accessibility sum (road, river, foot)	access_sum
	Accessibility 10 (road, river, foot)	access_10
Population	Population (Land scan)	pop_2007
Wealth	Poverty index	poverty
Culture	District population % who follow Islam	islam
	District population % who are Christian	christian
	Ethnic groups	ethnic_gp

distribution (absolute deviation); maximum 5000 trees with an interaction depth of 3 (including multiway interactions); bagging fraction of 0.5 (50% random samples used for fitting the trees); training fraction of 0.8 (20% data reserved for independent model testing); and fivefold cross-validation. Predictive performances of the models were assessed using the correlation between observed and predicted values.

Mapping model outputs

Response variables were imported into ArcGIS 10 (ESRI), and using a 1-km^2 grid-mask, mapped, then classified into tertiles (equal number of observations in each class). We present maps for Kalimantan only and restrict outputs to the following: (1) areas of known orangutan populations (Wich *et al.*, 2012b) with a 10-km buffer to allow for possible omission error in the distribution map and (2) areas with 'forest' cover, using a 2010 forest extent layer for Kalimantan (which included natural forest and agroforest/regrowth classes) described in Gaveau *et al.* (2013). To facilitate discussions on the mapped BRT outputs, we highlighted five regions in Kalimantan and related our main findings to these areas. These regions encompassed *P. p. pygmaeus* range in West Kalimantan province, close to the Sarawak boarder within and surrounding Betung Kerihun and Danau Sentarum National Parks (NP) (region 1), and the lowlands of West Kalimantan that encompass Gunung Niut Nature Reserve (region 2). Regions in *P. p. wurmbi* range included north of Sebangau

NP (region 3); within and north-east of Sebangau NP (region 4); and within both *P. p. pygmaeus* and *P. p. wurmbi* ranges along the West and Central Kalimantan border surrounding Bukit Baka and Bukit Raya NP (region 5). In East Kalimantan and in *P. p. morio* range, the region discussed is within and surrounding Kutai NP (region 6) (Fig. 1).

RESULTS

Orangutan sightings and conflict

Of the 512 villages surveyed in Kalimantan, 48% (n = 245) reported seeing orangutans around their village in the year prior to the survey. The BRT model for orangutan sightings performed well (Fig. 2a, Table 2). The likelihood of seeing an orangutan was greater in the following: low road density areas (the strongest associated variable), further from oil palm (> 60 km) and with increasing surrounding (logged) forest (Fig. 3a). Orangutan sighting likelihood was predicted high in regions 1, 4, 5 and parts of 3 and 6 (Fig. 4a).

Nineteen percentange of villages (n = 99) in Kalimantan reported human–orangutan conflicts. The human–orangutan conflict model performed well (Fig. 2b, Table 2) with higher predicted conflict in areas of very low or high road densities (showing a 'U'-shaped relationship), nearer to severely logged forests in regions with greater temperature seasonality (standard deviation of > 4.5°C) and precipitation < 2000 mm per year (Fig. 3b). Areas of high conflict potential were predicted for regions 1, 4 and 6 (Fig. 4b). The subset data conflict model (n = 245) had 80 (33%) villages that reported conflicts (Appendix S3), performing slightly better than the full dataset model, and largely influenced by the same spatial variables (Figures S3a & S4a, Table S2). Spatial predictions of conflict likelihood were also similar to the full dataset model, although they showed more moderate conflict risk in and around region 5 (Figure S5a).

Orangutan killings

Overall, 23% (n = 116) of villages in Kalimantan reported that one or more orangutans had been killed around the village in the year prior to survey (Figure S1). The BRT model showed moderate performance (Fig. 2c) with killing occurrences increasing with distance from village to the following: oil palm plantations (> 60 km from plantations), agroforests/forest regrowth (> 70 km); and other land cover types > 20 km), and greater surrounding orangutan habitat (Fig. 3c). The mapped output of this model infers high killing patterns in regions 1, 4, 5 and 6 (Fig. 4c). The subset data model (n = 245 villages) had 87 (36%) villages with

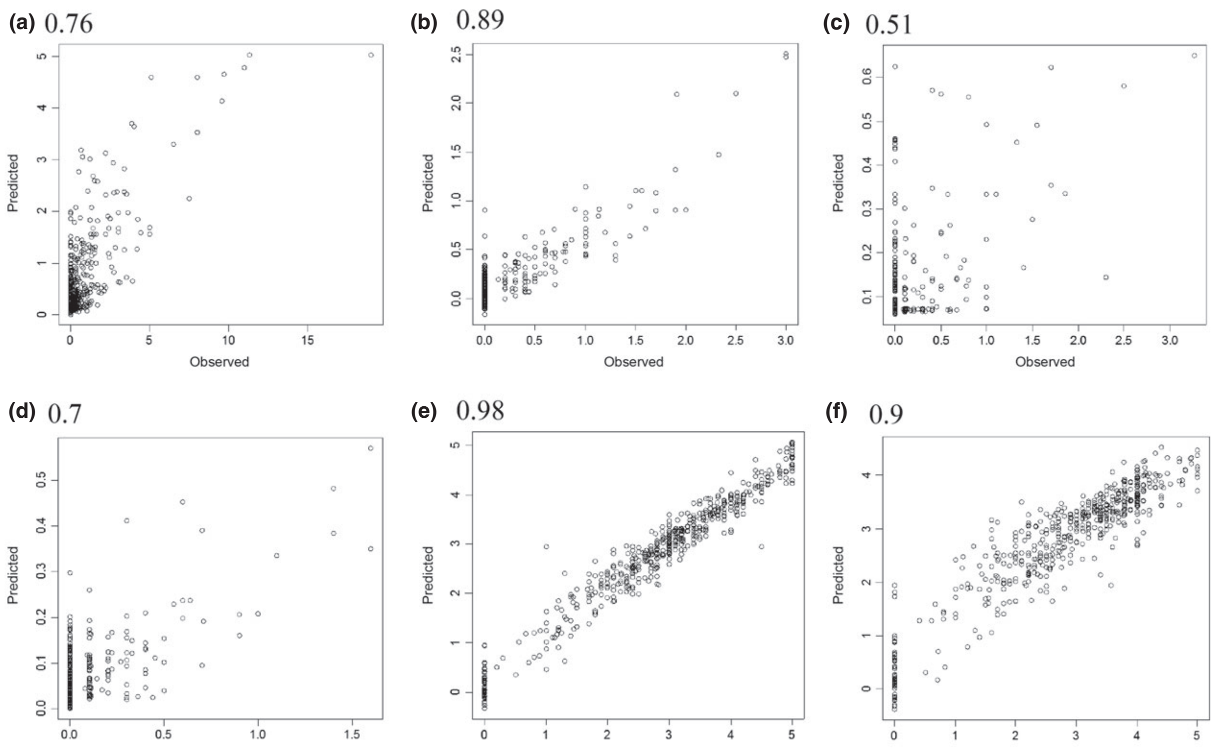

Figure 2 Correlations of goodness-of-fit and plots between observed and predicted responses for the six boosted regression tree models for the following: (a) likelihood of orangutans seen in the last year; (b) likelihood of human–orangutan conflict risk; (c) likelihood of orangutan killings occurring within 1 year prior to the surveys, by anyone in the village; (d) likelihood of orangutan killings by respondents within their lifetime; (e) villagers' perceptions of changes in orangutan populations 10 years ago compared to the time of the interview; and (f) villagers' perceptions of likely future changes in orangutan populations over the next 10 years, compared to the time of interview.

Table 2 Boosted regression tree models top 10 most influential spatial variables, their percentage contribution (%) and the summed total percentage of these top 10 variables.

Likelihood of								Perception of orangutan population			
Seeing an orangutan	%	Human–orangutan conflict	%	Orangutan killings around villages	%	Orangutan killings by respondents	%	Now compared to 10 years ago	%	In next 10 years compared to now	%
road_d	22	road_d	15	oilpalm_m	43	prec_annra	11	ethnic_gp	13	ethnic_gp	15
indtim_m	14	temp_seaso	14	ou_s	16	christian	9	indtim_m	7	prec_annra	8
logged_s	10	svlogged_m	9	otherlc_m	7	temp_annra	9	settlemt_d	7	settlemt_d	8
oilpalm_m	8	prec_annra	7	agroregr_m	7	ou_s	9	svlogged_m	6	logged_s	6
ou_s	7	pa_m	6	elevation	6	road_d	7	road_d	6	pa_s	6
christian	6	oilpalm_s	4	prec_annra	4	svlogged_m	7	prec_annra	5	carbon_s	6
svlogged_m	6	temp_annra	3	temp_annra	3	otherlc_m	6	mangrove_m	5	prec_seaso	5
prec_seaso	5	indtim_m	3	indtim_m	2	ou_m	4	ou_m	4	svlogged_m	4
logged_m	3	otherlc_s	3	road_d	2	islam	4	prec_seaso	4	access_sum	3
prec_annra	2	agroregr_m	3	pa_m	2	temp_seaso	4	pa_m	4	access_10	3
Total	83	Total	67	Total	92	Total	70	Total	61	Total	64

For explanation of codes, see Table 1.

reported orangutan killings in the year prior to survey (Figure S2). Model performance was similar to the full data-set model and largely influenced by the same principal spatial variables (Figures S3b & S4b, Table S2). High killing likelihood, however, was far less extensive and was largely restricted to region 5 (Appendix S3, Figure S5b).

In 20% (101) of surveyed villages in Kalimantan, at least one respondent reported killing an orangutan(s) in their lifetime, with the corresponding BRT model performing well (Fig. 2d, Table 2). Killing likelihood increased in areas where Christians form a higher proportion of the population (> 40% threshold) and in areas with more orangutan habitat, as well as ≥ 3400 mm annual precipitation and > 9.5 °C annual range in temperature (Fig. 3d). The likelihood of killings by respondents was high in regions 1 and 5, and several smaller areas (Fig. 4d).

Orangutan population trends

Thirty-six percentage (184) of villages in Kalimantan reported that orangutan populations had declined in the past decade; 21% (110) said orangutans were no longer present; 32% (163) reported no change; and 11% (55) reported they had never seen an orangutan in the area. The BRT model on perceptions of current orangutan populations compared to 10 years ago had excellent performance (Fig. 2e, Table 2). High likelihood areas of orangutan population decline within the past decade (possibly gone locally extinct) were associated with Ibanic, Kenyakh, Land Dyak/Western, Malay, Ngaju/Barito and nomadic ethnic groups, < 10 km from industrial timber plantations, in low settlement density areas, with higher road densities (Fig. 3e). Areas where orangutan populations may have gone locally extinct included parts of regions 2, 3, 5 and 6, whilst the majority of areas were predicted with local population declines, with few regions (e.g. 1 and 4) predicted to have stable populations (Fig. 4e).

Thirty-two percentage (163) of villages in Kalimantan predicted fewer orangutans in the next decade, whilst 33% (168) said orangutans would be locally extinct. The corresponding BRT model performed very well (Table 2) with the likelihood of local orangutan populations declining (or possibly going extinct) in the near future being higher in regions associated with Ibanic, Kenyakh, Land Dyak/Western, Malay, Ngaju/Barito and nomadic ethnic groups, in areas of lower (< 3600 mm) annual precipitation, fewer settlements and greater surrounding extent of logged forests (Fig. 3f). Decreasing/extinct local populations were predicted in regions 2, 3 and 4 and widespread throughout much of Kalimantan (Fig. 4f). Few areas were predicted to have stable or increasing populations, for example region 1, in part 5 and in the far western coastal flats, and at the Sabah border (Fig. 4f).

Correlations among predictor variables and among modelled responses

Several strong/moderate correlations were identified between the 39 spatial predictor variables, shown in Table S5 and

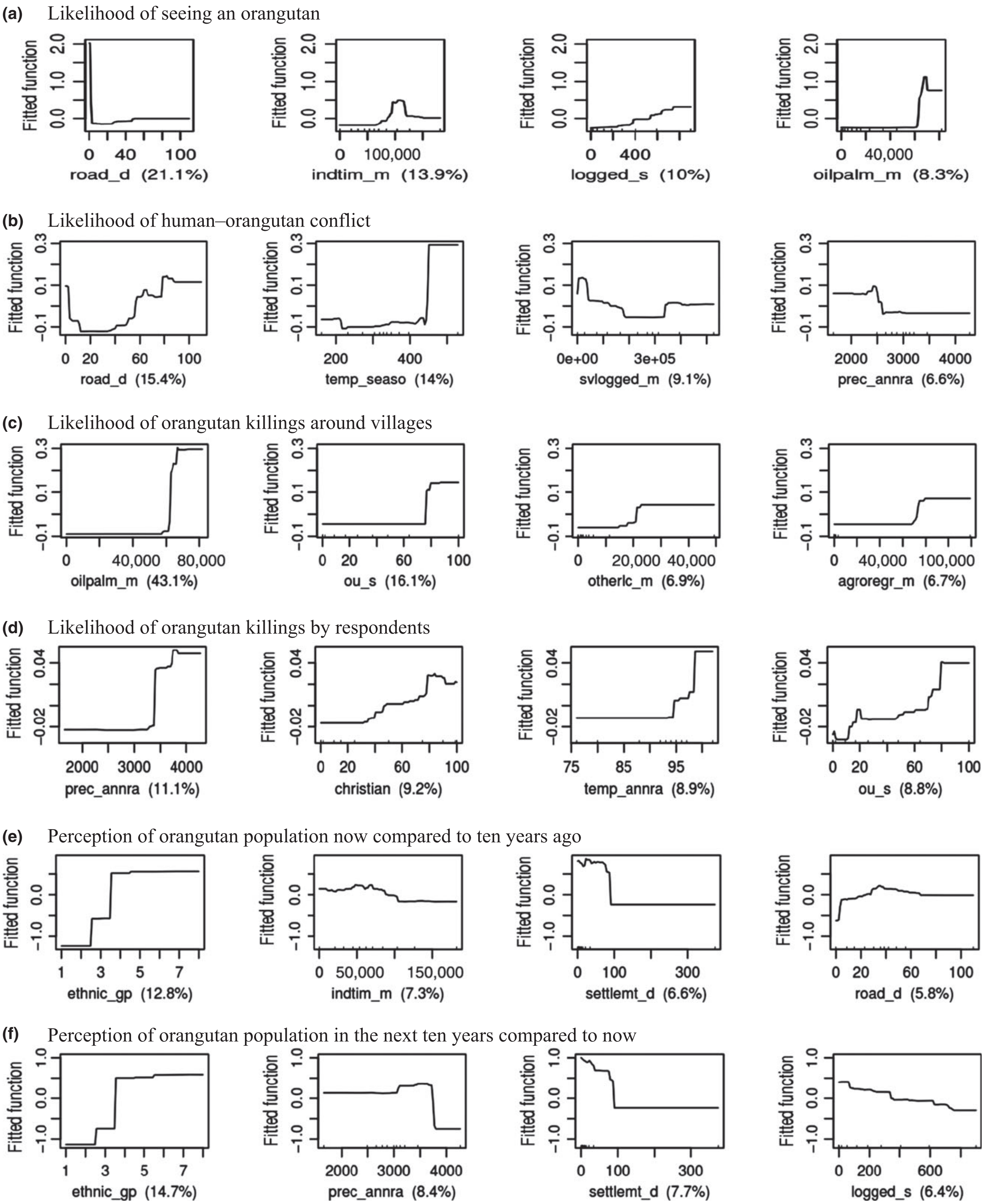

Figure 3 Plots for the top four most influential spatial predictor variables within the six boosted regression tree (BRT) models that relate to perceptions of human–orangutan interactions and orangutan population trends. Plots show the effect of spatial predictors on the respondent's response variable with relative importance values for each variable shown in parentheses on the *x*-axis.

described in Appendix S4. Predictions between the six BRT models (full dataset) showed only weak or no correlations across the models, with the exception between the orangutan sightings and orangutan killing around the village in the year prior to survey, and between the two population trends models (Table S3).

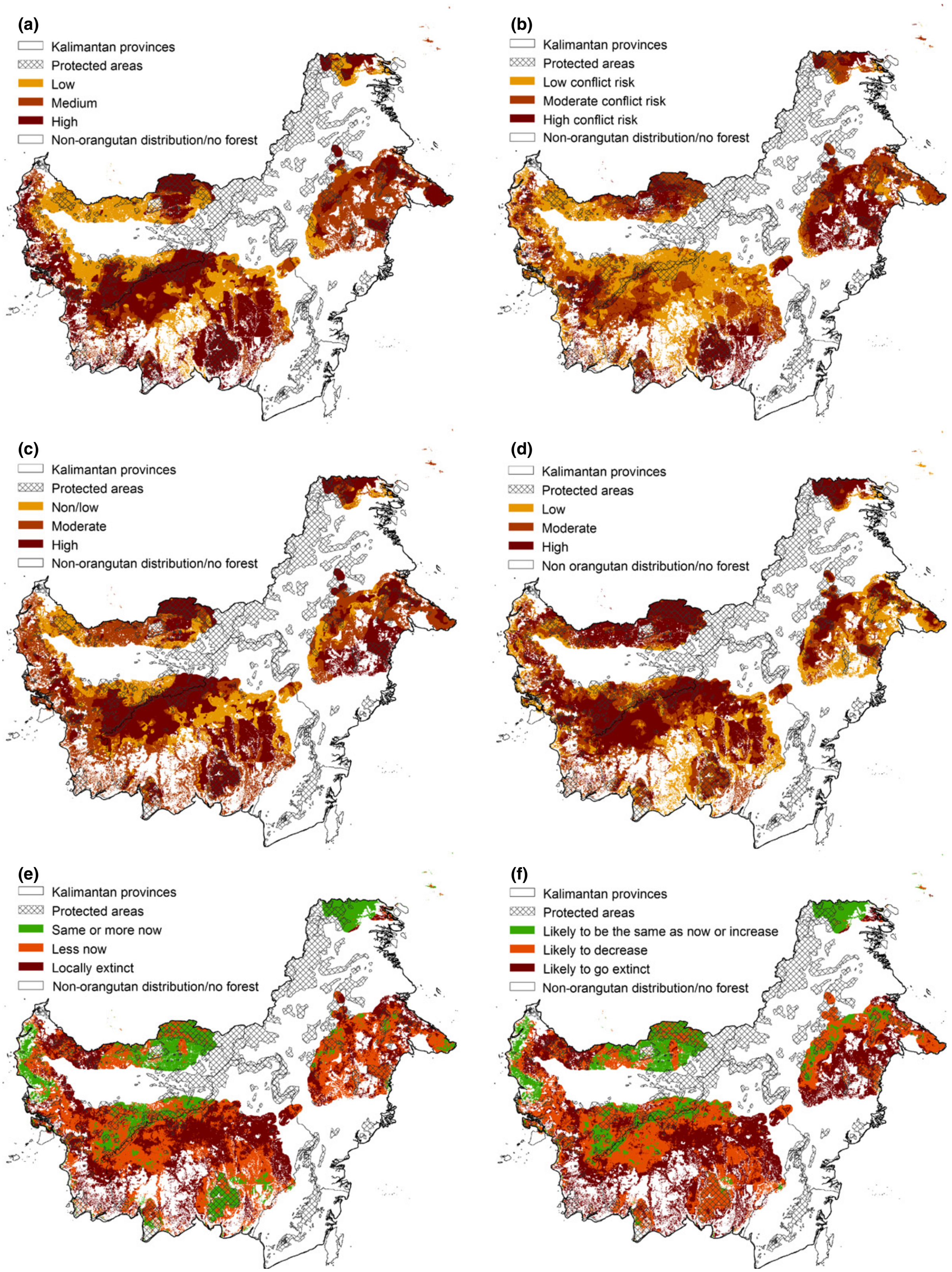

Figure 4 Mapped outputs from six boosted regression tree models (based on interviews from 513 villages) overlaid with protected areas (hatched) and provinces (black line). Each map shows the predicted likelihood of a given response mapped as tertiles for the likelihood of the following: (a) seeing an orangutan in the last year; (b) human–orangutan conflict risk; (c) orangutan killings occurring in the year prior to the surveys by anyone in the village; (d) orangutan killings by respondents within their lifetime, as well as (e) villagers' perceptions of changes in orangutan populations 10 years ago compared to the time of the interview; and (f) villagers' perceptions of likely future changes in orangutan populations over the next 10 years, compared to the time of interview.

DISCUSSION

It is likely that many orangutan populations will disappear in forthcoming decades unless threats are abated (Meijaard *et al.*, 2012). In our analyses, many areas of Kalimantan were predicted to see declines or local extinction of orangutan populations within a decade, with few areas of Kalimantan predicted to have stable orangutan populations, adding weight to concerns over short- and long-term viability of this species. We discuss the four main combinations of threats and population trends that emerge from our analysis and highlight conservation actions that are likely to be most effective in addressing each combination.

Stable population and high conflict/killings

In region 1 (*P. p. pygmaeus* range), stable or increasing local orangutan populations were predicted. Yet, despite perceived stability in this region, high killing predictions suggest tenuous population viability. Higher rates of killings in the region may be linked to religious and/or cultural practices of hunting orangutan for food. Previous studies in Borneo have found that more orangutans are killed for food than for any other reasons (such as conflict, pet trade, fear or self-defence) and that Christian respondents are more likely to kill orangutans for food than non-Christians (e.g. Davis *et al.*, 2013). Our models highlighted higher likelihoods of killings by respondents in areas with a higher proportion of Christian residents. The analyses showed greater distance from plantations/non-forest land cover and surrounding orangutan habitat were associated with an increase in killing trends suggesting higher killing rates from villagers within forested regions, consistent with the findings by Davis *et al.* (2013). Orangutan densities are largely unknown for region 1; however, sighting likelihood from our analyses was predicted to be high, suggesting that orangutan encounters may be relavively frequent. Although there are significant protected forests in region 1, surveys should be conducted to better understand the degree of orangutan threats and enhance management and enforcement of protected areas.

Historically stable but declining populations and high conflict/killings

The principal area perceived as historically having stable orangutan populations but current declines was in region 4 (*P. p. wurmbi* range), an area encompassing Sebangau NP which has one of the largest Bornean orangutan populations (circa 6700 individuals) (Singleton *et al.*, 2004). Despite its protected status, this area is threatened by illegal logging, fire and conversion of forest to agriculture, with establishment of plantations and agroforests in and around the protected area (Wich *et al.*, 2012b; Gaveau *et al.*, 2013). Several studies have demonstrated insufficient management and enforcement in mitigating illegal activities in protected areas in Indonesia (e.g. Gaveau *et al.*, 2013), with Sebangau NP being an exemplary case. In Sebangau NP, hunting of orangutan, as well as the Bornean gibbon, is of great concern to the viability of these species (Singleton *et al.*, 2004; Cheyne *et al.*, 2007). Our models predict high likelihood of persecutions within this region, with population declines over the next decade. Orangutan conservation in this region depends critically on reducing illegal practices through strengthened monitoring and law enforcement. Region 5 (in *P. p. wurmbi* and *P. p. pygmaeus* subspecies' ranges) also demonstrated potentially stable populations and similarly showed high likelihood of killing trends, likely related to hunting practices in the upland areas (Davis *et al.*, 2013). Outreach work within these communities may be the most effective approach for identifying and acting upon opportunities to reduce killings and sustain existing orangutan populations.

Declining populations and low conflict/killings

Vast extents within Kalimantan were predicted to have declining or locally extinct orangutan populations. In regions 2 (*P. p. pygmaeus*) and 3 (*P. p. wurmbi*), populations were perceived to be locally extinct, triangulated by low likelihood of seeing orangutan and low conflict/killing potential (and potentially no killings in the year prior to surveys), suggesting the absence of orangutan. Studies suggest region 2 previously supported large populations of orangutans, but widespread forest clearance for agriculture has resulted in the decline of orangutan numbers (Rijksen & Meijaard, 1999; Meijaard *et al.*, 2010b). The central mountains of region 3 have retained large areas of intact or logged rain forest, but orangutans are scarce, presumably because of historic hunting (Sharma *et al.*, 2012). In these two regions, the likelihood of killings by respondents within their lifetime was high and, when combined with low sighting likelihoods in the present, suggests that past killings may have facilitated population decline. Both regions contain significant areas of agroforestry/forest regrowth, and in region 2, very little natural forest remains (Gaveau *et al.*, 2013). Both regions would benefit from surveys to understand remaining population numbers. With little remaining forest in region 2, conservation efforts may require better habitat management/restoration for any remaining orangutan populations. In region 3, conserving existing forest cover may need to be combined with community outreach to prevent hunting and enhance cultural protection.

Declining populations and high conflict/killings

Our study demonstrates that 57% of villages surveyed in Kalimantan perceived declines or extinctions in local orangutan populations, with mapped outputs predicting vast areas of population decline/local extinctions. Such trends are consistent with the widespread incidence of killings in the year prior to surveys (Figure S1). A concurrent study estimated that between 750 and 1800 orangutans were killed in the year prior to the survey and that between 1950 and 3100 orangutans had been killed annually over the life of the respondents (Meijaard *et al.*, 2011b). Such mortality rates are unsustainable for orangutan which is a slow-breeding species. In region 6 (*P. p. morio* range), models of perceived population trends predicted orangutan decline and localized extinctions within the next 10 years. Conflict risk for this region was high, and this is likely to reflect pressures from rapid land cover change to plantations (Meijaard *et al.*, 2010a). Although studies have shown that orangutans can persist in fragmented landscapes (Meijaard *et al.*, 2010a; Campbell-Smith *et al.*, 2011b), use of non-forest areas may be limited (Ancrenaz *et al.*, 2014). Furthermore, killings by respondents within their lifetime were generally predicted as low/moderate. However, killings in recent periods were predicted to be high, indicating killing frequency may have increased and may be linked to recent land cover transformations that has caused rapid orangutan habitat loss, and possibly increased encounters with displaced individuals (Wich *et al.*, 2012b). Outreach to public and especially industry is vital to mitigate conflict/killings and promote responsible practices within plantations such as establishing corridor networks to facilitate orangutan movement through plantations (e.g. Ancrenaz *et al.*, 2014).

General conservation recommendations/conclusions

Effective conservation strategies are needed to mitigate further declines of orangutan populations. Presented information on combinations of threats and population trends can help target reactive conservation efforts (targeting areas where orangutans are on the brink of localized extinctions such as region 6) or proactive conservation efforts (targeting populations where orangutans are relatively stable such as region 1). If killings occur for food or as 'accidental bycatch' during hunting, conservation efforts should target local rural communities for education and outreach programmes, coupled with better law enforcement, to reduce or eliminate killing incidences. If killings occur because orangutans raid people's gardens, then peaceful ways to mitigate conflicts are needed (Ancrenaz *et al.*, 2007; Campbell-Smith *et al.*, 2011a). If local killings are related to the clearance of orangutan habitat, then actions could include the following: (1) protection of habitat, for example through revised land use planning (e.g. Paoli *et al.*, 2013); (2) effective conservation management of forest patches within individual plantations (Ancrenaz *et al.*, 2014); (3) public awareness campaigns; and (4) strengthened monitoring and law enforcement in protected areas and plantations to ensure that no orangutans are harmed.

Methodological limitations and strengths

Spatial mapping of the human–environment interface enables us to make advances in spatial understanding of complex systems (Bryan, 2010). Our approach offers a robust method for mapping perceptions relevant for species conservation planning, thereby promoting conservation effectiveness (Knight *et al.*, 2006). A range of potential issues arose in this study which we highlight here to facilitate wider use of these methods. Interviewer reliability posed an issue for certain NGOs – these were excluded from the analysis (Meijaard *et al.*, 2011b). Respondent reliability also posed a potential issue which is often problematic in interview-based methods (Tourangeau & Yan, 2007). We attempted to overcome this by assessing reliability – in our case the identification of our case study species. Reliability on associated killing/conflict accounts was more difficult to assess, and values should be regarded as 'baseline' information. Also, data collected on conflict, sightings and population status may include inaccuracies resulting from difficulties in recalling past events or trends. Nevertheless, these responses provide highly valuable information which is potentially unobtainable from other sources. Although the acquisition of such information needs to be carefully planned to ensure the quality of information (Davis & Wagner, 2003), survey-based methods can provision high-quality data at relatively low cost (Anadon *et al.*, 2009). For example, Meijaard *et al.* (2011a) estimated interview-based survey costs at US \$ 2 per km^2 versus US\$ 10-US \$ 17 per km^2 for line transect surveys to estimate population numbers (often used for orangutans) or US\$ 6 15 per km^2 for helicopter surveys. Moreover, if humans are the principal threat to wildlife, interviews and mapping methods can provide highly valuable information.

CONCLUSIONS

Understanding of threats and population trends (such as those provided in this study) is vital for conservation planning to direct appropriate conservation actions and resources. Our study demonstrates new approaches in mapping and spatial prediction to understand certain threats and population trends to conservation priority species to fulfil (in part) this knowledge gap, through the ecological perspective of local rural people coupled with spatial data and robust modelling methods. In the case of the Bornean orangutan, it is increasingly clear that meeting Indonesia's objectives for maintaining viable wild orangutan populations by 2017 and in the longer term will depend critically on the incorporation of new information, careful cost-effective conservation targeting in moderate/high-threat areas, enforcement of existing laws, and appropriate environmental education and outreach programmes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data framework.

Appendix S2 Observed orangutan killing localities across Kalimantan.

Appendix S3 Subset data for conflict and killing models.

Appendix S4 Correlations between the spatial predictor variables.

Figure S1 Localities of orangutan killing reports in full dataset (n = 512) across Kalimantan.

Figure S2 Localities of orangutan killing reports in subset data (n = 245) across Kalimantan.

Figure S3 Goodness of fit plots for subset data models (conflict and killing around village).

Figure S4 Plots for the top four most influential spatial variables in subset data models (conflict and killing around village).

Figure S5 Mapped outputs from subset data models (conflict and killing around village).

Table S1 Classes of land cover types.

Table S2 Top ten most influential spatial variables in subset data models (conflict and killing around village).

Table S3 Correlation matrix between the observed responses of the 6 models (based on full dataset).

Table S4 Correlation matrix between the 39 spatial predictor (explanatory) variables.

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