Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution

34 authors, including:

Jena Hickey
National Park Service
24 PUBLICATIONS **291** CITATIONS

SEE PROFILE

Nathan Nibbelink
University of Georgia
98 PUBLICATIONS **2,021** CITATIONS

SEE PROFILE

Janet Nackoney
University of Maryland, College Park
33 PUBLICATIONS **746** CITATIONS

SEE PROFILE

Stephen Blake
Max-Planck-Institut für Ornithologie, Teilinstitut Radolfzell
125 PUBLICATIONS **6,180** CITATIONS

SEE PROFILE

ORIGINAL PAPER

Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution

**Jena R. Hickey · Janet Nackoney · Nathan P. Nibbelink · Stephen Blake ·
Aime Bonyenge · Sally Coxe · Jef Dupain · Maurice Emetshu ·
Takeshi Furuichi · Falk Grossmann · Patrick Guislain · John Hart ·
Chie Hashimoto · Bernard Ikembelo · Omari Ilambu · Bila-Isia Inogwabini ·
Innocent Liengola · Albert Lotana Lokasola · Alain Lushimba ·
Fiona Maisels · Joel Masselink · Valentin Mbenzo ·
Norbert Mbangia Mulavwa · Pascal Naky · Nicolas Mwanza Ndunda ·
Pele Nkumu · Valentin Omasombo · Gay Edwards Reinartz ·
Robert Rose · Tetsuya Sakamaki · Samantha Strindberg ·
Hiroyuki Takemoto · Ashley Vosper · Hjalmar S. Kühl**

Abstract Habitat loss and hunting threaten bonobos (*Pan paniscus*), Endangered (IUCN)
great apes endemic to lowland rainforests of the Democratic Republic of Congo. Con-
servation planning requires a current, data-driven, rangewide map of probable bonobo
distribution and an understanding of key attributes of areas used by bonobos. We present a
rangewide suitability model for bonobos based on a maximum entropy algorithm in which
data associated with locations of bonobo nests helped predict suitable conditions across the
species' entire range. We systematically evaluated available biotic and abiotic factors,
including a bonobo-specific forest fragmentation layer (forest edge density), and produced

---

J. R. Hickey (✉)
Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA
e-mail: jrh367@cornell.edu

J. Nackoney
Department of Geographical Sciences, University of Maryland, 2181 LeFrak Hall,
College Park, MD 20742, USA
e-mail: jnackone@umd.edu

N. P. Nibbelink
Warnell School of Forestry and Natural Resources, University of Georgia,
Athens, GA 30602-2152, USA
e-mail: nate2@uga.edu

S. Blake
Max Planck Institute of Ornithology, Vogelwarte Radolfzell, Schlossallee 2,
78315 Radolfzell, Germany
e-mail: sblakewcs@gmail.com

a final model revealing the importance of simple threat-based factors in a data poor environment. We confronted the issue of survey bias in presence-only models and devised a novel evaluation approach applicable to other taxa by comparing models built with data from geographically distinct sub-regions that had higher survey effort. The model's classification accuracy was high (AUC = 0.82). Distance from agriculture and forest edge density best predicted bonobo occurrence with bonobo nests more likely to occur farther from agriculture and in areas of lower edge density. These results suggest that bonobos either avoid areas of higher human activity, fragmented forests, or both, and that humans reduce the effective habitat of bonobos. The model results contribute to an increased understanding of threats to bonobo populations, as well as help identify priority areas for future surveys and determine core bonobo protection areas.

Introduction

Wildlife conservation relies on understanding patterns of species occurrence. With the global human footprint ever growing and intensifying (Sanderson et al. 2002), approximate delineations of species' ranges exclusively based on historic data are no longer enough for

A. Bonyenge · M. Emetshu · B. Ikembelo · I. Liengola · P. Naky · P. Nkumu
Wildlife Conservation Society, 1725 Ave Col. Mondjiba Ngaelima, Kinshasa,
Democratic Republic of the Congo
e-mail: bonyenge@yahoo.fr

M. Emetshu
e-mail: mauriceemetshu@yahoo.fr

B. Ikembelo
e-mail: bernardikembelo@yahoo.fr

I. Liengola
e-mail: iliengola2002@yahoo.fr

P. Naky
e-mail: nakybopolo@yahoo.fr

P. Nkumu
e-mail: nkumupele@yahoo.fr

S. Coxe
Bonobo Conservation Initiative, 2701 Connecticut Ave. NW #702, Washington, DC 20008, USA
e-mail: scoxe@bonobo.org

J. Dupain
African Wildlife Foundation Conservation Centre, Ngong Road, Karen,
P.O. Box 310, Nairobi 00502, Kenya
e-mail: jdupain@awfafrica.org

T. Furuichi · C. Hashimoto · T. Sakamaki · H. Takemoto
Primate Research Institute, Kyoto University, Kanrin, Inuyama, Aichi 484-8506, Japan
e-mail: furuichi@pri.kyoto-u.ac.jp

C. Hashimoto
e-mail: hashimot@pri.kyoto-u.ac.jp

conservation and minimum-impact infrastructure planning. As such, spatially-explicit rangewide models that deliver fine-scaled information on suitable conditions are critical. Such models can inform land-use plans designed to maintain connected, viable populations of species. In the Democratic Republic of Congo (DRC), annual human population growth is increasing rapidly—estimates range from 2.6 % (UNDP 2011) to 3.2 % (USAID 2010)—driving increased deforestation in areas of previously intact forest (Hansen et al. 2008; OSFAC 2010). Increased poverty from the collapse of the agricultural sector during and following DRC's recent civil wars has also contributed to a rise in bushmeat hunting, which remains a substantial threat to the viability of many game species (Draulans and Van Krunkelsven 2002; Yamagiwa 2003; Beyers et al. 2011).

Bonobos (*Pan paniscus*) are great apes listed as Endangered on the IUCN Red List since 2007 (Fruth et al. 2008). They are endemic to the lowland rainforests of DRC and are threatened by both habitat loss and hunting (IUCN 2010). For conservation efforts to be successful, up-to-date information on the rangewide distribution of bonobos and an evaluation of their threats is required (Grossmann et al. 2008). A bonobo conservation-action planning meeting was held in Kinshasa, DRC in January 2011, with a large group of bonobo experts and representatives from DRC's government. Several objectives for bonobo conservation were defined, including the promotion of strategic land-use management and conservation plans at local, regional and national levels. Achieving this objective required spatial information about the probability of bonobo occurrence in unsampled areas and the characteristics and drivers of bonobo distribution.

T. Sakamaki
e-mail: sakamaki@pri.kyoto-u.ac.jp

H. Takemoto
e-mail: takemoto@pri.kyoto-u.ac.jp

F. Grossmann · F. Maisels · J. Masselink · R. Rose · S. Strindberg
Wildlife Conservation Society, 2300 Southern Blvd., Bronx, NY 10460, USA
e-mail: fgrossmann@wcs.org

F. Maisels
e-mail: fmaisels@wcs.org

J. Masselink
e-mail: jmasselink@gmail.com

R. Rose
e-mail: rrose@wcs.org

S. Strindberg
e-mail: sstrinberg@wcs.org

P. Guislain · G. E. Reinartz
Bonobo and Congo Biodiversity Initiative, Zoological Society of Milwaukee, 10005 W. Bluemound Rd., Milwaukee, WI 53226, USA
e-mail: patrickg@zoosociety.org

G. E. Reinartz
e-mail: gayr@zoosociety.org

J. Hart
Lukuru Foundation, Kinshasa, Democratic Republic of the Congo
e-mail: johnhartdrc@gmail.com

Junker et al. (2012) presented a first effort at providing such spatial information for all great ape species across Africa. Here, we provide a finer resolution (100 m^2 vs. 5 km^2) bonobo-specific rangewide suitability model that explores additional indices of threats. Model development began in a collaborative workshop held in Kinshasa immediately prior to the action-planning meeting. We used a maximum-entropy modeling approach (Max-Ent; Phillips et al. 2006; Elith et al. 2010) that combined bonobo nest locations with environmental layers to predict the spatial distribution of potentially suitable conditions. Recognizing that suitable conditions include food availability, shelter, and security from hunting, we used a suite of environmental variables to model bonobo distribution and evaluated their relative prediction strength. To date, spatial vegetation data lack sufficient detail to be relevant for bonobo foraging. We therefore focused on the presence of broad forest types where bonobos are known to nest, abiotic factors that likely influence vegetation (and indirectly, occurrence of forage species), and proxies for hunting pressure as measures of habitat security (Swenson 1982). For the purpose of this paper, we defined suitable conditions as those locations where bonobo nests occur, which necessarily include conditions with reduced risk of hunting.

MaxEnt is a modeling tool that uses presence-only occurrence data and has been found to perform favorably in comparison to other presence-only models (Elith et al. 2006; Hernandez et al. 2006). It has been widely applied in the species distribution modeling literature: primate examples include monkeys in Amazonia (Boubli and de Lima 2009), slow lorises in Southeast Asia (Thorn et al. 2009), and chimpanzees in West Africa (Torres et al. 2010).

O. Ilambu · B.-I. Inogwabini
World Wildlife Fund, DRC, 14, Avenue Sergent Moke, Kinshasa, Commune de Ngaliema, Kinshasa, Democratic Republic of the Congo
e-mail: oilambu@wwfcarpo.org

B.-I. Inogwabini
e-mail: bi4@kent.ac.uk

A. L. Lokasola
Kokolopori Bonobo Nature Reserve, Avenue Nguma Numero 80, Ma Campagne, Kinshasa, Democratic Republic of the Congo
e-mail: viesauvage@yahoo.fr

A. Lushimba
African Wildlife Foundation, Kinshasa Office, 12 Avenue Comité Urbain, Gombe, Kinshasa, Democratic Republic of the Congo
e-mail: alushimba@awfafrica.org

F. Maisels
School of Natural Sciences, Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK

V. Mbenzo
Congo Basin Ecosystems Conservation Support Program (PACEBCo), Kinshasa, Democratic Republic of the Congo
e-mail: va.mbenzo@pacebco-ceeac.org

N. M. Mulavwa · N. M. Ndunda
Center of Research in Ecology and Forestry (CREF), Ministry of Education and Scientific Research, Mabali, Democratic Republic of the Congo
e-mail: mbanginorbert@yahoo.fr

We present a rangewide map of modeled relative suitability for bonobos. The map and approach serve as a foundation for further refinement as improved habitat data become available. The DRC Government recognizes the need for sustainable land-use planning, and local and international non-government organizations have generated momentum toward achieving it (USAID 2010). Our map and results will assist planning efforts by providing necessary information for bonobo conservation prioritization.

Study area

The bonobo range, located in central DRC, is defined by the Congo River to the north and west, the Lualaba River to the east, and the Kasai/Sankuru Rivers to the south (IUCN 2010). Although the distribution of bonobos is currently thought to be discontinuous with isolated populations located in the western portion of the range, we included the entire area in our model because the collective knowledge on bonobo occurrence, especially in unsurveyed areas, is still expanding. We therefore developed a contiguous boundary based initially on the IUCN (2010) range and then expanded it to encompass all known bonobo occurrences southward to the Kasai River, thereby eliminating any isolated pockets (Fig. 1). The total area of this range is approximately 563,330 km^2.

Materials and methods

Bonobo data

Multiple entities collected the presence-only bonobo data used in this model. These data were compiled as part of the IUCN/SSC primate specialist group (PSG) Apes, Populations, Environments, and Surveys (A.P.E.S.) database managed by the Max Planck Institute for Evolutionary Anthropology. The IUCN/SSC A.P.E.S. database provides a global picture of the distribution and status of great apes and informs their long-term management and conservation. During the Kinshasa workshop, we evaluated the presence-only data and performed quality assessment and control prior to modeling. We used bonobo nest locations collected between years 2003 and 2010 from the IUCN/SSC A.P.E.S. database, rather than all signs (e.g. feeding remains or tracks) in order to characterize habitat where bonobos nest rather than areas used only for transient movement. Numerous teams collected data along randomly- or systematically-located line transects, or recce walks; the

N. M. Ndunda
e-mail: mwanzandunda@yahoo.fr

V. Omasombo
Congolese Institute for the Conservation of Nature (ICCN), Kinshasa,
Democratic Republic of the Congo
e-mail: valomasombo@yahoo.fr

A. Vosper
Wildlife Conservation Society, Pointe Noire, Zanaga, Democratic Republic of the Congo
e-mail: ashley.vosper@gmail.com

H. S. Kühl
Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany
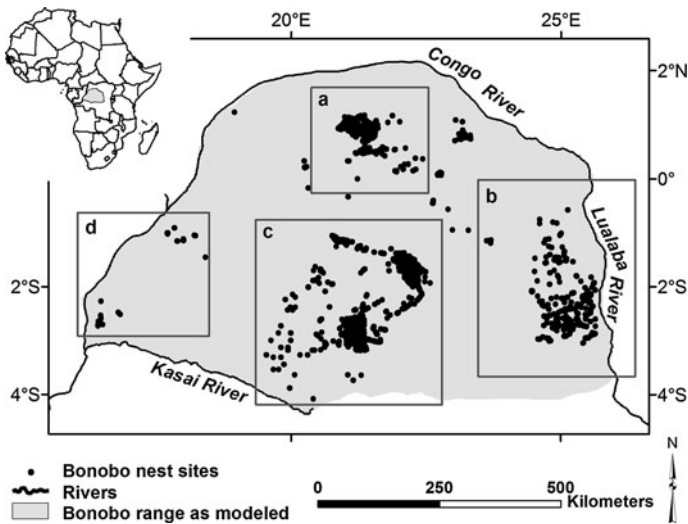e-mail: kuehl@eva.mpg.de

Fig. 1 A map of the bonobo range as defined for the purpose of this effort to model suitable conditions for bonobos rangewide. All wild bonobos inhabit the area south of the Congo River, Democratic Republic of Congo. Specific regions referred to in the text correspond to the boxes shown: **a** Maringa–Lopori–Wamba Landscape (MLW), **b** Tshuapa–Lomami–Lualaba Landscape (TL2), **c** Salonga National Park (SNP), and **d** Lac Tumba (LT), respectively

latter followed the path of least resistance and focused on areas where bonobo signs were found. Because bonobo nests and nest sites tend to be clustered, we reduced the effects of spatial auto-correlation by aggregating the individual nest or nest-site locations to 100 × 100 m blocks (the same resolution as the environmental predictor layers). A block containing one or more nests or nest sites was termed a *nest block*. Because groups of nests tend to be located within 30 m or less (Mulavwa et al. 2010), this block size corresponded well to the scale of nest groups, lowering the risk that a single nest group was split between two blocks. We compiled data for 2,364 nest blocks throughout the bonobo range (Fig. 1).

Predictor variables

We collaboratively developed and evaluated a suite of environmental predictors relevant to bonobos. MaxEnt allows for the incorporation of a diverse range of environmental predictor variables (hereafter referred to as "predictors" or "environmental layers") including biotic, abiotic, and threat-based data. However, MaxEnt requires that data values exist for each pixel across the entire modeled range. Certain data describing factors that influence bonobo presence, such as detailed vegetation layers and understory information (including bonobo forage species), are not classified and mapped for the bonobo range. This is due to the vast size and extreme inaccessibility of the region, a history of highly localized research effort, and the sheer logistical and economic challenges to ground truth remotely sensed data in Central Africa.

To construct the model, we focused on two broad biotic predictors (percent forest and presence of intact forest), select abiotic factors that may influence vegetation (and hence, forage, such as precipitation and soil type), and measures of potential human pressure. Environmental layers were assembled from a variety of sources with varying resolutions.

We qualitatively assessed each predictor variable's expected influence on bonobo occurrence (Table 1). We resampled the environmental layers to 100 m resolution in ArcGIS to standardize the pixel size. The Africover data (FAO 2000) contained six landcover categories: agriculture, broadleaved rainforest, swamp rainforest, shrub, urban, and water. Because we found that most nest blocks (99.9 %) were located in just two forest cover types (broadleaved rainforest and swamp rainforest), we re-classified these data into a single forest cover type. We then calculated percent forest on that cover type based on a 3×3 cell neighborhood of 100 m cells (0.09 km^2) using FRAGSTATS 3.3 (McGarigal et al. 2002). This neighborhood analysis addressed potential GPS error and decreased the possibility of misclassification of any given cell. While bonobos nest in terra-firma forest more often (Mohneke and Fruth 2008; Reinartz et al. 2008), we included swamp forest in the percent-forest variable because Mulavwa et al. (2010) reported 13 % of nest groups in swamp forest, thereby supporting suitability for nesting.

Calculation

MaxEnt (version 3.3.1) predicts relative suitability of conditions based on presence-only data. It does not require known absences; instead, MaxEnt relies on random background points to characterize the range and variation of values for each environmental layer across the study area. Using the "species with data" (SWD) format and 10,000 random background points, MaxEnt compared the environmental values of nest blocks to the environmental values observed throughout the bonobo range to predict probability of suitable conditions in unsurveyed areas (Elith et al. 2010). It is noteworthy that MaxEnt performs best with relatively broad sampling coverage within the area of interest (Phillips et al. 2009). Although there was clustering of nest locations where sampling intensity was high, nest-block locations were well-distributed throughout the bonobo range (Fig. 1).

Recent research (Yackulic et al. 2013) highlighted common misconceptions when using MaxEnt, noting the relevance of detection probability to model inference, the consequences of using data with sample selection bias, and the importance of critically examining modeled relationships. We consider those concerns here. Although we do not have a direct estimate of detection probability for all nests in our dataset, we have reason to expect it to be high and not to vary substantially with environmental predictors. Hickey (2012) estimated the probability of nest detection as 0.93 when there were a total of 4 observers and found no support for variance in detection probability by forest type. Most, if not all, nest data for the present study were collected with teams of ≥ 4 observers; therefore, for this rangewide dataset, we believe that detection probability is unlikely to influence model inference. However, using presence-only data can sometimes produce results that are geographically biased to regions located near the presence points (Phillips 2008; Phillips et al. 2009). This effect can be most pronounced if those areas are highly surveyed relative to the full dataset (Phillips et al. 2009). To test for such bias, we ran iterative models withholding nest-block locations and background points from specific regions to evaluate how well each reduced-data model performed in the area of withheld data. This procedure informally evaluated the sensitivity of the models to potential bias from highly sampled sites and the ability of the models to predict into unsampled regions. Specifically, we tested a succession of separate models, independently withholding nest data from each of the following highly-sampled regions: Maringa–Lopori–Wamba (MLW), Tshuapa–Lomami–Lualaba (TL2), and Salonga national park (SNP) (Fig. 1a–c, respectively). We also ran another series of models that each used only the data from one intensively-sampled region

Table 1 List of environmental predictor variables originally used and those used in the final model predicting relative suitability of conditions for bonobos rangewide, Democratic Republic of Congo

Category	Name	Description	Influence forage	Expected relationship			Source
				Forage availability	Security from hunting	Bonobo Presence	
Forest metrics	Percent forest[a]	Percentage of broadleaf terra-firma and swamp forest in a 9-cell neighbourhood (= 0.09 km²) reclassified from six landcover types	Yes	+	+	+	FAO (2000)
Forest metrics	Intact forest	Presence of blocks of forest >500 km²	Yes	+	+	+	Potapov et al. (2008)
Forest metrics	Forest edge density[a]	A measure of forest fragmentation at 57 m resolution, then resampled up	Yes	U	–	–	Hickey et al. (2012)
Climate	Monthly Mean Precipitation	mm/month	Yes	+	No	+	Hijmans et al. (2005)
Terrain	Elevation	1 km Digital Elevation Model	Yes	U	U	U	USGS (2000)
Terrain	Soil lithology	Surface rock type	Yes	U	No	U	van Engelen et al. (2006)
Terrain	Soil types	Dominant soil types	Yes	U	No	U	van Engelen et al. (2006)
Terrain	Compound Topographic Index	From HYDRO1k elevation derivative database	Yes	U	No	U	USGS (2000)
Terrain	Distance from rivers[a]	Distance to nearest river or stream in km calculated from HYDRO1k elevation derivative database	Yes	U	+	+	USGS (2000)
Human impact	Distance from agriculture[a]	Distance to nearest agricultural complex in km as reclassified from landcover types	Yes	+	+	+	FAO (2000)
Human impact	Distance from roads	Distance to nearest road in km	No	U	+	+	WRI (2010)
Human impact	Presence of forest loss	Locations of areas experiencing deforestation between the years 1990–2000 and 2000–2010	Yes	U	–	–	OSFAC (2010)

Table 1 continued

Expected relationship

Category	Name	Description	Influence forage	Forage availability	Security from hunting	Bonobo Presence	Source
Human impact	Distance to forest loss	Distance to nearest areas experiencing deforestation between the years 1990–2000 and 2000–2010	Yes	U	+	+	OSFAC (2010)

Yes predictor variable expected to influence the location of bonobo forage species

No predictor variable not expected to relate to the life-history component listed

U relationship unknown

+ Positive correlation expected between predictor variable and mechanism influencing bonobo presence

− Negative correlation expected between predictor variable and mechanism influencing bonobo presence

[a] Retained in final model

at a time, plus a model that used only data from a lightly sampled area (39 nest blocks) called Lac Tumba (LT) (Fig. 1d). These sensitivity tests allowed us to evaluate how well models built with presence data from each region predicted other regions of known occurrence, and whether the relative importance of different predictor variables changed based on the region from which presence data originated.

We varied the suite of included environmental layers to test their predictive performance and to refine their selection based on diagnostics (explained below). We rejected predictors exhibiting too narrow a range of values because they added little discerning capability to the models (e.g. certain datasets, such as soil type, were mapped at such coarse resolution that only one value dominated the entire bonobo range). For each MaxEnt analysis in the series, we used a random 70 % of the nest blocks as training data to build the model and withheld 30 % to independently test model accuracy.

A common metric for evaluating the classification accuracy of MaxEnt models is the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Phillips et al. 2006). An AUC of 0.5 represents a prediction no better than random, whereas a theoretically perfect prediction would approach an AUC of 1, with no errors of omission or commission. Omission and commission error, or false-negative and false-positive prediction respectively, are used to calculate sensitivity and specificity. Traditionally, a graph of the true positive rate (sensitivity) on the y-axis and the false positive rate (1-specificity) on the x-axis gives the AUC. MaxEnt, however, calculates the AUC using the fractional predicted area on the x-axis (Phillips et al. 2006), resulting in a theoretical maximum equal to $[1 - (\text{predicted area}/2)]$ (Wiley et al. 2003). This adjustment accounts for the fact that the background points are not true absences and therefore do not indicate false positives. Standard deviation of the test AUC provides an estimate of significance (DeLong et al. 1988; Phillips 2006).

We also ran a jackknife analysis to determine the relative contribution of each environmental predictor to the models' performance. In this procedure, MaxEnt removed one predictor and ran the model once on the individual predictor and again on the remaining predictors. Using this approach, MaxEnt calculated the difference in the training and test gains of each predictor alone, the model without that predictor, and the full model with all predictors included. *Gain* is closely related to deviance, a measure of goodness of fit used in generalized additive and generalized linear models; it starts at 0 and increases asymptotically during the model run (Phillips 2006). Training and test gains relate to training and test data, respectively. High test gains reflect predictor variables that better predict locations not used to build the model (test data). We removed environmental predictors that contributed negligibly to prediction (low gains). To avoid multicollinearity, we calculated Pearson's correlation coefficient, r, and removed predictor variables that were strongly correlated ($r \geq 0.49$). However, in order to assess model sensitivity to such removal and to determine the direction and strength of relationships between nest blocks and removed correlated predictors, we ran a series of models in which the retained predictor was substituted by the corresponding removed predictor. For binary suitability maps, we selected the "maximum sensitivity plus specificity" threshold because it balances omission and commission errors thereby generating neither overly cautious nor overly optimistic predictions regarding suitable conditions. All other settings, including regularization, were left at default values.

Results

The final output of the MaxEnt model (Fig. 2) highlights locations most likely suitable for bonobos based on the final model containing distance from agriculture, edge density,
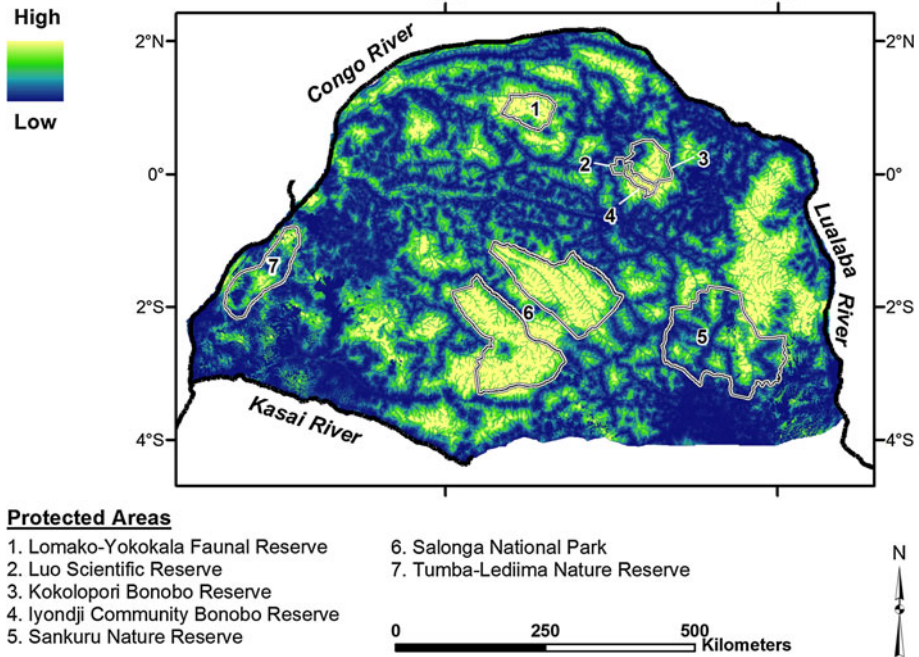
Fig. 2 Final rangewide map of suitable conditions for bonobos, based on locations of bonobo nest blocks and the strongest non-correlated predictor variables using a maximum-entropy approach. The polygons denote boundaries of official protected areas at the time of writing

percent forest, and distance from river. The jackknife analyses showed that the first three of these were the best predictors of bonobo nest presence (Table 2; Fig. 3). We included distance from river in the final model because it increased model accuracy and was not correlated with the other three predictors. Each of the predictors was threat-based except percent forest. Distance from agriculture contributed most to the final model and to all models with one region withheld, making it the most important predictor. In the final model, approximately 28 % (156,211 km^2) of the bonobo range was predicted suitable based on the maximum test sensitivity plus specificity threshold (values greater than 0.3). This cut-off value was 0.3, producing a maximum classification accuracy when values greater than 0.3 were classified as suitable. Within the area of suitable conditions, about 46 % has had at least some level of survey effort and 27.5 % (42,979 km^2) was located in official protected areas. The majority of Iyondji Community Bonobo Reserve, Lomako–Yokokala Faunal Reserve, SNP, and Kokolopori Bonobo Reserve were predicted suitable (87, 86, 82 and 64 %, respectively) whereas less than 50 % each of Luo Scientific Reserve, Sankuru Reserve, and Tumba–Lediima Reserve were predicted as suitable.

Predictor-exclusion rules rejected certain variables from the final model as follows. We removed forest-loss variables because they contributed negligibly (training gains <0.05 each). Distance from agriculture and distance from roads were highly correlated (Pearson's $r = 0.72$), and therefore we removed the weaker predictor of the two, distance from roads. Nevertheless, distance from roads was a strong predictor of bonobo nest occurrence, with

Table 2 MaxEnt diagnostics for each predictor variable modeling the relative suitability of conditions for bonobos rangewide using each predictor variable by itself

Predictor variable	Training gain	Test gain	AUC
Distance from agriculture	0.58	0.50	0.77
Edge density	0.34	0.35	0.73
Percent forest	0.16	0.15	0.58
Distance from river	0.10	0.08	0.6

Gain is a measure of relative goodness-of-fit (Phillips 2006). An AUC of 1 would be perfect prediction whereas 0.5 would be no better than random

nests more likely to occur farther from roads. Model runs replacing distance from agriculture by distance from roads produced very similar results, with distance from roads being the strongest predictor in the absence of distance from agriculture. Presence of intact forest was negatively correlated with edge density ($r = -0.55$) and was removed, leaving the variable with the highest test gain (edge density) as the only remaining forest pattern metric. We removed soil and lithology due to minimal variation throughout the range. Similarly, elevation and precipitation exhibited a narrow range of values, with 145–672 m and 118–179 mm/month, respectively. With the selected settings (default feature types and regularization), MaxEnt over-fit the model to these two variables, creating complex relationships that were not biologically defensible, so we omitted them.

Training and test AUCs (0.82 and 0.80, respectively) indicated strong prediction accuracy for the final model. MaxEnt calculated the theoretical maximum test AUC [$1 -$ (predicted area/2)] of the data as 0.816. The small standard deviation (±0.007) of the test AUC confirmed that model performance was significantly better than random (AUC = 0.5). In addition, the series of models for which we iteratively removed data from each highly-sampled region resulted in maps that still predicted the withheld regions as likely suitable (not shown). This confirmed that the final model (1) predicted suitable conditions beyond regions of known occurrence, (2) was robust to missing data despite the absence of surveys in some areas, and (3) was not overly biased toward predicting suitable conditions in close proximity to presence points. If the latter were true, the withhold-one-region models would not have consistently predicted the missing region as suitable.

The withhold-one-region models generally supported the final model, whereas models built using region-specific nest blocks showed some noteworthy differences in terms of both transferability and predictor variable importance. For comparison purposes, we applied the final model's threshold of 0.3 to all region-specific models (Fig. 4). The models built with MLW-only (Fig. 1a) and SNP-only (Fig. 1c) data agreed most with the final model (44.6 and 63.5 % spatial overlap, respectively). The SNP model predicted similarly to the MLW model (overlapping 91 % of the MLW model), yet the SNP output had larger areas of high suitability. The MLW model predicted 13 % of the range as suitable while the SNP model predicted 18 % (the final rangewide model predicted 28 % of the range as suitable). The TL2-only model was the most liberal, predicting nearly 44 % of the range as suitable. The LT-only model was the most dissimilar of the four region-specific models; it predicted only 11 % of the range as suitable, and those locations were nearly the spatial inverse of the final model's prediction with only 8 % spatial overlap.
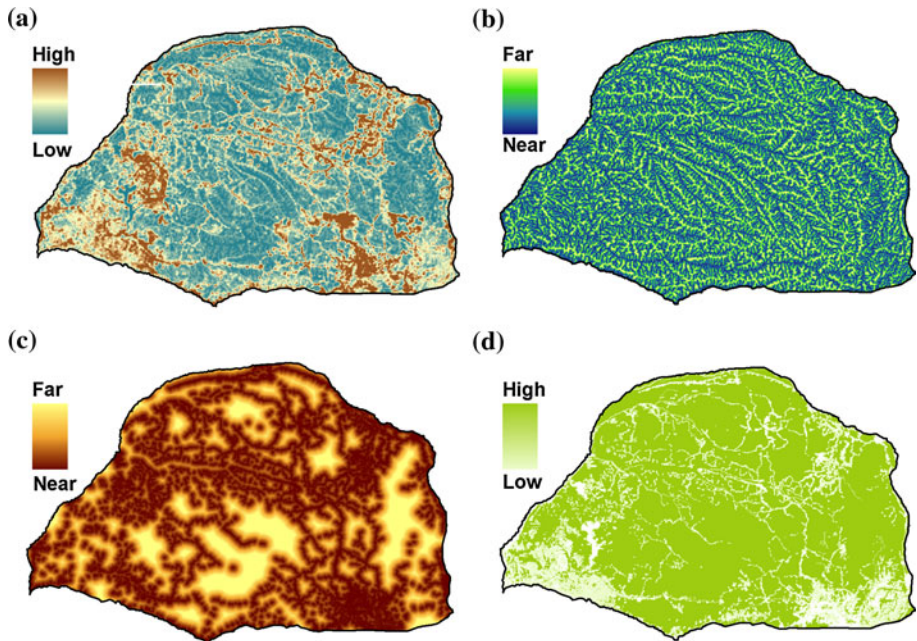
Fig. 3 Maps of the selected environmental variables used in the final model to predict relative suitability of conditions for bonobos: **a** edge density (km/km²), **b** distance from river (km), **c** distance from agriculture (km), and **d** percent-forest landcover. All maps are drawn at 100 m resolution

Of the four predictor variables, distance from agriculture had the highest test gain for all models except the MLW-only model, for which edge density was higher. Edge density was one of the top two predictors for all region-specific models except TL2, which was more influenced by percent forest. Distance from river had test gains between 0.14 and 0.24 for all region-specific models except the TL2 model, where it had a test gain of 0.06.

The response curves (Supplemental Fig. 1) show the relationship between each predictor and suitability of conditions for bonobos based on the final model. As expected, distance from agriculture and distance from rivers were positively correlated with bonobo occurrence, with nests more often occurring far from agriculture and rivers. Edge density was negatively correlated with bonobo occurrence, suggesting that bonobos tend to nest in areas of low edge density rather than in highly fragmented forests. Percent forest was a broad-scale predictor, positively correlated with bonobo occurrence.

As described earlier, elevation was excluded from the final model; however, prior to removal, it too served as a broad predictor suggesting that bonobos tend to occur above approximately 400 m elevation. Few surveys occurred below 400 m elevation; this likely caused a sampling bias that created this apparent elevational pattern. When elevation was included in the model, the mapped output predicted large swaths of terra-firma forest in the south-west and a smaller area in the north-west of the range as *un*suitable. Yet, when elevation was excluded from the model, the output depicted these same regions as suitable (Supplemental Fig. 2). Based on our knowledge of bonobo ecology, we find no support for this type of elevation-related limitation to their distribution given the presence of appropriate vegetation and absence of potential threats.
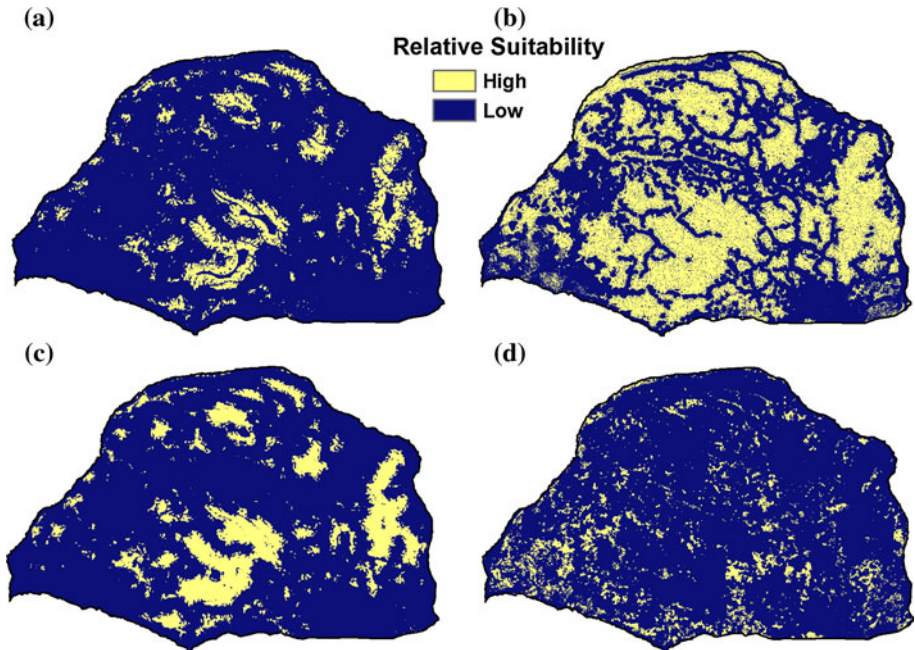
Fig. 4 A comparison of suitable conditions for bonobos as predicted by four rangewide models differing in their presence-only input data. Each was built from nest-block data limited to the following corresponding regions **a** MLW-only, **b** TL2-only, **c** SNP-only, and **d** LT-only, Democratic Republic of Congo. Note the similarity between **a**, **c**, and the final model (Fig. 2)

Discussion

Results from our iterative modeling approach strongly suggest that threats associated with human activity (forest fragmentation and proximity to agriculture, roads and rivers) affect the bonobo distribution. Human impact has become the key predictor of the bonobo rangewide distribution and overrides the importance of ecological conditions as measured in this analysis. We view these predictors as indicators of hunting impact. Areas closer to agriculture and roads are closer to human populations who tend to hunt in the surrounding forest (Robinson 1996; Hart et al. 2008). Roads and navigable rivers provide human access to areas that would otherwise likely be less vulnerable to hunting (Wilkie et al. 2000; Blake et al. 2007). The higher number of nests occurring far from rivers could also be indicative of proportionately higher use of terra-firma rather than seasonally inundated forests by bonobos. This relationship and the importance of swamp forests for bonobo nesting need further study. Edge density distills information on forest fragmentation occurring from agriculture, logging, major rivers, and roads (all of which create edge) into a single metric describing hunter accessibility. Very likely, it is poaching associated with these metrics that is the single common threat influencing bonobo occurrence. However, at the regional/local scale, there will be some exceptions due to cultural taboos against eating bonobos. Such taboos are in a state of flux because of changing values associated with immigrant populations (Fruth et al. 2008); therefore, poaching of bonobos may begin to occur in new areas, further magnifying this threat.

MaxEnt proved an effective tool for developing a useful distribution model where presence-only data were available. Other great ape modeling studies that benefited from both presence and absence data (e.g. Wich et al. 2011; Stokes et al. 2010) applied more traditional modeling methods like generalized linear models and generalized additive models. Because our study compiled bonobo observations from numerous data providers, absence data were not always available, and we recommend the use of iterative MaxEnt modeling for similar efforts where presence-only data are used. For other ape species threatened by hunting, a similar analysis could elucidate important patterns relating ape occurrences to landscape metrics and hunter accessibility. However, the specific relationship between forest edge density and ape occurrence is likely to be case specific and vary by species, habitat type, habitat condition, prevailing hunting and land-use patterns, and effectiveness of law enforcement.

In the final model, threat-based variables were better predictors of suitability for bonobos than were biotic and abiotic factors. However, this could be due to greater availability of data describing human threats at the correct spatial scale than were available for other biotic and abiotic factors. Because hunting persists throughout most of the bonobo range, including in areas that are legally protected (Dupain and Van Elsacker 2001; Hart et al. 2008), it is difficult to determine environmental variables that would predict suitable conditions in the absence of hunting. Finer-scale analyses of relative hunting pressure are recommended to further examine these effects. While distance from roads was not included in the final model due to multicollinearity with distance from agriculture, it was in fact one of the strongest predictors of bonobo nest occurrence (second only to its correlated variable, distance from agriculture). As such, proximity to roads should also be considered an important threat to bonobos. We recommend repeating this study's approach when more detailed biotic and abiotic data relevant to bonobos become available.

The first bonobo conservation action plan (Thompson-Handler et al. 1995) recognized that very little was known about bonobos and outlined an expansive area that needed to be surveyed to determine bonobo distribution, abundance and the environmental factors influencing bonobo presence. Here, we show the results of a comprehensive compilation of bonobo nest data collected since then, and offer a current rangewide bonobo distribution model (Fig. 2) that can be used to inform future bonobo conservation actions and plans. A similar approach of iterative modeling would likely prove useful to develop robust maps of predicted distributions of other taxa and serve as a basis for associated conservation action plans.

Due to spatially comprehensive data requirements, the model provided here does not benefit from finer-resolution data nor more detailed understandings of local areas well-known to particular researchers. Instead, this type of knowledge of bonobo occurrence can be used in combination with the prediction map on a case-by-case basis. Future modeling would benefit from higher resolution environmental data, particularly for vegetation.

When building predictive models, it is important to critically consider classification accuracy (AUC). In some previous studies using MaxEnt (Phillips et al. 2009; Veloz 2009), small sample sizes of geographically clumped data produced inflated measures of AUC, especially when projecting to large extents (Anderson and Gonzalez 2011). For such studies, the data were biased by the characteristics found in those limited geographic areas, yet high accuracies were reported (all AUCs >0.9 when extrapolating to areas ≥100 km from known presences, VanDerWal et al. 2009). Suggestions for corrective action have included restricting the geographic distribution of background points used by MaxEnt to surveyed areas in order to match potential bias in the presence-only data (Phillips et al. 2009). Our sensitivity test of a model in which we used LT-only data (39 nest sites)

underscored the caution needed when modeling large areas with small presence-only datasets (Fig. 4d), because the LT-only output is implausible given the other known nest locations throughout the range. In contrast, the strength of the full dataset used in our final model is that the data are numerous (>2,000 nest blocks), points span the entire modeled area, clusters of those points cover vast expanses, and surveyed regions represent a broad portion of each predictor's range of values. Due to these characteristics, we did not restrict background points to surveyed areas but instead used 10,000 random points distributed throughout the entire range. We interpret the test AUC (0.80) of this study to be biologically reasonable based on the input data and, after iterative modeling, find no evidence that it is inflated. The high AUC demonstrates that the model exhibits high classification accuracy and therefore is likely to be useful for predicting areas of relative suitability.

The final model predicted numerous unsampled areas as likely suitable for bonobos, suggesting that it is not overly biased to vicinities near presence points. The succession of test models built by sequentially removing presence data from each highly-sampled region (i.e., MLW, TL2 and SNP) demonstrated high spatial overlap with each other and with the final model. Such agreement further increased our confidence in the model's portrayal of suitable conditions for bonobos. Finally, our series of test models built using just one highly-sampled region at a time confirmed that the full set of compiled presence data sufficiently portrayed the range of conditions (described by the predictors) that bonobos have generally tolerated, given that humans are part of the landscape. This novel method of addressing survey bias, a common problem in species distribution modeling, could be applied to other studies, particularly in order to assist the development of conservation plans for other great apes.

However, all models are simplified interpretations of the real world with inherent error. The model may highlight areas as suitable that, in the field, contain little or no evidence of bonobos. Reasons why such areas might not harbor bonobos could include: recent hunting, biotic interactions, existence of conditions outside the range of model training (e.g. an important predictor variable may be missing), or simply that bonobos have not moved into that area, but could in the future. There were both advantages and disadvantages to using bonobo nest data collected over a span of seven years. Strengths were that more areas could be surveyed over the longer duration and the likelihood of detecting bonobo nests was improved in areas where repeat surveys occurred. Therefore, the study was not merely a snapshot of bonobo presence, but instead considered their presence over a longer time period. A potential drawback to basing the model on this extended data collection period, however, was that it may overestimate suitability in areas where bonobo populations have since declined. Another limitation of the model was that predictor variables were restricted to those for which spatially explicit data existed across the entire range, which constrained our ability to test a wide range of environmental predictors. Moreover, there was uncertainty regarding the best way to compute the percent-forest variable; we could define forest as terra-firma forest alone, or we could include both swamp forest and terra-firma forest in the definition. There is evidence that, in addition to terra-firma rainforest, bonobos do nest in swamp forests (Mohneke and Fruth 2008; Reinartz et al. 2008; Mulavwa et al. 2010) at a higher proportion than indicated by the rangewide dataset. We concluded that swamp forest is underrepresented in survey effort, partially due to its sampling difficulty, and therefore included it in our computation of percent forest, thereby removing the influence of this potential survey bias on the MaxEnt algorithm.

The iterative MaxEnt modeling approach identified the most important factors determining the current bonobo distribution. Distance from agriculture was the strongest predictor of bonobo presence, with suitability increasing farther from agricultural areas.

Furthermore, the region-specific models revealed local exceptions. In MLW, edge density best predicted suitable conditions for bonobos whereas in TL2 percent-forest predicted better than edge density. These outcomes were likely explained by the difference in the range of values represented for each predictor within each region. Despite such local patterns, the MLW-only, SNP-only, and TL2-only models exhibited high spatial agreement with each other and with the final model. By contrast, only the LT data produced an anomalous and demonstrably inaccurate rangewide model. While LT nests did occur near agriculture and at intermediate edge density values, these represented the extreme values for bonobo nest blocks and were not indicative of the rangewide relationship between nest blocks and these variables. These results demonstrated both the geographic variation of factors determining bonobo presence, and the importance of using well-distributed presence-only data when extrapolating to broad areas across the entire range.

The final suitability map provides a necessary foundation for developing sound actions that are needed to maintain viable bonobo populations. For example, the map can be used to spatially prioritize regions with highest suitability in order to concentrate conservation effort therein. Further, the map identifies certain unsurveyed areas as potentially suitable that may be important for bonobo conservation. In fact, at least 54 % of area predicted suitable has yet to be surveyed. Conducting additional bonobo surveys in these areas will be especially important as such areas may either currently harbour unsurveyed bonobo populations or support a natural expansion of the current bonobo distribution. Additionally, because this distribution model does not predict density of bonobos, continued monitoring of known populations remains necessary to better assess bonobo abundance.

Here, the best predictors (distance from agriculture and edge density) are both effects of human activity, representing habitat loss in addition to hunter accessibility. Others have noted the importance of habitat loss, fragmentation and shape of habitat patches, and distance from humans to primate populations (Arroyo-Rodriguez et al. 2008). Therefore, where possible, we recommend any future agricultural, logging or infrastructure development concentrate in areas of least suitability and avoid areas of high suitability. Overall, we urge that priority actions focus on reducing bonobo hunting mortality. Concrete activities to achieve this goal that have proven useful in other regions may also be applicable to bonobos, e.g., increasing the effectiveness of law enforcement by establishing links to ecological monitoring programs (N'Goran et al. 2012) or improving protected area effectiveness by creating zones of increased wildlife protection through long-term presence of research and tourism (Campbell et al. 2011; Tranquilli et al. 2012). We hope that our analysis will contribute significantly to the development of these and other land-use management plans aimed at protecting highly suitable areas, reducing threats to bonobos, and promoting conservation and sustainable natural resource management throughout the bonobo range.

References

Anderson RP, Gonzalez I (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. Ecol Model 222:2796–2811

Arroyo-Rodriguez V, Mandujano S, Benítez-Malvido J (2008) Landscape attributes affecting patch occupancy by howler monkeys (*Alouatta palliata mexicana*) at Los Tuxtlas, Mexico. Am J Primatol 70:69–77

Beyers RL, Hart JA, Sinclair ARE, Grossmann F, Klinkenberg B, Dino S (2011) Resource wars and conflict ivory: the impact of civil conflict on elephants in the Democratic Republic of Congo—the case of the Okapi Reserve. PLoS One 6(11):e27129. doi:10.1371/journal.pone.0027129

Blake S, Strindberg S, Boudjan P, Makombo C, Bila-Isia I et al (2007) Forest elephant crisis in the Congo Basin. PLoS Biol 5(4):e111. doi:10.1371/journal.pbio.0050111s

Boubli JP, de Lima MG (2009) Modeling the geographical distribution and fundamental niches of *Cacajao* spp. and *Chiropotes israelita* in Northwestern Amazonia via a maximum entropy algorithm. International J Primatol 30:217–228

Campbell G, Kuehl HS, Diarrassouba A, N'Goran PK, Boesch C (2011) Long-term research sites as refugia for threatened and over-harvested species. Biol Lett 7:723–726

DeLong ER, DeLong D, Clarke-Pearson D (1988) Comparing the areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. Biometrics 44:837–845

Draulans D, Van Krunkelsven E (2002) The impact of war on forest areas in the Democratic Republic of Congo. Oryx 36:35–40

Dupain J, Van Elsacker L (2001) The status of the bonobo in the Democratic Republic of Congo. In: Galdikas BMF, Briggs NE, Sheeran LK, Shapiro GL, Goodall J (eds) All Apes Great and Small Volume 1: African Apes. Kluwer Academic/Plenum Publishers, New York, pp 57–74

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates C (2010) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57

FAO (2000) Africover multipurpose land cover databases for Democratic Republic of Congo. Food and Agriculture Organization (FAO) of the United Nations, Rome. www.africover.org. Accessed 23 July 2011

Fruth B, Benishay JM, Bila-Isia I, Coxe S, Dupain J, Furuichi T, Hart J, Hart T, Hashimoto C, Hohmann G, Hurley M, Ilambu O, Mulavwa M, Ndunda M, Omasombo V, Reinartz G, Scherlis J, Steel L, Thompson J (2008) *Pan paniscus*. IUCN Red List of Threatened Species, Version 2010.4 (IUCN 2010). www.iucnredlist.org. Accessed 8 June 2011

Grossmann F, Hart J, Vosper A, Ilambu O (2008) Range occupation and population estimates of bonobos in the Salonga National Park: application to large-scale surveys of bonobos in the Democratic Republic of Congo. In: Furuichi T, Thompson J (eds) The bonobos behavior, ecology, and conservation. Springer, New York, pp 189–216

Hansen MC, Roy D, Lindquist E, Adusei B, Justice CO, Altstatt AA (2008) A method for integrating MODIS and Landsat data for systematic monitoring of forest cover and change in the Congo Basin. Remote Sens Environ 112:2495–2513

Hart J, Grossmann F, Vosper A, Ilanga J (2008) Human hunting and its impact on bonobos in the salonga national park, Democratic Republic of Congo. In: Furuichi T, Thompson J (eds) The bonobos behavior, ecology, and conservation. Springer, New York, pp 245–271

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29:773–785

Hickey JR (2012) Modeling bonobo (*Pan paniscus*) occurrence in relation to bushmeat hunting, slash-and-burn agriculture, and timber harvest: harmonizing bonobo conservation with sustainable development. Dissertation, University of Georgia

Hickey JR, Carroll JP, Nibbelink NP (2012) Applying landscape metrics to characterize potential habitat of bonobos (*Pan paniscus*) in the Maringa–Lopori–Wamba landscape, Democratic Republic of Congo. International J Primatol 33:381–400

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

IUCN (2010) IUCN Red List of Threatened Species, Version 2010.4. www.iucnredlist.org. Accessed 7 Jun 2011

IUCN/SSC A.P.E.S. Database. http://apes.eva.mpg.de. Accessed 1 Feb 2011

Junker J, Blake S, Boesch C et al (2012) Recent decline in suitable environmental conditions of African great apes. Divers Distrib 18:1077–1091

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html

Mohneke M, Fruth B (2008) Bonobo (*Pan paniscus*) density estimation in the SW-salonga national park, Democratic Republic of Congo: common methodology revisited. In: Furuichi T, Thompson J (eds) The bonobos behavior, ecology, and conservation. Springer, New York, pp 151–166

Mulavwa MN, Yangozene K, Yamba-Yamba M, Motema-Salo B, Mwanza NN, Furuichi T (2010) Nest groups of wild bonobos at Wamba: selection of vegetation and tree species and relationships between nest group size and party size. Am J Primatol 72:575–586

N'Goran PK, Boesch C, Mundry R, N'Goran EK, Herbinger I, Yapi FA, Kühl HS (2012) Hunting, law enforcement and African primate conservation. Conserv Biol 26:565–571

OSFAC (Observatoire Satellital des forêts d'Afrique Central) (2010) Forêts d'Afrique centrale évaluées par télédétection (FACET): forest cover and forest cover loss in the Democratic Republic of Congo from 2000 to 2010. South Dakota State University and University of Maryland, Brookings and College Park. ISBN 978-0-9797182-5-0

Phillips SJ (2006) A brief tutorial on Maxent. AT&T Research, Florham Park. http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc

Phillips SJ (2008) Transferability, sample selection bias and background data in presence-only modeling: a response to Peterson et al. (2007). Ecography 31:272–278

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

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

Potapov P, Yaroshenko A, Turubanova S et al. (2008) Mapping the world's intact forest landscapes by remote sensing. Ecol Soc 13(2):51. http://www.ecologyandsociety.org/vol13/iss2/art51/

Reinartz GE, Guislain P, Mboyo Bolinga TD, Isomana E, Inogwabini B, Bokomo N, Ngamankosi M, Wema Wema L (2008) Ecological factors influencing bonobo density and distribution in the salonga national park: applications for population assessment. In: Furuichi T, Thompson J (eds) The bonobos: behavior, ecology, and conservation. Springer, New York, pp 167–188

Robinson JG (1996) Hunting wildlife in forest patches: an ephemeral resource. In: Schelhas J, Greenberg R (eds) Forest Patches in Tropical Landscapes. Island Press, Washington, DC, pp 111–130

Sanderson EW, Malanding J, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. Bioscience 52:891–904

Stokes EJ, Strindberg S, Bakabana PC, Elkan PW, Iyenguet FC et al (2010) Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. PLoS One 5(4):e10294. doi:10.1371/journal.pone.0010294

Swenson JE (1982) Effects of hunting on habitat use by mule deer on mixed-grass prairie in Montana. Wildl Soc Bull 10:115–120

Thompson-Handler N, Malenky RK, Reinartz GE (1995) Action plan for *Pan paniscus*: report on free ranging populations and proposals for their preservation. Zoological Society of Milwaukee County, Milwaukee

Thorn JS, Nijman V, Smith D, Nekaris KAI (2009) Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *nycticebus*). Biodivers Distrib 15:289–298

Torres J, Brito JC, Vasconcelos MJ, Catarino L, Gonçalves J, Honrado J (2010) Ensemble models of habitat suitability relate chimpanzee (*Pan troglodytes*) conservation to forest and landscape dynamics in western Africa. Biolog Conserv 143:416–425

Tranquilli S, Abedi-Lartey M, Amsini F et al (2012) Lack of conservation effort rapidly increases African great ape extinction risk. Conserv Lett 5:48–55

UNDP (2011) Human development report 2011. United Nations development programme. Palgrave Macmillan, New York. ISBN: 9780230363311. http://hdr.undp.org/en/media/HDR_2011_EN_Complete.pdf

USAID (2010) Democratic Republic of Congo: biodiversity and tropical forestry assessment (118/119) final report. Prosperity, livelihoods and conserving ecosystems indefinite quantity contract (PLACE IQC) contract number EPP-I-03-06-00021-00. http://pdf.usaid.gov/pdf_docs/PNADS946.pdf

USGS (2000) HYDRO1k elevation derivative database. US geological survey earth resources observation and science (EROS) Center, Sioux Falls. http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30/hydro/africa. Accessed 1 Sept 2010

van Engelen VWP, Verdoodt A, Dijkshoorn JA, Van Ranst E (2006) Soil and terrain database of central Africa (DR of Congo, Burundi and Rwanda). Report 2006/07, ISRIC World Soil Information, Wageningen. http://www.isric.org. Accessed 1 Sept 2010

VanDerWal J, Shoo LP, Graham C, Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecol Model 220:589–594

Veloz SD (2009) Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. J Biogeogr 36:2290–2299

Wich SA, Fredriksson GM, Usher G, Peters HH, Priatna D, Basalamah F, Susanto W, Kühl HS (2011) Hunting of Sumatran orang-utans and its importance in determining distribution and density. Biol Conserv 146:163–169

Wiley EO, McNyset KM, Peterson AT, Robins CR, Stewart AM (2003) Niche modeling and geographic range predictions in the marine environment using a machine-learning algorithm. Oceanography 16:120–127

Wilkie DS, Morelli GA, Shaw E, Rotberg F, Auzel P (2000) Roads, development and conservation in the Congo basin. Conserv Biol 14:1614–1622

WRI (2010) Interactive forest atlas for Democratic Republic of Congo (Atlas forestier interactif de la République Démocratique du Congo), version 1.0. World resources institute and the ministry of the environment. Conservation of Nature and Tourism of the Democratic Republic of Congo, Washington, DC, USA. http://www.wri.org/publication/interactive-forest-atlas-democratic-republic-of-congo

Yackulic CB, Chandler R, Zipkin EF, Royle JA, Nichols JD, Grant EHC, Veran S (2013) Presence-only modelling using MAXENT: when can we trust the inferences? Methods Ecol Evol 4:236–243

Yamagiwa J (2003) Bushmeat poaching and the conservation crisis in Kahuzi-Biega National Park, Democratic Republic of the Congo. J. Sustain For 16:111–130