Global Change Biology
celebrating 20 years

Global Change Biology (2015), doi: 10.1111/gcb.12814

Anticipated climate and land-cover changes reveal refuge areas for Borneo's orang-utans

MATTHEW J. STRUEBIG[1], MANUELA FISCHER[2,3], DAVID L. A. GAVEAU[4], ERIK MEIJAARD[4,5,6], SERGE A. WICH[7,8], CATHERINE GONNER[1], RACHEL SYKES[1], ANDREAS WILTING[2] and STEPHANIE KRAMER-SCHADT[2]

[1]*Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury, CT2 7NR, UK,* [2]*Leibniz Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Straße 17, 10315 Berlin, Germany,* [3]*Department of Forestry and Ecosystem Science, University of Melbourne, Creswick, Vic. 3366, Australia,* [4]*Center for International Forestry Research (CIFOR), P.O. Box 0113 BOCBD, Bogor 16000, Indonesia,* [5]*Borneo Futures, People and Nature Consulting International, Jakarta, Indonesia,* [6]*Australian Research Council Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, Brisbane, Qld, Australia,* [7]*Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, UK,* [8]*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH, Amsterdam, the Netherlands*

Abstract

Habitat loss and climate change pose a double jeopardy for many threatened taxa, making the identification of optimal habitat for the future a conservation priority. Using a case study of the endangered Bornean orang-utan, we identify environmental refuges by integrating bioclimatic models with projected deforestation and oil-palm agriculture suitability from the 1950s to 2080s. We coupled a maximum entropy algorithm with information on habitat needs to predict suitable habitat for the present day and 1950s. We then projected to the 2020s, 2050s and 2080s in models incorporating only land-cover change, climate change or both processes combined. For future climate, we incorporated projections from four model and emission scenario combinations. For future land cover, we developed spatial deforestation predictions from 10 years of satellite data. Refuges were delineated as suitable forested habitats identified by all models that were also unsuitable for oil palm – a major threat to tropical biodiversity. Our analyses indicate that in 2010 up to 260 000 km^2 of Borneo was suitable habitat within the core orang-utan range; an 18–24% reduction since the 1950s. Land-cover models predicted further decline of 15–30% by the 2080s. Although habitat extent under future climate conditions varied among projections, there was majority consensus, particularly in north-eastern and western regions. Across projections habitat loss due to climate change alone averaged 63% by 2080, but 74% when also considering land-cover change. Refuge areas amounted to 2000–42 000 km^2 depending on thresholds used, with 900–17 000 km^2 outside the current species range. We demonstrate that efforts to halt deforestation could mediate some orang-utan habitat loss, but further decline of the most suitable areas is to be expected given projected changes to climate. Protected refuge areas could therefore become increasingly important for ongoing translocation efforts. We present an approach to help identify such areas for highly threatened species given environmental changes expected this century.

Keywords: assisted colonization, biodiversity, deforestation, habitat suitability, orangutan, South-East Asia, species distribution modelling, translocation

Received 12 August 2014 and accepted 13 November 2014

Introduction

Habitat loss and climate change can lead to changes in species distributions, including range shifts, contractions, expansions and fragmentation (Parmesan, 2006; Chen *et al.*, 2011). Although the relative impacts on biodiversity remain uncertain, the two threats are expected to act synergistically, thus creating a double jeopardy for many taxa (Brook *et al.*, 2008; Mantyka-Pringle *et al.*, 2012; Beale *et al.*, 2013). Identifying the extent to which species could be affected by both processes is therefore important for effective conservation management.

Despite growing recognition of the combined influence of multiple environmental threats on biodiversity, most studies that project species distributions into the

Correspondence: Matthew Struebig, Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury, CT2 7NR, UK, tel. +44 1227 827139, fax +44 1227 827289, e-mail: m.j.struebig@kent.ac.uk and Andreas Wilting, Leibniz Institute for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Straße 17, 10315 Berlin, Germany, tel. +49 30 5168 333, fax +49 30 5126 104, e-mail: wilting@izw-berlin.de

future base their projections largely on climate and keep land-cover variables constant. This may be because climate is typically considered to be the main driver of distribution change at large geographic scales (Pearson & Dawson, 2003; Bellard *et al.*, 2012) or that climate is expected to change more rapidly than land cover (e.g. in Europe, Barbet-Massin *et al.*, 2012). Patterns of land-cover change are also difficult to predict in the long term and so are often overlooked in future assessments. In contrast to the freely available climate projections of the Intergovernmental Panel on Climate Change (IPCC), for much of the world, spatially explicit land-cover projections have simply been unavailable (Stanton *et al.*, 2012). The implications of neglecting potential changes to land cover in distribution models might be particularly important in tropical regions. The tropics host a disproportionate number of extinction-prone species (Brook *et al.*, 2008; De Chazal & Rounsevell, 2009), while continuing to experience high rates of habitat loss (Hansen *et al.*, 2013), particularly in the species-rich lowlands (Gaveau *et al.*, 2009a,b). Many tropical taxa have limited distributional ranges and dispersal capabilities that may exacerbate their vulnerability to environmental change (Tewksbury *et al.*, 2008). Upslope range shifts are expected to be particularly characteristic within the confines of narrow latitudinal temperature gradients seen in the tropics; a process that could lead to a net loss of lowland species (Colwell *et al.*, 2008).

Orang-utans are the largest arboreal species in the world, and their long-term viability, like many other tropical species, is closely linked to the presence of lowland tropical rainforest (Wich *et al.*, 2008). As an endemic and endangered great ape, the Bornean orang-utan (*Pongo pygmaeus*) attracts significant conservation resources, yet populations have exhibited a sharp decline in the last 30 years, with recent estimates approximating 54 000 individuals left in the wild (Wich *et al.*, 2008). The species persists at low densities within the territories of Indonesia (four of five provinces in Kalimantan) and Malaysia (Sabah and Sarawak) where it is threatened by expanding agriculture, illegal logging and hunting (Meijaard *et al.*, 2012; Wich *et al.*, 2012). These densities tend to be very low in monotonous and uniform forest systems with little variety in fruiting resources (e.g. mangroves and upper montane forests, and plantations), higher in forest dominated by dipterocarps on mineral soils and often highest in alluvial and peat swamp forests (Husson *et al.*, 2009). Unlike other great apes, orang-utans rely mostly on fruit and are largely solitary, both socio-ecological adaptations thought to have been adopted following past climate change in the Holocene (Lehmann *et al.*, 2010). Climatic factors pertaining to temperature and rainfall are also known to limit abundance and distribution in at least part of the current species' range; a finding partially attributed to the availability of preferred and fallback foods during drought (Gregory *et al.*, 2012). Combined, these land cover and climate threats could seriously hinder efforts to protect this charismatic species from extinction, which in turn could lead to diminished public support for conservation (Junker *et al.*, 2012).

The extent of tropical deforestation in part explains why conservation efforts continue to focus on threats from land-cover change rather than the implications of climate forecasts in these regions. Mirroring trends across the tropics, the loss of natural forests, including key orang-utan habitats on mineral soils and peatland (Rijksen & Meijaard, 1999), has been unprecedented in South-East Asia (Miettinen *et al.*, 2011; Hansen *et al.*, 2013). When large-scale commercial logging began during the 1970s 558 000 km^2 of forest (i.e. 76% of the island) remained on Borneo, but over 168 000 km^2 had been cleared by 2010 and approximately 28% remained intact (Gaveau *et al.*, 2014). In recent years, large-scale agriculture has played a defining role in deforestation and associated biodiversity loss (Fitzherbert *et al.*, 2008; Koh *et al.*, 2011; Laurance *et al.*, 2014); at least 10% of the island has been converted to industrial plantations and nearly half is earmarked for development (Gaveau *et al.*, 2013). Although orang-utans are sometimes recorded in plantation-forest mosaics (Meijaard *et al.*, 2010a), densities are much lower than those found in intact forests or carefully managed logging concessions (Ancrenaz *et al.*, 2004, 2010; Husson *et al.*, 2009). Moreover, long-term persistence in human-dominated landscapes is often compromised by killing or poaching due to agricultural conflicts (Meijaard *et al.*, 2011), leaving little opportunity for individuals to respond to diminishing habitat and the effects of a changing climate.

The extent and immediacy of these threats have led to translocation of individuals from conflict areas to forests deemed suitable over the long term; an intervention that is estimated to cost conservation up to US $14 000 per animal per year, amounting to several million dollars annually (Meijaard *et al.*, 2012). This makes the identification of translocation sites all the more important in an era of climate change. During past climate perturbations, the survival of many taxa was facilitated by refugial habitats, and so, climate and land-cover criteria are potentially useful to identify places where species could persist and later expand during anthropogenic environmental changes (Keppel & Wardell-Johnson, 2012; Reside *et al.*, 2014). In this context, suitability assessments can reveal where optimal habitat is likely to remain, thereby supporting decisions of where to target management intervention, or whether it is even warranted, both inside and outside of a species' range (Thomas, 2011; Guisan *et al.*, 2013). The burgeoning field of species distribution modelling provides tools to guide these decisions (Thomas, 2011; Guisan *et al.*, 2013; Reside *et al.*, 2014), which is typically performed by statistical association of species locality records and environmental data (Elith *et al.*, 2010). A recent appraisal of African great apes demonstrated dramatic declines in suitable environmental conditions during the last decade (Junker *et al.*, 2012). For the Bornean orang-utan predicted population declines in the Malaysian state of Sabah are mostly attributed to land-cover changes projected for this century (Gregory *et al.*, 2012). A range-wide assessment recently concluded that the species currently inhabits around 155 000 km^2 (Wich *et al.*, 2012), but for the vast majority of this area long-term projections are unavailable.

Here, we extend this appraisal by providing range-wide projections of habitat suitability under land cover and climate change forecasts this century. Under our modelling framework, we (1) project the extent of suitable habitat into future time periods both within and outside the currently recognized orang-utan range and (2) consider the relative influence of predicted changes in land cover and climate, while (3) accounting for uncertainty arising from climate forecasts using several global circulation model (GCMs) and emission scenario combinations. By encompassing >732 000 km^2, mainland Borneo is a size at which the processes of both land cover and climate change are expected to affect biodiversity and be detectable (Pearson & Dawson, 2003). Therefore, we make use of recently mapped deforestation data to develop land-cover change projections on which to base our analyses. By doing so, we are able to provide trajectories of possible distributional change and use this information to identify land, both inside and outside of the current species range, that might serve as future refuge for this endangered species in an era of environmental change.

Materials and methods

Modelling framework

Rapid deforestation over the last decade meant that land use changed at many orang-utan localities during the time frame of data collection, leading to substantial mismatch between species presences and land-cover classifications. To maximize the use of locality data, we therefore delineated the extent of suitable orang-utan habitat in each time slice and environmental change scenario using a modelling framework that treated the potential influences of climate and land cover separately (Wilting *et al.*, 2010).

First, we used a maximum entropy algorithm (MaxEnt; Phillips *et al.*, 2006) to model environmental suitability for orang-utan under baseline climate conditions leading to the present day (interpolations representative of 1950s–2000), and project this spatial information into future time slices during the 21st century for the 2020s, 2050s and 2080s (hereafter the 'bioclimatic model'). To better account for orang-utan habitat needs, we then refined MaxEnt outputs using land-cover data and expert-derived information on species' sensitivity to human disturbance to calculate habitat suitability in each time slice (hereafter the 'habitat suitability model'). These habitat suitability surfaces were obtained in three different ways, namely for (1) baseline climate but future land cover (i.e. 'land cover only'); (2) projected climate but land cover fixed to baseline conditions (i.e. 'climate only'); and (3) both projected climate and land cover for each time slice (i.e. 'climate + land cover'). Finally, to identify potential refuges for orang-utans over the course of the century, we identified forests that were consistently suitable under all current and future model predictions, while being unsuitable for cultivating oil palm (the primary agrarian threat to orang-utans, Meijaard *et al.*, 2012).

To place our projections into a historical context, we also predicted the former extent of suitable habitat by hindcasting to conditions before the 1950s, a time when most data used to quantify current climate were first collected (Hijmans *et al.*, 2005) and before major land-cover changes occurred on Borneo (Gaveau *et al.*, 2014). Potential uncertainty associated with source environmental data was also investigated by modelling under several climate projections.

Environmental predictors used in bioclimatic modelling

For baseline climate conditions, we used 19 gridded temperature and precipitation parameters downscaled to 1 km^2 resolution (Hijmans *et al.*, 2005; Table S1). For future climate, we used the same variables projected via two general circulation models (GCMs: Commonwealth Scientific and Industrial Research Organisation Australia, CSIRO-Mk3; and Hadley Centre for Climate Prediction and Research UK, HADCM3) under two emission scenarios (A2 and B2, representing a worst case and best case, respectively). These four variants were chosen to account for uncertainties in single models and to reflect the range of projected values available for the time frame and resolution of the study (Appendix S1). Climate forecasts from the various sources differed in the extent to which they deviated from observed conditions (Struebig *et al.*, In Press), providing potential uncertainty for extrapolating to unobserved settings (Elith *et al.*, 2010). However, the vast majority of projected values fell within the ranges observed in the sampling region for the current day (Fig. S1) indicating that the overall effect on our predictions would be minimal.

We incorporated a measure of topographic ruggedness ranging from 1 (flat) to 7 (extremely rugged), as topographic heterogeneity may affect distributions by influencing accessibility and microclimate, as well as the movement capabilities and availability of shelter for wildlife (Turner, 2005). Vegetation near watercourses may be particularly suitable for great apes, while streams and rivers might also serve as navigational cues for wildlife and sources of access for people (Junker *et al.*, 2012). We therefore included three 'distance to water' layers as environmental predictors, each reflecting a different water catchment size (Kramer-Schadt *et al.*, 2013). Finally, as orang-utan populations are known to be sizeable in swamp forests and relatively low in limestone karst forests (Husson *et al.*, 2009), we incorporated a distance function to these landscape features as additional predictors as they were not well represented within other variables (Table S1).

Modelling formed part of a broader appraisal of Borneo mammal distributions (Struebig *et al.*, In Press), in which predictor variables were checked for multicollinearity. Models based on a subset of uncorrelated variables yielded similar outcomes, and any remaining collinearity effects were minimal when sampling bias was corrected (Kramer-Schadt *et al.*, 2013). Therefore, we kept predictor variables fixed for all taxa, and so, in order to make our findings comparable to results for other species, we present complex models using all environmental variables.

Presence localities, sampling bias correction and projecting the bioclimatic model, M

The orang-utan occurrences on which we based our MaxEnt models comprised a subset of 6711 records collected between 1990 and 2011 during the most comprehensive surveys on the island (Ancrenaz *et al.*, 2004, 2010; Husson *et al.*, 2009; Wich *et al.*, 2012). Sampling effort was not evenly distributed; the Malaysian state of Sabah was much more intensively surveyed, and surveys in Indonesian Borneo concentrated around research sites. Because uneven sampling effort can have adverse consequences for distribution models (Phillips *et al.*, 2009), leading to high omission or commission errors (Kramer-Schadt *et al.*, 2013), we accounted for this potential problem by spatial filtering and manipulating background data. These strategies are demonstrated to greatly improve model predictions (Beck *et al.*, 2014; Varela *et al.*, 2014), including specifically in our study region and data structure (Kramer-Schadt *et al.*, 2013). For spatial filtering, we used only one presence locality randomly selected within a radius of 2 km; a value chosen to correspond to the upper estimates of home range size for Bornean orang-utans (Singleton *et al.*, 2009) and leaving 298 spatially independent records on which to base our analyses. Background manipulation was undertaken by creating a 'bias file' of relative sampling effort (or record density) to incorporate within the MaxEnt process. We used the procedure outlined in Kramer-Schadt *et al.* (2013) to map sampling density, summing records across the Moore neighbourhood of each cell and assigning values of 0.1 (i.e. 10% sampling effort) to cells with no records.

We incorporated the orang-utan occurrence records, bias grid and baseline environmental predictors into a MAXENT model (version 3.3.3a; Phillips *et al.*, 2006, with settings: random test percentage = 25; regularization multiplier = 1; maximum number of background points = 10 000), using the mean predicted probabilities of 10 replicates for subsequent analyses. From this baseline model, M_{cur}, we projected orang-utan presence probabilities into 12 future scenarios (three time slices, two GCMs, two emission scenarios), M.

Incorporating land cover, L, into past, present and future forecasts

Baseline habitat suitability models incorporated 2010 land-cover data derived from 50 m resolution PALSAR imagery by SarVision (Hoekman *et al.*, 2009), but updated with elevation information and resampled to match the 1 km resolution of climate variables (Kramer-Schadt *et al.*, 2013). The resulting land-cover map comprised 17 habitat-elevation classes representing intact forests (4 classes), swamps (2), fragmented/degraded forest mosaics (4), burnt forest (1), plantations/crops (3), water/fishponds (2) and no data (1) (Table S1). For the past coverage, we reclassified all nonforest or mosaic forest classes to their forested counterparts with the aid of wetlands maps (Appendix S2).

For future time slices, we modelled deforestation to predict forest loss over the island in any given time slice and then reclassified deforested areas as plantation or forest mosaic land covers. The deforestation base map was produced by fitting a generalized linear model with binomial error distribution and logit link function (i.e. a logistic regression) to predict the probability of forest absence between 2000 and 2010 in Kalimantan using a time series of Landsat TM satellite data (Appendix S2). Forest maps and definitions followed Gaveau *et al.* (2013), and deforestation by 2010 was defined as $\geq$ 0.2 km^2 forest loss within a 1 km^2 cell. Forest loss was determined within a sample of 451 training cells that were randomly generated within fully forested stands in the 2000 map. We then randomly selected an equal number of cells that experienced no deforestation (i.e. forest presence) to build a binary model and assessed spatial autocorrelation in the model residuals using Moran's I.

During the 2000–2010 period used to train the model, the mean annual deforestation rate for Borneo approximated 3234 km^2 yr^{-1} (2341 km^2 yr^{-1} for Kalimantan). We extended this rate to future time periods (32 338 km^2 forest lost by 2020, 129 354 km^2 by 2050 and 226 370 km^2 by 2080), and for each year of interest we identified the number of cells with the highest deforestation probabilities that equated to these areas. We then reclassified the predicted areas as plantation or forest mosaic land classes according to prior land use (Appendix S2). Extending the rate in this way assumed no reforestation and that the pace of deforestation would remain unchanged in the future; an intentional and plausible worst-case scenario for land-cover change against which to compare the influence of climate.

Delineating habitat suitability

We defined a habitat suitability index (HSI) in a given time slice, y, using the following equation adapted from Wilting *et al.* (2010), $HSI_y = (M_{yc,es}{}^2 * L_{yl}{}^3 * P)^{1/6}$, where M comprises the probability of orang-utan occurrence (MaxEnt outputs) under a given emission scenario (A2, B2) and GCM (CSIRO, HAD) combination es, and time slice yc (2010, 2020, 2050, 2080); L is the land-cover class for orang-utan under land-cover scenario yl, P is human population density weighted by sensitivity of orang-utans to human population pressure, and yc, es and yl refer to current conditions or 2020, 2050 and 2080 time slices of the respective emission scenarios. Defining the index in this way gave a greater emphasis to suitable habitats that were also away from human settlements, while allowing us to systematically test the influence of climate change and land-cover change on the final habitat suitability maps (i.e. by fixing climate to baseline conditions and changing land cover, or *vice versa*).

Values for L were derived from six leading primate experts with >100 years of combined experience studying orang-utans across Borneo, including published research on the effects of habitat degradation and contributions to population viability assessments for the species (Marshall *et al.*, 2009). Each provided habitat suitability scores (ordinal scale of 0–1, unsuitable–suitable, in five classes) for the land-cover classes available (Table S1). Experts also provided values for P as estimates of orang-utan sensitivity to a range of human population densities (ordinal scale 0–1, unsuitable–suitable, five classes) (Table S1). Human population density was extracted from the LandScan 2007 spatial database (Oak Ridge, UT-Battelle, LLC) and fixed to 2007 values since projected data for 2020–2080 were unavailable. High population densities were typically alongside roads, rivers and large agricultural areas, as well as urban settlements.

To compare the extent of suitable habitat between the various models and scenarios, we converted HSI scores into binary (i.e. suitable, unsuitable) predictions. We first used a 10% omission error threshold, a commonly applied criterion in distribution modelling studies (e.g. Pearson *et al.*, 2007), to generate a liberal suitability classification that would be insensitive to outliers and incorporate a larger predicted area (i.e. 90% of possible predicted values). In addition, as area estimates are inevitably sensitive to threshold choice, we also provide estimates from a 25% error threshold to give a stricter representation of primary orang-utan habitat. Although somewhat arbitrary, using fixed omission thresholds in this way provided upper and lower bounds of possible habitat extent that could be consistently applied across environmental projections. The decision for these specific threshold values followed initial consultation with the primate experts who confirmed that the 25% threshold (i.e. the top 75% of suitable habitat) best reflected the core distribution of the species known for the present day (*sensu* Wich *et al.*, 2012 and http://www.iucnredlist.org/details/17975/0), while giving some opportunity to identify potentially suitable areas outside the range. Suitable area predictions are reported within the core orang-utan range currently recognized, as well as for the whole of Borneo.

Identifying potential future refuges for orang-utan

We defined future refuges as areas expected to support orang-utan habitat under the ensemble of projected environmental changes, while also being buffered by further land development. To extract these areas, we first identified the land consistently identified as suitable for orang-utans in 2010, 2050 and 2080 under all environmental scenarios (four outcomes under 'land cover + climate change' models). We then extracted 2010 intact forest areas from this coverage, as these classes were ranked the greatest suitability by the primate experts. As a further indicator of refuge potential, we also excluded land suitable for oil palm, assuming that most forthcoming land-use wildlife conflicts on Borneo would arise from expansion of this crop, as they have performed in the recent past (Fitzherbert *et al.*, 2008). To map crop suitability, we expanded an approach established in consultation with the oil-palm industry (Gingold *et al.*, 2012) to delimit productive areas over Borneo according to edaphic, elevation/slope and rainfall criteria (Appendix S3). To best serve conservation plans, we present these results for the three orang-utan subspecies currently recognized for the island, by overlaying refuge maps with subspecies extent maps. Subspecies range boundaries are largely defined by the presence of large rivers rather than variation in their ecological requirements, as these features are known to impede dispersal (Wich *et al.*, 2012).

Results

The bioclimatic model

MaxEnt analyses for 2010 conditions converged well and yielded models with good discriminatory power (AUC = 0.72 ± 0.03) despite spatial filtering and background manipulation of source locality data (which tend to reduce AUC values – Kramer-Schadt *et al.*, 2013), indicating that the models could be considered useful for projections. The difference between calibration and evaluation AUC values was also small (0.07), indicating a model unlikely to overfit calibration data (Warren & Seifert, 2010). Environmental parameters with the greatest contribution to model goodness-of-fit were precipitation in the driest month (16%), annual temperature range (14%), distance to wetlands (13%) and diurnal temperature range (10%). Low suitability for three of these parameters, as defined by MaxEnt response curves, coincided with low suitability scores in the overall model (Fig. S2). Importantly, the primate experts consulted also considered the 2010 model to provide a useful representation of possible orang-utan habitat (using a 10% error threshold) and particularly of the primary parts of the species range (25% error threshold).

Habitat suitability for current and past conditions

Experts consistently ranked lowland and swamp forests as the most suitable habitats for orang-utans, followed by hill forests, then forest mosaics (Table S1). Greatest suitability was attributed to areas with low human population densities (0–3 people km^{-2}). Much of the lowland and upland regions of Borneo

(0–1000 m) exhibited modest to high suitability according to the HSI, with the exception of highly degraded areas (i.e. plantations), primarily near the coast (Fig. 1). Substantial upland habitat outside the core range was also deemed moderately suitable. Using a 10% error threshold, HSI models predicted approximately 560 000 km^2 of Borneo to be currently suitable orang-utan habitat, of which 260 000 km^2 lay within the current core range (*sensu* Wich *et al.*, 2012). This represented a reduction of approximately 18% of the habitat available prior to major land-cover changes according to the models hindcasting to conditions before the 1950s (Table 1).

Projected impacts of land-cover change

Our predictive model of deforestation explained 85.1% of the 2000–2010 training data, with good model fit ($R^2 = 0.506$). Under this model, lowland forests (<500 a.s.l) on mineral soils and allocated for conversion were most likely to be deforested. By contrast, lower deforestation probabilities were evident for peatlands, in protected areas, logging concessions and in other forests far from roads and cities (Table S2).

As a result deforestation early in the projection period mostly occurred on land designated for conversion in the northwest and south of the island, primarily in

Table 1 Projected change in the extent of suitable orang-utan habitat over Borneo between the 1950s and 2080s under different environmental change scenarios and model predictions. The magnitude of habitat loss is calculated between the 1950s and 2010 for current conditions, and between 2010 and the 2080s for the future. Projections are presented for two suitability thresholds, inside and outside of the core range (i.e. the current range extent) *sensu* Wich *et al.* (2012).

	10% threshold				25% threshold			
	Area (thousands of km^2)			Suitable habitat loss (%)	Area (thousands of km^2)			Suitable habitat loss (%)
Inside core orang-utan range								
Before major land-cover change (1950s)	316				290			
Current (2010)	260			18	220			24
Time slices	2020	2050	2080		2020	2050	2080	
Land cover only	251	237	219	15	209	177	155	30
Climate only								
CSIRO-Mk3, A2	233	205	79	69	106	46	4	98
HADCM3, A2	205	130	82	68	102	33	10	95
CSIRO-Mk3, B2	225	178	133	49	115	34	15	93
HADCM3, B2	222	151	111	57	107	47	20	91
Land cover + climate								
CSIRO-Mk3, A2	221	165	49	81	103	44	4	98
HADCM3, A2	196	110	58	78	99	31	8	96
CSIRO-Mk3, B2	214	144	83	68	112	33	14	94
HADCM3, B2	212	128	80	69	103	44	16	93
Outside core orang-utan range								
Before major land-cover change (1950s)	341				168			
Current (2010)	300			12	135			20
Time slices	2020	2050	2080		2020	2050	2080	
Land cover only	290	268	254	15	128	111	99	26
Climate only								
CSIRO-Mk3, A2	248	212	50	83	57	41	2	99
HADCM3, A2	234	112	36	88	46	15	4	97
CSIRO-Mk3, B2	244	137	83	73	66	13	7	95
HADCM3, B2	237	118	60	80	52	14	7	95
Land cover + climate								
CSIRO-Mk3, A2	240	191	42	86	55	39	2	99
HADCM3, A2	227	105	31	90	45	14	4	97
CSIRO-Mk3, B2	236	123	71	76	65	13	7	95
HADCM3, B2	231	109	52	83	50	14	6	95

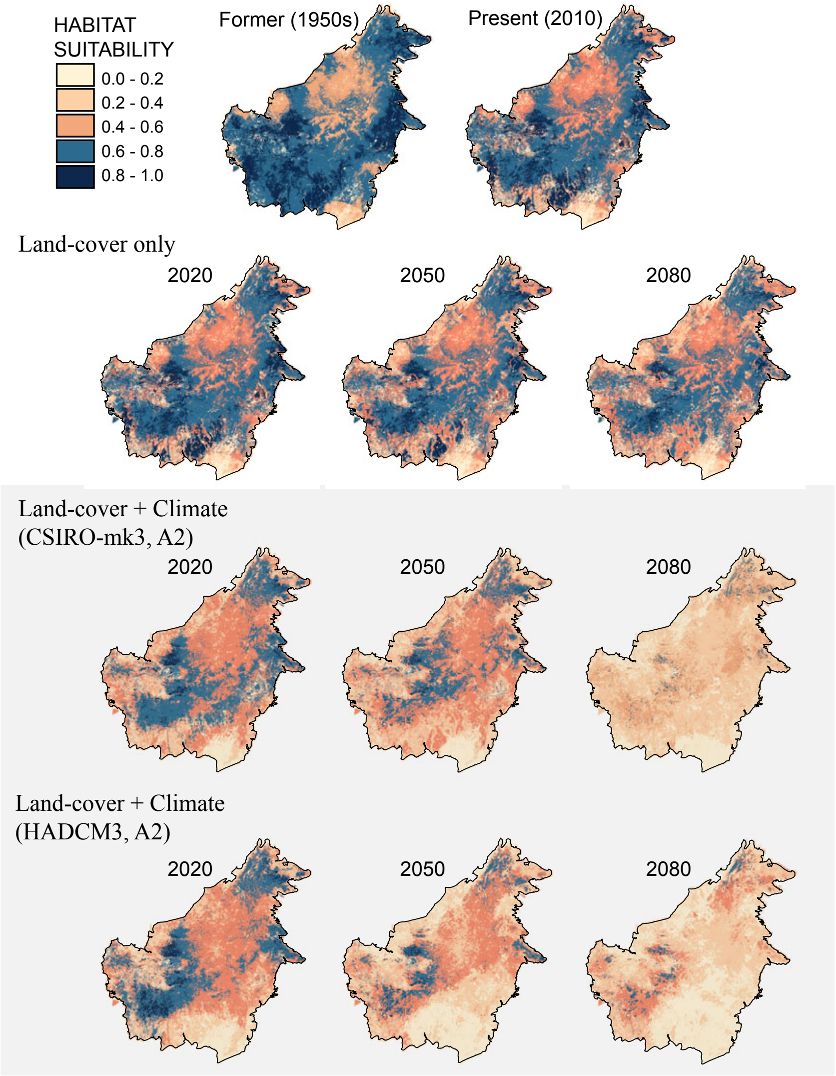

Fig. 1 Predicted suitable orang-utan habitat following projected changes to land cover and climate. Suitability modelling derived from a habitat suitability index based on several land cover and climate conditions. Climate data from two global circulation models and two emission scenarios (results from A2 and B2 emission scenarios were similar, so for clarity, only results from A2 are shown).

Sarawak and Central Kalimantan (Fig. 2), following trends in recent years. By the 2050s, predictions extended to all states, revealing deforestation in less accessible conversion forest as well as land designated for timber production. This trend continued to the 2080s, but also lowland forest reserves were targeted. Under these projected land-cover changes, HSI calculations revealed a gradual reduction in suitable habitat after 2010 with a decline of 15% of core orang-utan habitat by the 2080s (Table 1).

Habitat decline under a changing climate

The extent of suitable orang-utan habitat in future climate conditions varied among the GCMs and emission scenarios used, although there was consensus across all models over most of the area (Fig. 1; Table 1). Models incorporating changes to climate only during the projection time frame all pointed to a large decline in suitable habitat; approximately 63% loss between 2010 and 2080 (median across models, Table 1). Under these conditions, the north-east and western parts of Borneo were consistently identified as suitable habitats throughout the 21st century, but the extent of habitat decline in south-central regions varied across models (Fig. 1).

The main sources of variation were attributed to choice of presence threshold, then GCM, and to a much lower extent, the emission scenario used in analyses (Fig. S1; Appendix S1). Although there was majority

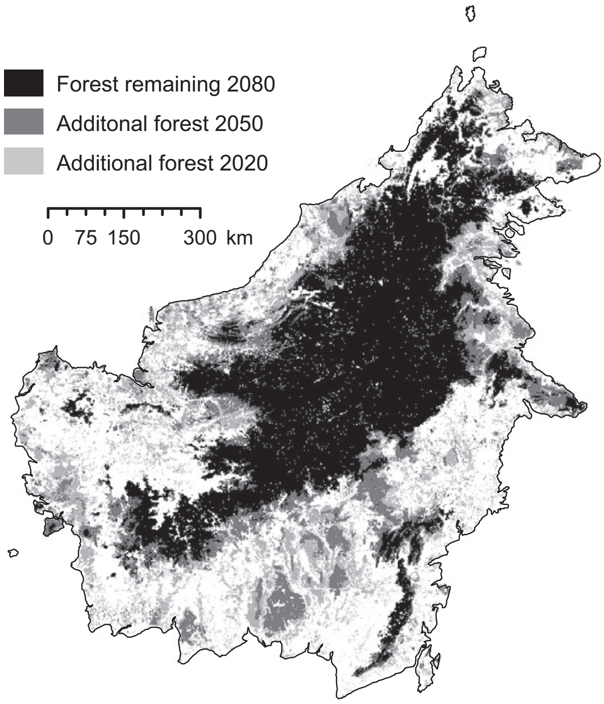

Fig. 2 Trajectory of forest loss for Borneo as predicted by a spatial deforestation model based on 2000–2010 trends.

consensus among GCMs overall, models using HADCM3 yielded lower suitability values in the south-east compared to those using CSIRO-Mk3 data. This coincided with the area of least agreement between the two climate projections (Appendix S1, Fig. S1). This variation could be attributed to differences in suitability defined by MaxEnt response curves, primarily for three climate predictors that contributed the most to the bioclimatic model (Fig. S2). Conversely, no clear pattern emerged with choice of emission scenario, and climate projections were similar between the two options (Appendix S1).

Combined effects of land cover and climate change

Models that combined the influence of changing land cover and climate yielded similar predictions to those based on climate change only, although the extent of suitable habitat loss was exacerbated by the two processes incorporated into models together (Fig. 1). Under this combined environmental change scenario, models predicted an average of 74% habitat loss between 2010 and 2080 (Table 1).

Future orang-utan refuges

By intersecting forest areas deemed suitable for orang-utan but unsuitable for oil palm during the projection period, a median of approximately 92 000 km^2 of Borneo (or 16% of 2010 habitat) was identified as potential refuge habitat by the various model forecasts using the 10% error threshold (Table 2). Most of this land was in lowland (57%, <500 m.a.s.l), or hill forest (33%, 501–1000 m.a.s.l) areas. Large consensus was reached among the various model forecasts for refuge habitats, with 2000–42 000 km^2 of land consistently identified using the two presence thresholds (Fig. 3).

For *P. p. pygmaeus* – the north-western subspecies – an average of 21 000 km^2 of refuge habitat would likely remain by 2080 using 10% error threshold estimates, with approximately 16 000 km^2 consistently identified by half the models (Table 2). Much of this area was in protected forests, the bulk within four conservation estates in West Kalimantan and Sarawak (Appendix S4). For *P. p. morio* – the north-eastern subspecies – around 35 000 km^2 of land was identified as potential refuge in eastern Kalimantan and Sabah, of which 27 000 km^2 was identified by half the models. The largest extent of refuge habitat was identified for *P. p. wurmbii* – the southern subspecies – both inside and outside the core range extent. For this subspecies, 23 000–46 000 km^2 of land was identified as refuge, with 29 000 km^2 being consistently identified by half the models (Table 2). However, the vast majority of this habitat remained in the western part of the range, and southern populations were poorly represented in protected refuges. (Appendix S4; Fig. 3). Despite optimistic projections under the 10% error threshold, use of the stricter 25% error threshold revealed a much lower extent of suitable refuge habitat overall, with only a subset of 14 000 km^2 (2% of 2010 habitat) identified, at elevational distribution comparable to the previous assessment (68%, < 500 m.a.s.l; 31%, 501–1000 m.a.s.l).

Discussion

The potential for synergistic effects of land cover and climate change on biodiversity is well recognized (Brook *et al.*, 2008), but so far relatively few distribution modelling studies have included both these threats in future forecasts (Barbet-Massin *et al.*, 2012; Schweiger *et al.*, 2012; Martin *et al.*, 2013). Our assessment of the endangered Bornean orang-utan predicted a trajectory of habitat loss following anticipated future changes to land cover and climate. Our models suggest that 220 000–260 000 km^2 of land within the core range on Borneo was potentially suitable for orang-utan in 2010. This is greater than previous estimates (e.g. Wich *et al.*, 2012) as our predictions also include mid-elevation and degraded mosaic habitats that are known to support orang-utans in some areas, but at low densities (Husson *et al.*, 2009). While clearly suboptimal for orang-utans

Table 2 Potential extent of refuges from future land cover and climate change for the three subspecies of orang-utan on Borneo. Refuge areas are forested, unsuitable for oil palm and consistently classified as suitable habitat between 2010 and 2080 under the combined 'land cover + climate change' models. Values are presented both within and outside the core known range (*sensu* Wich *et al.*, 2012) for the 10% and 25% omission error thresholds. Consensus among predictions is derived from overlays of the four model outcomes

	Core areas, within known range extent (thousands of km^2)			Outside known range extent (thousands of km^2)		
	pygmaeus	*wurmbii*	*morio*	*pygmaeus*	*wurmbii*	*morio*
(a) Using 10% error threshold						
Climate projections						
CSIRO-Mk3, A2	7.1	12.1	19.7	8.0	11.0	16.6
HADCM3, A2	10.1	22.7	9.8	6.6	9.0	8.7
CSIRO-Mk3, B2	12.7	26.5	25.9	15.4	19.2	25.3
HADCM3, B2	13.5	26.7	19.7	10.8	14.4	14.0
Median across projections:	11.4	24.6	19.7	9.4	12.7	15.3
Consensus among models						
4 models	6.5	9.3	9.3	4.2	5.7	6.9
3 models	3.0	9.1	6.6	2.7	5.3	4.5
2 models	3.3	8.4	5.7	4.0	4.1	6.9
(b) Using 25% error threshold						
Climate projections						
CSIRO-Mk3, A2	0.9	0.6	1.9	0.2	0.8	0.6
HADCM3, A2	2.6	3.6	1.3	0.3	2.1	1.1
CSIRO-Mk3, B2	4.0	4.4	4.6	0.6	3.7	1.4
HADCM3, B2	4.6	6.5	3.1	0.4	4.0	0.8
Median across projections:	3.3	4.0	2.5	0.3	2.9	0.5
Consensus among models						
4 models	0.8	0.4	0.4	0.1	0.5	0.1
3 models	1.2	2.2	1.4	0.1	1.3	0.3
2 models	2.0	2.3	1.4	0.3	1.7	0.8

(Meijaard *et al.*, 2011) this additional area might become increasingly important following environmental forecasts this century.

Projected effects of land cover and climate change

Under land-cover change projections (i.e. treating climate variables as static), we estimate that around 15–30% of core orang-utan habitat will be lost by 2080, a rate comparable to that already experienced since the 1950s: approximately 2–4% per decade (Table 1). Conversely, under climate change projections, rates of habitat loss are expected to be much greater – more than triple those under land-cover change projections alone. Models that incorporate the effects of both land cover and climate change point to an average of 74% habitat loss by 2080 (11% per decade) using 10% error thresholds, suggesting that the effects of a changing climate might greatly exacerbate the ongoing impacts of land-cover change on Borneo. Much of this is expected to be primary habitat in the lowlands, as indicated by stricter 25% error thresholds.

It is somewhat surprising, given the high rates of deforestation reported for Borneo (Langner *et al.*, 2007) and the worst-case scenario depicted in our land-use trajectory, that the contribution of land-cover change to the trajectory of orang-utan habitat loss was relatively small compared to that from climate. This is also contrary to the findings of Gregory *et al.* (2012) who demonstrated that land-cover change would have a far greater impact on orang-utan population sizes in Sabah. This discrepancy can in part be explained by moderate suitability weights assigned to mosaic habitats in our assessment, meaning that some degraded areas would be given similar weighting to pristine forests regardless of population size. The broader extent of our study also has implications, as at the scale of Borneo, both deforestation and climate processes disproportionately affect the same areas (i.e. lowlands of Central Kalimantan and Sarawak, Fig. 2; Appendix S1).

Including land-cover data specifically within bioclimatic models can significantly increase explanatory power (Tingley & Herman, 2009), although we note that this was not possible within our study system due

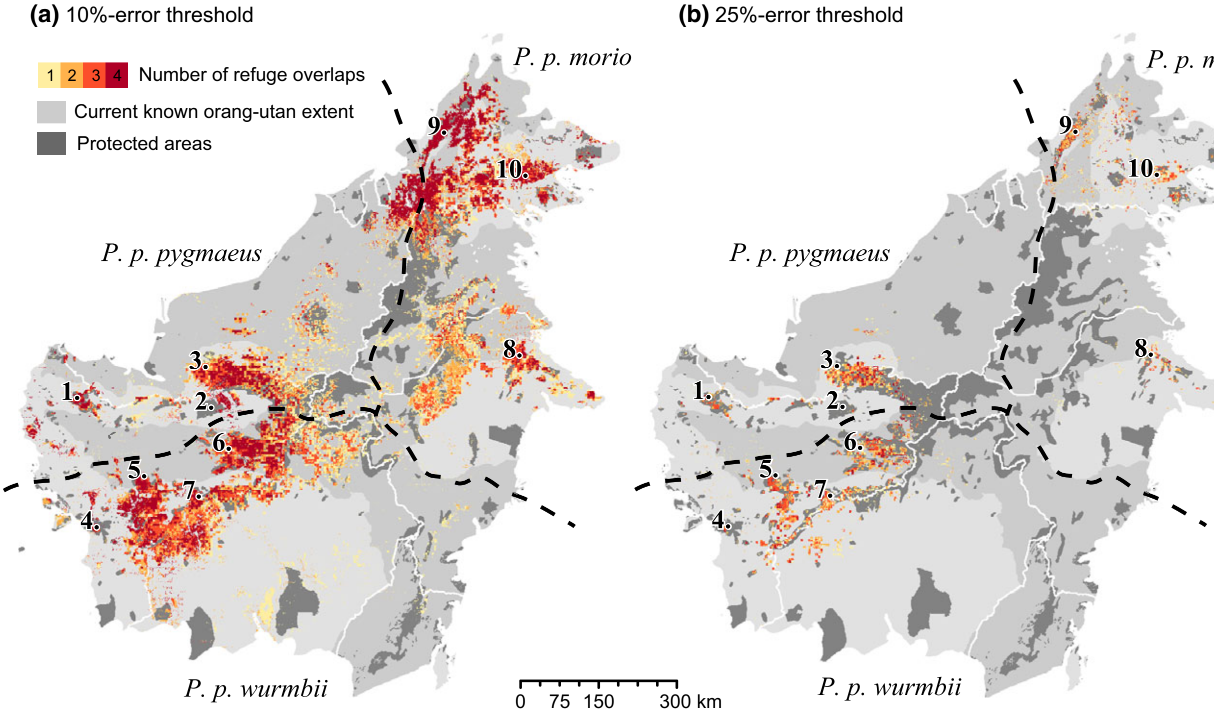

Fig. 3 Potential refuges for Bornean orang-utan under predictions of both land cover and climate change. Refuge areas are forested, unsuitable for oil palm, while being suitable for orang-utans between 2010 and 2080 according to 10% error (a) and 25% error (b) thresholds. Consensus among models based on four climate data is indicated by overlays (red indicating 100% agreement). Subspecies boundaries are indicated by dashed lines, and protected areas are indicated by dark shading – numbers refer to key reserves identified for both error thresholds as listed in Table S4.

to the rapid pace of land-use change during the data collection time frame. Our deforestation predictions echoed recent trends at the beginning of the projection time frame (2020s, 2050s), and it is highly probable that without policy changes deforestation rates would continue mid-century given the large pool of unprotected lowland forest remaining (Gaveau *et al.*, 2014). However, for longer term projections (2080s), our model could be improved by allowing for forest regeneration and a slowing of the deforestation rate. Regeneration can and does occur in tropical South-East Asia if land is not converted to agriculture. There are renewed efforts to map these areas (D. G. Gaveau *pers. obs.*), although we also note that many of these sites were likely reclassified as forest mosaics with medium habitat suitability under our assessment. We also note that for the purposes of this appraisal, using a worst-case land-cover change was valuable for comparing against the effects of climate change.

The importance of climate has also been emphasized in recent studies that incorporated both habitat and climate variables directly into distribution models. In a study of European butterflies, for example, climate explained the most important part of current distributions, and land-use change scenarios poorly represented current and future habitat suitability, even at fine spatial scale (Martin *et al.*, 2013). Likewise, habitat models for European birds predicted smaller range shifts than climate models, although this was attributed to improved model accuracy under the climate-only scenario (Barbet-Massin *et al.*, 2012).

Variation in model predictions

Despite substantial consensus among the suitability models across much of the currently recognized orang-utan range, our approach uncovered some variation in model projections. After variation ascribed to the different presence thresholds, the main differences in the predicted habitat extent were attributed to choice of GCM, with projections based on HADCM3 data predicting a lower extent of suitable habitat in the southern lowlands (Central Kalimantan). This large area (Sabangau-Katingan peat swamp forests) is known to support high orang-utan densities (Husson *et al.*, 2009) and is thus regarded as a stronghold for *P. p. wurmbii*. Further investigations of model outcomes from additional GCM projections, including regionally downscaled data as they become available following the latest IPCC assessment period, are therefore warranted. However, we note that there was majority consensus among the thresholds used in our analyses and that any such variation is likely to be strongest when differences between current and future climate conditions are high, something that does not characterize equatorial regions as much as higher latitudes. We also acknowledge that additional variation would arise from using alternative species distribution models, although we note that for our study region and biased data set the virtues of MaxEnt are well established (Elith *et al.*, 2010), and that the primate experts we engaged agreed the baseline model gave a realistic portrayal of present-day habitat suitability. Moreover, we reiterate that variation among model outcomes is to be expected in forecasting studies (Buisson *et al.*, 2010; Araújo & Peterson, 2012) and that our ensemble approach provides a range of possible outcomes against which more detailed analyses pertinent to smaller spatial scales can be compared. Such analyses would benefit from incorporating other data important for orang-utan survival, such as population sizes and hunting pressures, which are available for some (though notably not all) areas (Meijaard *et al.*, 2011; Gregory *et al.*, 2012).

Potential future refuges for Borneo orang-utan

We defined orang-utan refuges as intact forests that were consistently suitable under current and future environmental change scenarios. Ideally such refuges would be spared from development (Reside *et al.*, 2014), and so, we also extracted only areas deemed unsuitable for oil-palm cultivation, a leading threat to Borneo's biodiversity. Although we used an established procedure to identify suitable land for oil palm, the edaphic, geographical and climatic criteria used do not solely dictate where the crop can and cannot be grown, and at least some recent oil-palm expansion has occurred in substandard regions (Koh *et al.*, 2011). In addition, crop suitability assessments are based on present-day growth characteristics of commercially available cultivars and do not account for potential genetic improvements that could increase drought or flood resistance (Cochard *et al.*, 2005). However, while improved cultivars will likely be developed in due course, suitability assessments are still useful to predict where land-use conflicts are likely to be, particularly for small-holder farmers for which uptake of new cultivars might be slow, or for regions where people reject large-scale agricultural expansion (Abram *et al.*, 2014).

Combined, our projections reveal potential refuge habitat that is fragmented among protected areas within the extent of each orang-utan subspecies. The amount of refuge habitat potentially available is worryingly unrepresentative for eastern populations of the subspecies with the largest current range (*P. p. wurmbii*, and to some extent *P. p. morio*), for which substantial areas of Borneo's lowlands could become less suitable over time due to the combined influence of deforestation and changing climate. Nonetheless, the same appraisal also highlights forests outside of the core range that might serve as potentially suitable habitat in the future and which are well represented within reserves and logging concessions (Fig. 3; Appendix S4).

Viability of refuges and implications for orang-utan conservation

Although we are able to identify potentially suitable refuge habitat, it is highly unlikely that the dispersal capabilities and population dynamics of the orang-utan would enable individuals to move to these areas within the pace of environmental change predicted. Importantly for meta-population functioning, female orang-utans are philopatric and males disperse (Nietlisbach *et al.*, 2012). As a result, breeding populations (consisting mainly of dominant males, females and their young) tend to occur in the most ecologically suitable areas with the lowest levels of threat. Non-dominant males disperse from these areas, sometimes over long distances, as indicated by single orang-utans recorded hundreds of kilometres from the nearest breeding population (Rijksen & Meijaard, 1999). However, the strict limitations to female dispersal make colonization of marginally suitable habitats or recolonization of poorly populated areas (e.g. where orang-utans were hunted out in the past), a slow process (Meijaard *et al.*, 2010b). In addition, deteriorating ecological conditions could lead to increased mortality rates biased to females, because these individuals are unlikely to disperse far in search of more suitable habitat (Ancrenaz *et al.*, 2014). Sex-biased dispersal rates in orang-utans could thus negatively influence reproductive rates in both residential populations with decreasing ecological conditions and in new areas that are becoming ecologically suitable.

To maximize the likelihood that both male and female orang-utans could disperse from ecologically poor to highly suitability areas, maintaining connectivity between existing stronghold orang-utan populations and the refuge areas we identify is crucial (Gregory *et al.*, 2014). These conservation corridors would ideally also be suitable for other threatened species, as recent evaluations in northern Borneo are beginning to demonstrate (Brodie *et al.*, 2014). Nevertheless, present spatial and development planning in the different regions of Borneo does not yet include ecological principles such as forest connectivity, and so a major change of planning systems and processes would be required.

The flow of orangutans to recipient sites could also be boosted through future introductions pending further investigation on their suitability and cost-effectiveness. The effectiveness of such introductions, or assisted colonizations in the context of environmental change, has caused considerable debate in conservation, with arguments for and against the strategy purported in almost equal measure (Seddon, 2010). Our study suggests that within an emerging decision framework concerning the need for assisted colonization (Chauvenet *et al.*, 2013; Schwartz & Martin, 2013), the case for the Bornean orang-utan would be clear; namely that the risk of decline or extensive local extinction under environmental change is high. Habitat modelling, such as that used in our assessment, could therefore inform the selection of introduction sites. However, given the relatively coarse resolution of climate data and the Borneo-wide scale of analysis, the refuge habitats we identify are likely to miss fine-scale characteristics of microrefugia that might be central to long-term survival (Ashcroft, 2010). Translocation decisions also require a better understanding of other factors (e.g. hunting) that are pertinent to orang-utan survival at local scales. Further needs assessment is therefore warranted at the subspecies and management unit levels, which should incorporate information on habitat quality (e.g. food availability as an important determinant of orang-utan density), population dynamics (Gregory *et al*., 2012) and risk (Husson *et al*., 2009; Ewen *et al*., 2012; Kelle *et al*., 2013), and how these factors could vary under global change. Land-cover changes notwithstanding, forests on Borneo are expected to remain largely in their current state, as climate conditions associated with their distribution are not expected to vary substantially between present and future projections (Zelazowski *et al*., 2011). Although potential changes to forest phenology, and hence orang-utan food availability, remain poorly understood (Malhi *et al*., 2014), time budget models indicate that time available for foraging and resting behaviours could nevertheless be a significant constraint on the orang-utan's ability to adapt to climate change (Carne *et al*., 2006).

While translocation, reintroduction and supplementation are common management tools in orang-utan conservation, they have been implemented with mixed success (Russon, 2009). Still, these strategies generally have high public and governmental support, and there are already examples of orang-utan releases into regions of Central and East Kalimantan where no wild populations previously existed (BOSF, 2013). The feasibility of such introductions elsewhere on Borneo should therefore be assessed alongside other climate change adaptations such as corridor development, but continue to be seen as a last resort. In either case, the identification of refuge areas will become increasingly important for the conservation of orang-utan and other threatened species, especially in the context of extensive land cover and climate changes that are predicted for this century.

Acknowledgements

The study was supported by the Great Apes Survival Partnership of the United Nations Environment Programme via funding from the Norway Government, as well as the Arcus Foundation, and a Leverhulme Trust Research Fellowship awarded to MJS. We thank all contributors to the orang-utan data in the original assessment, and the Indonesian and Malaysian government agencies who supported their research. Nicola Abram, Mark Ancrenaz, Carolyn Devens, Surya Purnama, Andjar Rafiastanto and Lili Sadikin provided additional records from Sabah and Central Kalimantan. Perry van Duijnhoven helped with Figure S2. In addition, we are grateful to primate experts who advised on habitat suitability, including Henry Bernard, Susan Cheyne, Mark Harrison and Simon Husson.

References

Abram NK, Meijaard E, Ancrenaz M *et al.* (2014) Spatially explicit perceptions of ecosystem services and land cover change in forested regions of Borneo. *Ecosystem Services*, **7**, 116–127.

Ancrenaz M, Gimenez O, Ambu L *et al.* (2004) Aerial surveys give new estimates for orangutans in Sabah, Malaysia. *PLoS Biology*, **3**, e3.

Ancrenaz M, Ambu L, Sunjoto I, Ahmad E, Manokaran K, Meijaard E, Lackman I (2010) Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orang-utans (*P. p. morio*) can be maintained in slightly logged forests. *PLoS ONE*, **5**, e11510.

Ancrenaz M, Sollmann R, Meijaard E *et al.* (2014) Coming down from the trees: is terrestrial activity in Bornean orangutans natural or disturbance driven? *Scientific Reports*, **4**, 4024, doi: 10.1038/srep04024.

Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modelling. *Ecology*, **93**, 1527–1539.

Ashcroft MB (2010) Identifying refugia from climate change. *Journal of Biogeography*, **37**, 1407–1413.

Barbet-Massin M, Thuiller W, Jiguet F (2012) The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology*, **18**, 881–890.

Beale CM, Baker NE, Brewer MJ, Lennon JJ (2013) Protected area networks and savannah bird biodiversity in the face of climate change and land degradation. *Ecology Letters*, **16**, 1061–1068.

Beck J, Böller M, Erhardt A, Schwanghart W (2014) Spatial bias in the GBIF database and its effect on modelling species' geographic distributions. *Ecological Informatics*, **19**, 10–15.

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

BOSF (2013) *Annual report 2012*. The Borneo Orangutan Survival Foundation, Bogor, Indonesia.

Brodie JF, Giordano AJ, Dickson B *et al.* (2014) Evaluating multispecies landscape connectivity in a threatened tropical mammal community. *Conservation Biology*, in press, doi: 10.1111/cobi.12337.

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, **23**, 453–460.

Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G (2010) Uncertainty in ensemble forecasting of species distribution. *Global Change Biology*, **16**, 1145–1157.

Carne C, Semple S, Lehmann J (2006) The effects of climate change on orangutans: a time budget model. In: *Climate Models*. (ed. Druyan LM), pp. 313. Available at: http://www.intechopen.com/books/climate-models, InTech (accessed 2 December 2014)

Chauvenet ALM, Ewen JG, Armstrong DP, Blackburn TM, Pettorelli N (2013) Maximizing the success of assisted colonizations. *Animal Conservation*, **16**, 161–169.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Cochard B, Amblard P, Durand-Gasselin T (2005) Oil palm genetic improvement and sustainable development. *Oléagineux, Corps Gras, Lipides*, **12**, 141–147.

Colwell RK, Brehm G, Cardelius CL, Gilman AC, Longino JY (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **322**, 258–261.

De Chazal J, Rounsevell MDA (2009) Land-use and climate change within assessments of biodiversity change: a review. *Global Environmental Change*, **19**, 306–315.

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution*, **1**, 330–342.

Ewen JG, Armstrong DP, Parker KA, Seddon PJ (eds.) (2012) *Reintroduction Biology: Integrating Science and Management*. Blackwell Publishing Ltd, UK.

Fitzherbert EB, Struebig M, Morel A, Danielsen F, Brühl C, Donald PF, Phalan B (2008) How will oil palm expansion affect biodiversity? *Trends in Ecology & Evolution*, **23**, 538–545.

Gaveau DLA, Epting J, Lyne O, Linkie M, Kumara I, Kanninen M, Leader-Williams N (2009a) Evaluating whether protected areas reduce tropical deforestation in Sumatra. *Journal of Biogeography*, **36**, 2165–2175.

Gaveau DLA, Wich S, Epting J, Juhn D, Kanninen M, Leader-Williams N (2009b) The future of forests and orangutans (*Pongo abelii*) in Sumatra: predicting impacts of oil palm plantations, road construction, and mechanisms for reducing carbon emissions from deforestation. *Environmental Research Letters*, **4**, 034013.

Gaveau DLA, Kshatriya M, Sheil D *et al.* (2013) Reconciling forest conservation and logging in Indonesian Borneo. *PLoS ONE*, **8**, e69887.

Gaveau DLA, Sloan S, Molidena E *et al.* (2014) Four decades of forest persistence, clearance and logging on Borneo. *PLoS ONE*, **8**, e0101654.

Gingold B, Rosenbarger A, Muliastra YIKD *et al.* (2012) *How to Identify Degraded Land for Sustainable Palm Oil in Indonesia*. World Resources Institute and Sekala, Washington D.C.

Gregory SD, Brook BW, Goossens B, Ancrenaz M, Alfred R, Ambu LN, Fordham DA (2012) Long-term field data and climate-habitat models show that orangutan persistence depends on effective forest management and greenhouse gas mitigation. *PLoS ONE*, **7**, e43846.

Gregory SD, Ancrenaz M, Brook BW, Goossens B, Alfred R, Ambu LN, Fordham DA (2014) Forecasts of habitat suitability improve habitat corridor efficacy in rapidly changing environments. *Diversity and Distributions*, **20**, 1044–1057.

Guisan A, Tingley R, Baumgartner JB *et al.* (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, **16**, 1424–1435.

Hansen MC, Potapov PV, Moore R *et al.* (2013) High-resolution global maps of 21st-century forest cover change. *Science*, **342**, 850–853.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hoekman D, Vissers M, Wielaard N (2009) *PALSAR land cover mapping methodology validation study Borneo*. Wagingen University, The Netherlands.

Husson S, Wich S, Marshall AJ *et al.* (2009) Orang-utan distribution, density, abundance and impacts of disturbance. In: *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (eds Wich S, Atmoko SSU, Setia MS, Van Schaik CP), pp. 77–96. Oxford University Press, Oxford.

Junker J, Blake S, Boesch C *et al.* (2012) Recent decline in suitable environmental conditions for African great apes. *Diversity and Distributions*, **18**, 1077–1091.

Kelle D, Fechter D, Singer A, Pratje P, Storch I (2013) Determining sensitive parameters for the population viability of reintroduced Sumatran Orangutans (*Pongo abelii*). *International Journal of Primatology*, **34**, 423–442.

Keppel G, Wardell-Johnson GW (2012) Refugia: keys to climate change management. *Global Change Biology*, **18**, 2389–2391.

Koh LP, Miettinen J, Liew SC, Ghazoul J (2011) Remotely sensed evidence of tropical peatland conversion to oil palm. *Proceedings of the National Academy of Sciences*, **108**, 5127–5132.

Kramer-Schadt S, Niedballa J, Pilgrim JD *et al.* (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions*, **19**, 1366–1379.

Langner A, Miettinen J, Siegert F (2007) Land cover change 2002-2005 in Borneo and the role of fire derived from MODIS imagery. *Global Change Biology*, **13**, 2329–2340.

Laurance WF, Sayer J, Cassman KG (2014) Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, **29**, 107–116.

Lehmann J, Korstjens AH, Dunbar RIM (2010) Apes in a changing world – the effects of global warming on the behaviour and distribution of African apes. *Journal of Biogeography*, **37**, 2217–2231.

Malhi Y, Gardner TA, Goldsmith GR *et al.* (2014) Tropical Forests in the Anthropocene. *Annual Review of Environment and Resources*, **39**, 125–159.

Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239–1252.

Marshall AJ, Lacy RC, Ancrenaz M *et al.* (2009) Orangutan population biology, life history, and conservation. In: *Orangutans: geographic variation in behavioral ecology and conservation* (eds Wich S, Atmoko SSU, Setia MS, Van Schaik CP), pp. 311–326. Oxford University Press, Oxford.

Martin Y, Van Dyck H, Dendoncker N, Titeux N (2013) Testing instead of assuming the importance of land use change scenarios to model species distributions under climate change. *Global Ecology and Biogeography*, **22**, 1204–1216.

Meijaard E, Albar G, Nardiyono, Rayadin Y, Ancrenaz M, Spehar S (2010a) Unexpected ecological resilience in Bornean orangutans and implications for pulp and paper plantation management. *PLoS ONE*, **5**, e12813.

Meijaard E, Welsh A, Ancrenaz M, Wich S, Nijman V, Marshall A (2010b) Declining orangutan encounter rates from Wallace to the present suggest the species was once more abundant. *PLoS ONE*, **5**, e12042.

Meijaard E, Buchori D, Hadiprakarsa Y *et al.* (2011) Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. *PLoS ONE*, **6**, e27491.

Meijaard E, Wich S, Ancrenaz M, Marshall AJ (2012) Not by science alone: why orangutan conservationists must think outside the box. *Annals of the New York Academy of Sciences*, **1249**, 29–44.

Miettinen J, Shi C, Liew SC (2011) Deforestation rates in insular Southeast Asia between 2000 and 2010. *Global Change Biology*, **17**, 2261–2270.

Nietlisbach P, Arora N, Nater A, Goossens B, Van Schaik CP, Krützen M (2012) Heavily male-biased long-distance dispersal of orang-utans (genus: *Pongo*), as revealed by Y-chromosomal and mitochondrial genetic markers. *Molecular Ecology*, **21**, 3173–3186.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Reviews of Ecology, Evolution and Systematics*, **37**, 637–669.

Pearson R, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, **34**, 102–117.

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.

Reside AE, Welbergen JA, Phillips BL *et al.* (2014) Characteristics of climate change refugia for Australian biodiversity. *Austral Ecology*, **39**, 887–897.

Rijksen HD, Meijaard E (1999) *Our Vanishing Relative. The Status of Wild Orang-Utans at the Close of the Twentieth Century*. Kluwer Academic Publishers, Dordrecht, Netherlands.

Russon AE (2009) Orangutan rehabilitation and reintroduction: successes, failures and role in conservation. In: *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (eds Wich S, Atmoko SSU, Setia MS, Van Schaik CP), pp. 327–403. Oxford University Press, Oxford.

Schwartz MW, Martin TG (2013) Translocation of imperiled species under changing climates. *Annals of the New York Academy of Sciences*, **1286**, 15–28.

Schweiger O, Heikkinen RK, Harpke A *et al.* (2012) Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Global Ecology and Biogeography*, **21**, 88–99.

Seddon PJ (2010) From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restoration Ecology*, **18**, 796–802.

Singleton I, Knott CD, Morrogh-Bernard HC, Wich S, Van Shaik CP (2009) Ranging behavior of orangutan and social organization. In: *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (eds Wich S, Atmoko SSU, Setia MS, Van Schaik CP), pp. 205–215. Oxford University Press, Oxford.

Stanton JC, Pearson RG, Horning N, Ersts P, Reşit Akçakaya H (2012) Combining static and dynamic variables in species distribution models under climate change. *Methods in Ecology and Evolution*, **3**, 349–357.

Struebig M, Wilting A, Gaveau DLA, Meijaard E, Smith R, The Borneo Mammal Distribution Consortium, Fischer M, Metcalfe K, Kramer-Schadt S (In Press). Targeted conservation to safeguard a biodiversity hotspot from climate and land-cover change. *Current Biology*, doi: 10.1016/j.cub.2014.11.067.

Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the heat on tropical animals. *Science*, **320**, 1296–1297.

Thomas CD (2011) Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology and Evolution*, **26**, 216–221.

Tingley R, Herman TB (2009) Land-cover data improve bioclimatic models for anurans and turtles at a regional scale. *Journal of Biogeography*, **36**, 1656–1672.

Turner M (2005) Landscape ecology: what is the state of the science. *Annual Reviews of Ecology, Evolution and Systematics*, **36**, 319–344.

Varela S, Anderson RP, García-Valdés R, Fernández-González F (2014) Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. *Ecography*, **37**, 1084–1091.

Warren DL, Seifert SN (2010) Ecological niche modelling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342.

Wich SA, Meijaard E, Marshall AJ *et al.* (2008) Distribution and conservation status of the orang-utan (*Pongo* spp.) on Borneo and Sumatra: how many remain? *Oryx*, **42**, 329–339.

Wich S, Gaveau DLA, Abram N *et al.* (2012) Understanding the impacts of land-use policies on a threatened species: is there a future for the Bornean Orang-utan? *PLoS ONE*, **7**, e49142.

Wilting A, Cord A, Hearn AJ *et al.* (2010) Modelling the species distribution of flat-headed cats (*Prionailurus planiceps*), an endangered south-east Asian small felid. *PLoS ONE*, **5**, e9612.

Zelazowski P, Malhi Y, Huntingford C, Sitch S, Fisher JB (2011) Changes in the potential distribution of humid tropical forests on a warmer planet. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **369**, 137–160.

Supporting Information

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

Appendix S1. Further description of source data and bioclimatic modelling for Bornean orang-utan.
Appendix S2. Further description of the predictive deforestation model for Borneo.
Appendix S3. Mapping suitable land for oil palm cultivation.
Appendix S4. Potential refuges from future environmental change for the Bornean orang-utan.