MODELING HABITAT SUITABILITY FOR *Pan troglodytes verus* IN MONTANE RAINFORESTS

A Thesis

by

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MASTER OF SCIENCE

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Tropical forests and the biodiversity within them are rapidly declining in the face of an increasing human population. Resource management and conservation of endangered species requires an understanding of how species perceive and respond to their environment so efforts can focus on areas of high importance for the species of concern. Species Distribution Modeling (SDM) is an appropriate tool for identifying conservation areas of concern and importance. In this study, maximum entropy SDM was used to identify areas of suitable chimpanzee (*Pan troglodytes verus*) habitat within the Greater Nimba Landscape of Guinea, Africa. This is an ideal location to study the effects of landscape structure on habitat suitability due to the topographic variation of the landscape and the Critically Endangered status of the chimpanzee communities in this area. Suitable habitat was predicted based on the location of direct and indirect signs of chimpanzee presence and the spatial distribution of 12 biophysical variables within the study area. Model performance was assessed by examining the area under the curve (AUC) for the test data.

The overall predictive performance of the model was 0.721 (random expectation results in AUC = 0.5). Models with AUC values greater than 0.70 are considered to have fair discriminative abilities and are ecologically useful. In addition to a map showing suitable chimpanzee habitat, the model identified the biophysical variables contributing most to habitat suitability (permutation importance). The variables most influencing
habitat suitability for chimpanzees in the study area were normalized the difference vegetation index (37.8%), elevation (27.3%), hierarchical slope position (11.5%), brightness (6.6%), and distance to rivers (5.4%). Moreover, the final model highlighted the isolation and fragmentation of chimpanzee habitat within the Greater Nimba Landscape. Understanding the factors influencing chimpanzee habitat suitability, specifically the biophysical variables considered in this study, will greatly contribute to efforts to conserve Endangered chimpanzees.
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1. INTRODUCTION

From 2000 to 2012, 2.3 million km$^2$ of forest were lost globally from anthropogenic forces with the greatest loss occurring in tropical regions (Hansen et al., 2013). Despite covering only 7% of the earth’s surface, tropical forests support over 60% of all living species (Tranquilli et al., 2014). Beyond habitat provisioning, tropical forests provide vital ecosystem services such as climate regulation at regional and global scales (Lawrence and Vandecar, 2015; Spracklen et al., 2012) and prevention of flooding and erosion (Millennium Ecosystem Assessment, 2005). As tropical forests decline in the face of increasing human population, so does biodiversity. Animal populations whose diets consist primarily of fruit, such as chimpanzees (*Pan troglodytes*), play vital ecological roles as seed dispersers for a wide variety of trees and have significant effects on the regeneration of tropical forests (Chapman, 1995; Chapman and Onderdonk, 1998; Gross-Camp et al., 2009). The absence of keystone species, such as chimpanzees, will irreversibly alter the functioning of ecosystems, both locally and globally (Tranquilli et al., 2014).

The IUCN (International Union for Conservation of Nature) has placed the *Pan troglodytes* taxon in the red list category of Endangered species since 1995 and their numbers continue to decline (Humle et al., 2016b). This includes all four subspecies of chimpanzees: Western (*P.t. verus*), Central (*P.t. troglodytes*), Eastern (*P. t. schweinfurthii*), and Nigeria-Cameroon chimpanzee (*P.t. elliottii*). The current estimate of the total population size of chimpanzees is approximately 200,000 individuals. This
estimate indicates a 66% decline within a 30-year span (Kormos et al., 2003). The principal threats to chimpanzees are habitat loss and/or degradation, hunting, and disease (Humle et al., 2016b). Chimpanzees in Guinea are the largest remaining population of the western subspecies, which are listed as Critically Endangered (Humle et al., 2016a; Kormos et al., 2003). Recognizing the devastating effects of habitat destruction and loss of biodiversity has led to an increasing number of protected areas (PAs) not only in Guinea, but throughout Africa. There are four PAs in Guinea: Massif du Ziama Strict Nature Reserve, Badiar National Park, Haut Niger National Park, and the Mount Nimba Strict Nature Reserve. An estimated 5-20% of the chimpanzee population in Guinea reside in these areas, whereas the rest live outside of PAs (Kormos et al., 2003).

Unfortunately, PAs face threats from human encroachment and neighboring land-use changes. From 2000 to 2012, the Mount Nimba Strict Nature Reserve (Mt. Nimba SNR hereafter) lost 1.5 km$^2$ of forest within its boundary and 21.7 km$^2$ within a 10 km buffer around the reserve (Allan et al., 2017). Laurance et al. (2012) found that changes both within and outside PAs are determinants of ecosystem health. For example, changes in the landscape structure of areas surrounding PAs may increase area isolation and edge effects (Laurance et al., 2012). Increasing isolation of chimpanzee communities leads to reductions in gene flow, important for sustaining healthy, viable populations (Morin et. al., 1994). Moreover, increasing competition for land and resources will lead to increases in human-chimpanzee interaction and conflict (Hockings et al., 2015; McLennan and Hill, 2012). In Bossou, Guinea, the chimpanzees rely heavily on cultivars (cassava, papaya, and bananas), THV (Zingeberaceae and Marantaceae
families), and oil palm (*Elaeis guineensis*) during periods of fruit scarcity (Humle, 2011). Many of these fallback food sources are in human impacted areas, so an increase in reliance on these foods will also cause an increase in human-chimpanzee conflict (Humle, 2011). Hence, not only will a decrease in forested areas due to human encroachment bring more humans into current chimpanzee habitat, it may result in chimpanzees ranging into areas currently dominated by human activities to access more food resources. In light of these threats and dynamic habitat-species relationships, there is a pressing need for habitat and species specific knowledge about population size, ecology, habitat loss, and human-chimpanzee interactions (Estrada et al., 2017).

To effectively protect chimpanzees and their habitats, it is crucial to understand how chimpanzees respond to their environment, so efforts can focus on areas of highest importance for their long-term survival. Identifying the environmental factors that influence chimpanzee habitat selection is a critical component of developing effective conservation plans (Rushton et al., 2004). Species distribution models (SDMs) are one way to evaluate the environmental variables related to species distribution. SDMs have gained traction as useful tools for mapping suitable habitat (also referred to as habitat suitability models) employed in reserve design, habitat management and conservation planning (Franklin, 2010). In this study, I used a maximum entropy modeling framework, namely Maxent, because it works well with presence only datasets like those available for this study (Elith et al., 2011; Phillips et al., 2006; Phillips and Dudík, 2008; Torres et al., 2010).
The aim of this study was to evaluate how the spatial distribution of biophysical features relates to the distribution of chimpanzees in the Mt. Nimba SNR. The specific objectives were (1) to quantify and map the spatial distribution of biophysical features within the study area, (2) use SDM to identify areas most suitable for chimpanzees, and (3) analyze the importance of each biophysical feature in modeling suitable chimpanzee habitat.
2. BACKGROUND

2.1 Conservation

2.1.1 Reasons for Conservation

Reasons for species conservation are varied, but they can be categorized into two rationales that are not mutually exclusive. The first rationale for conservation is that all living organisms have intrinsic value, or value in that they exist as living organisms. And in so much as they have intrinsic value, they should be protected. Intrinsic value is separate from any function or service an organism performs. In the past few centuries, philosophers, economists, and scientists, such as Immanuel Kant (1785), Aldo Leopold (1949), Peter Singer (1975), and J. Baird Callicott (1999), have proposed many different bases for why organisms have intrinsic value or why they do not. Although basing conservation on this rationale alone can be difficult, many organizations and governing bodies have included the intrinsic value of living organisms as part of their tenets. For example, the Society for Conservation Biology holds the “intrinsic value of in the natural diversity of organisms, the complexity of ecological systems, and the resilience created by evolutionary processes” as one of its five “organizational values” (SCB, 2011) and the U.N. Convention on Biodiversity states in its preamble that contracting parties be “conscious of the intrinsic value of biodiversity…” (United Nations, 1992).

The second rationale for species conservation is that all living organisms have extrinsic value in that they provide services to humans as well as other living organisms (i.e. they have instrumental value). For example, one can argue that chimpanzees have
extrinsic value as our closest living relative because by gaining a clearer understanding of chimpanzee behavior, scientists are capable of better understanding how humans have evolved. Thus, an argument could be made that chimpanzees must be protected from extinction, because they inform our understanding of human evolution. Additionally, chimpanzees have extrinsic value in that they provide ecosystem services as seed dispersers of numerous tree and plant species (Chapman, 1995; Chapman and Onderdonk, 1998; Gross-Camp et al., 2009). As such, they should be protected if these tree and plant species are to persist. Extrinsic value can also be derived from cultural and religious values. For example, the Manon people, inhabiting the area around the Mount Nimba Strict Nature Reserve, believe that chimpanzees are the reincarnation of their ancestors. As such, chimpanzees provide cultural services, a form of ecosystem service defined in the United Nation’s Millennium Ecosystem Assessment (2005).

No matter the rationale behind a researcher’s motivation for conservation, chimpanzees have value that is worth protecting. Once we recognize this value, researchers must identify the forces threatening chimpanzees in order to best protect and ensure the survival of the species.

2.1.2 Principal threats to chimpanzees

The principal threats to chimpanzees throughout Africa are habitat loss and degradation, poaching, and disease (Humle et al., 2016b). This section gives an overview of these threats.
Habitat loss and degradation are one of the main threats to chimpanzees across Africa (Kormos et al., 2003; Arcus Foundation, 2014). For chimpanzees inhabiting tropical forests, one of the major causes of habitat degradation and loss is deforestation. An estimated 32,000 km$^2$ of forests are lost each year in Africa (Arcus Foundation, 2014). Junker et al. (2012) conducted a continent wide assessment of the distribution of suitable environmental conditions (SECs) for all apes across Africa. They found that within its geographic range, chimpanzees lost approximately 21% of their SECs between 1990 and 2000. In Guinea alone, the proportion of SECs lost between 1990 and 2000 was 4.5% (Junker et al., 2012; Arcus Foundation, 2014). These estimates were based on species-level models using climatic, anthropogenic disturbance, and vegetation variables at a 5 x 5 km spatial resolution. The causes of deforestation include the expansion of subsistence farming, large-scale commercial farming, and extractive industries (Arcus Foundation, 2014).

Another major threat to the long-term survival of chimpanzees is poaching. Poaching is the illegal hunting and capturing of wild animals. Species most impacted by poaching are those that are long-lived, large-bodied, and reproduce at a slow rate (Kormos et al., 2003). Because chimpanzees meet all of these criteria, they are a species extremely vulnerable to poaching. The poaching of chimpanzees commonly occurs for bushmeat and the pet trade. Hunting pressure varies regionally and locally depending on cultural and religious traditions. For example, the Manon community living near the Mt. Nimba SNR believes chimpanzees are their reincarnated ancestors. Thus, chimpanzees are not hunted or consumed because it is a religious taboo. Despite the majority of the
local people holding firm to this belief, people from different religious and cultural traditions may travel to the region for its diverse wildlife and prospects of bushmeat. Additionally, although chimpanzees are not commonly the targets for hunters in this region, they are at risk of getting caught in snares set for other wildlife, such as bush pigs and duikers. Hunting for other wildlife, even in protected areas, is common. For example, in 2012, researchers found 82 traps and 30 bullet casings, and heard 23 gunshots while conducting fieldwork in the Mt. Nimba SNR (Koops, unpublished data).

In addition to poaching and habitat degradation, disease is a significant risk for chimpanzees. Infectious diseases, such as the Ebola virus and other zoonoses like influenza, have the potential to cause massive declines in ape populations. Because chimpanzees and humans are physiologically and genetically similar, human encroachment into chimpanzee habitats increases the rate of disease transmission between chimpanzees and humans as the encounter rate between the two also increases (Humle, 2011). In Gabon and the Republic of Congo, the Ebola virus is believed to have caused a massive reduction in gorilla and chimpanzee populations in the mid-1990s and early 2000s (Leendertz et al., 2016; Walsh et al., 2003). Between 1960 and 2006, Williams et al. (2008) found that more than 50% of the deaths occurring in the Kasekela community of chimpanzees in Gombe National Park, Tanzania, were due to illnesses such as polio, respiratory infections, and mange. In Bossou, Guinea, a respiratory illness epidemic in 2003 resulted in the death of five chimpanzees (Humle, 2011; Matsuzawa et al., 2004). This significantly reduced the size of the Bossou community from 19 chimpanzees to only 12. Although the exact origins of the illnesses in the examples
above are not clear, it is evident that chimpanzees are highly susceptible to many of the same illnesses as humans. Thus, any increases in human-chimpanzee encounters are threats to the survival of both species.

2.2 Habitat Suitability Modeling for Conservation

Despite the many threats to the survival of chimpanzees, new technologies and methods are constantly emerging that can help researchers and conservation practitioners combat these threats. One tool that is quickly gaining traction in conservation-oriented research is species distribution modeling (SDM). Species distribution models estimate conditions suitable for species survival by examining the relationships between species’ occurrence and associated environmental conditions. SDMs are based on three conceptual frameworks: ecological, data, and statistical (Austin, 2002).

The ecological framework refers to the ecological theory driving the research study. For example, the central concept of landscape ecology is that all landscapes have a structure that influences its function and vice versa (Coulson and Tchakerian, 2010). In other words, pattern influences process and process in turn influences patterns within a landscape. Thus, given this landscape ecological theory, one could posit that the distribution of biophysical variables, such as slope and aspect, across a user-defined landscape will influence the distribution of species across that same landscape.

The data framework refers to the methods used for data collection and measurement, such as whether to use remotely sensed data, the spatial resolution of that data, and whether the study includes species presence and absence data or just species
presence data. For example, a study might need to integrate remotely sensed data with field data to assist in more accurately classifying landscape structure.

The statistical framework refers to the choice of statistical methods used for model formulation, calibration, and validation (Austin, 2002). For instance, this might include a choice between using a generalized linear model, a generalized additive model, or a machine learning method such as maximum entropy to model species distribution. Moreover, the parameters used to calibrate and validate a model play a major role in a model’s effectiveness (Elith et al., 2011).

The ecological, data, and statistical frameworks underpinning SDM are intertwined. Decisions made within one framework influence the decisions made in another. For example, when presence but not absence data are available for a species, it limits the choice of statistical methods that can be applied to the data. As long as one understands the decisions necessary for model construction and how choices made within each conceptual framework influence the final model, SDM can have a wide range of applications. One common application of SDM is for creating maps of habitat suitability (referred to as habitat suitability modeling) that can be employed in reserve design, habitat management, and conservation planning (Franklin, 2010). For example, Leblond et al. (2014) developed habitat suitability models for Boreal caribou in eastern Canada that can be used to inform logging and industrial development policies. Habitat suitability modeling has also been used with connectivity analyses to assess the potential for species recovery (Cianfrani et al., 2013) as well as long-term viability and overall species conservation (Ramirez-reyes et al., 2016).
3. METHODS

3.1 Study Site

The Mt. Nimba SNR is a UNESCO World Heritage Site in Danger. The Mt. Nimba SNR encompasses most of the Nimba Mountain range in Guinea and parts of Côte d'Ivoire on the southeastern side of the mountain range. Covering approximately 175 km², the reserve is dominated by wet, evergreen forests with diverse topographical features including rocky peaks, rough cliffs, bare granite, steep river valleys, high altitude savannahs and rounded hilltops (Guillaumet and Adjano, 1971; Koops, 2011; Kormos et al., 2003). The reserve is home to a variety of flora and fauna, including the critically endangered endemic Mt. Nimba viviparous toad (*Nimbaphrynoides occidentalis*) and Critically Endangered chimpanzees (*P. t. verus*).

The study site (N 07.37°, W 08.28°), spanning 30 km², is located on the Guinean side of the Nimba Mountains within the Mt. Nimba SNR (Figure 1). The site is largely composed of primary tropical forests, but as the terrain becomes steeper, it transitions to a mosaic of terrestrial herbaceous vegetation, montane forest, and high altitude grasslands (Koops, 2011). The elevation ranges from 595 m to 1511 m. The climate is characterized by a rainy season from February to October and a dry season lasting from November to February (Koops et al, 2012, 2013). The site is adjacent to the small village of Seringbara, located about 6 km from Bossou at the foot of the Nimba Mountains (Koops, 2011). Bossou is home to a community of chimpanzees (currently 7 individuals) that have been the focus of research for over 30 years by the Kyoto University Primate Research Institute (KUPRI) (Matsuzawa and Humle, 2011). Seringbara and Bossou are
separated by savannah that few chimpanzees traverse (Matsuzawa et al., 2011). This study focuses on two communities of chimpanzees within the Mt. Nimba SNR, known as the Seringbara communities, both composed of approximately 30-40 individuals (Koops, unpublished data). The Seringbara communities have been the focus of habituation efforts and behavioral ecology studies since 2003, yet the chimpanzees remain mostly unhabituated to humans (Koops, 2011).

![Figure 1 Location of the study area on the Guinean side of the Mt. Nimba SNR in West Africa.](image)

### 3.2 Occurrence Data

Between January 2012 and April 2014, I was part of a team of researcher assistants and local field assistants collecting data on chimpanzee behavior at the Seringbara study site on the Guinean side of the Mt. Nimba SNR directed by K. Koops (University of Cambridge & University of Zurich). Research teams maintained a nearly constant
presence in the forest during this period, only missing data collection for one to two days a month. Field days focused on tracking and directly observing chimpanzees to obtain data on chimpanzee ranging, grouping, diet, nest building, and tool use. Direct observations of chimpanzees can be difficult in the wild, especially when communities are not fully habituated, such as the Seringbara communities. For this reason, nests, fecal samples, ant dipping sites, and feeding traces (i.e. wadges) were considered indirect indicators of chimpanzee presence and included as occurrence points along with direct chimpanzee sightings. All occurrence points were collected with GPS devices.

Data on chimpanzee presence were recorded using handheld Global Positioning System (GPS) devices during daily tracking of the chimpanzees. In total, 1386 occurrence points were recorded at different locations. Occurrence points were not evenly distributed throughout the study area due to sampling bias. In a study comparing the different methods commonly used to correct for sampling bias, Fourcade et al. (2014) found that systematic spatial filtering, consistently outperformed most other methods regardless of the species or type of bias. Systematic spatial filtering uses a grid of a user defined cell size and randomly keeps one occurrence point per cell. I used R 3.3.2 to place a grid (30 m resolution) over the study area and randomly select one occurrence point from each grid cell. The total occurrence points were filtered and reduced to N=947 for use in the final model (Figure 2). R scripts used to spatially filter the occurrence points are found in Appendix A.
3.3 Predictor Variables

Raster layers of predictor variables (Table 1) dealing with landscape structure and land cover, herein referred to as biophysical variables, were prepared at a 30-meter spatial resolution. An initial set of 17 biophysical variables (Table 1) were assessed, as detailed below, before being narrowed down to 12 variables for the final model. Minimum distance, supervised classification of a Landsat 8 image, obtained during the study period (December 26, 2013), was used in ENVI 5.0.2 to delineate 5 land cover
types: dense forest, mixed forest, bare ground, village, and savannah (Appendix B). These 5 classes were chosen based on expert knowledge of the region after analyzing the spectral groupings of the supervised classification. Dense forests consist of mostly primary, undisturbed forest. Mixed forests are mostly secondary, disturbed forests with less dense vegetation and less canopy cover. Bare ground includes cleared areas, sparsely vegetated grasslands, and bare rock. Savannah consists of very dense, tall grass areas lacking trees. The village class includes buildings, huts, and other anthropogenic structures interspersed with bare ground. The minimum distance land cover classification procedure performed well (overall accuracy of 90.78% and kappa coefficient of 0.8653) in distinguishing between macro habitats, such as savannah and forest, but was not able to distinguish microhabitats, such as vegetation types, at the spatial resolution of the image (30 m). Because chimpanzees have sophisticated mental mapping capabilities (Ban et al., 2014; Boesch and Boesch, 1984; Normand et al., 2009; Normand and Boesch, 2009) and are able to perceive their surroundings at the level of individual trees and forest patches, vegetation indices were calculated to capture differences at micro scales (Pintea et al., 2003; Torres et al., 2010). Landsat 8 imagery from 6 different dates within the data collection period was used to derive an average normalized difference vegetation index (NDVI) raster. NDVI is an indication of relative biomass (i.e. healthy, photosynthetically active vegetation) within each raster cell and can range from -1 (water or bare ground) to 1 (healthy, dense vegetation). It is calculated as using the near-infrared and red bands of a satellite image \((\text{NIR} - \text{R})/(\text{NIR} + \text{R})\) (Campbell and Wynne, 2011). In addition, I captured microhabitat characteristics within
the study area using a tasseled cap transformation of the original Landsat 8 image. This process transforms the original spectral data into a new coordinate system with 4 orthogonal axes (Campbell and Wynne, 2011). Each of these axes carries specific information that can be interpreted as (1) soil and surface brightness (brightness), (2) photosynthetically active vegetation (greenness), (3) soil moisture (wetness), and (4) atmospheric noise (Crist and Cicone, 1984).

Studies of the Seringbara chimpanzees (Koops, 2011; Koops et al., 2012, 2013), as well as other primates (Clee et al., 2015; Gregory et al., 2014; Hickey et al., 2013; Plumptre et al., 2010; Serckx et al., 2016; Torres et al., 2010; Wich et al., 2012), indicate that climate, vegetation, and anthropogenic factors may play a significant role in identifying suitable habitat. In particular, the dietary preferences of Seringbara chimpanzees indicate that the availability of fruit affects their ranging patterns (Koops, 2011; Koops et al., 2013). Many of the tree species producing fruit utilized by the chimpanzees occur in primary forests and at elevations higher than 800 m (e.g. Parinari excelsa) (Koops, 2011). Therefore, the other biophysical variables included in the initial model were chosen for their ability to serve as proxies for these factors (Franklin, 2009).

The following variables were generated using ArcMap 10.2.2 and R 3.3.2 (R Core Team, 2005) and derived from a digital elevation model (DEM) from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model Version 2 (NASA, JPL, 2009): elevation, slope, aspect, topographic position index, roughness, integrated moisture index, heat load index, landform curvature, compound topographic index surface relief, and hierarchical slope
position (Table 1). The R script for calculating hierarchical slope position is found in Appendix C. The distance to rivers variable was generated in ArcMap 10.2.2 using a shapefile of rivers within the Greater Nimba Landscape and calculating the Euclidean distance of each 30 m² cell from the nearest river.

I examined correlation between variables to reduce the effect that collinearity might have on interpreting Maxent results (Dormann et al., 2013; Kumar et al., 2014; Rodder et al., 2013). Correlation was calculated using Pearson’s product moment correlation (r). For a set of highly correlated variables (|r| >0.7), the variable with the highest predictive power (training gain), in the preliminary model using all 17 biophysical variables, was retained (Dormann et al., 2013; Estes et al., 2010; Hickey et al., 2013).
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<tbody>
<tr>
<td>Elevation*</td>
<td>elevation</td>
<td>Meters</td>
<td>Height above sea level</td>
<td>ASTER GDEM v.2</td>
<td>ArcMap 10.2.2</td>
</tr>
<tr>
<td>Aspect*</td>
<td>aspect</td>
<td>Degrees</td>
<td>Direction a slope faces</td>
<td>ASTER GDEM v.2</td>
<td>ArcMap 10.2.2</td>
</tr>
<tr>
<td>Slope</td>
<td>slope</td>
<td>Degrees</td>
<td>Steepness of a surface</td>
<td>ASTER GDEM v.2</td>
<td>ArcMap 10.2.2</td>
</tr>
<tr>
<td>Normalized Difference Vegetation Index*</td>
<td>NDVI</td>
<td>unitless</td>
<td>Index of relative biomass (average of 6 dates within study period)</td>
<td>Landsat 8</td>
<td>-</td>
</tr>
<tr>
<td>Wetness</td>
<td>wetness</td>
<td>unitless</td>
<td>Soil moisture content</td>
<td>Landsat 8</td>
<td>Baig et al., 2014</td>
</tr>
<tr>
<td>Brightness*</td>
<td>brightness</td>
<td>unitless</td>
<td>Soil brightness</td>
<td>Landsat 8</td>
<td>Baig et al., 2014</td>
</tr>
<tr>
<td>Land Cover Class</td>
<td>LCC</td>
<td>unitless</td>
<td>Categorization of land cover types</td>
<td>Landsat 8</td>
<td>-</td>
</tr>
<tr>
<td>Topographic Position Index</td>
<td>TPI</td>
<td>unitless</td>
<td>Difference between elevation at one point and the mean elevation around it</td>
<td>ASTER GDEM v.2</td>
<td>De Reu et al., 2013; Guisan et al., 1999</td>
</tr>
<tr>
<td>Integrated Moisture Index*</td>
<td>IMI</td>
<td>unitless</td>
<td>Estimate of soil moisture based on topography</td>
<td>ASTER GDEM v.2</td>
<td>Iverson et al., 1997</td>
</tr>
<tr>
<td>Heat load index*</td>
<td>HLI</td>
<td>unitless</td>
<td>Measurement of heat load considering steepness of slope and aspect</td>
<td>ASTER GDEM v.2</td>
<td>McCune and Keon, 2002</td>
</tr>
<tr>
<td>Landform/slope curvature*</td>
<td>curvature</td>
<td>unitless</td>
<td>Index of concavity/convexity</td>
<td>ASTER GDEM v.2</td>
<td>Bolstad and Lillesand, 1992; McNab, 1993, 1989</td>
</tr>
<tr>
<td>Compound topographic index*</td>
<td>CTI</td>
<td>unitless</td>
<td>Steady state wetness index</td>
<td>ASTER GDEM v.2</td>
<td>Gessler et al., 1995; Moore et al., 1993</td>
</tr>
<tr>
<td>Surface relief*</td>
<td>relief</td>
<td>unitless</td>
<td>Measure of rugosity</td>
<td>ASTER GDEM v.2</td>
<td>Pike and Wilson, 1971</td>
</tr>
<tr>
<td>Roughness*</td>
<td>roughness</td>
<td>unitless</td>
<td>Measure of surface roughness</td>
<td>ASTER GDEM v.2</td>
<td>Blaszczynski, 1997; Riley et al., 1999</td>
</tr>
<tr>
<td>Hierarchical slope position*</td>
<td>HSP</td>
<td>unitless</td>
<td>Relative topographic exposure</td>
<td>ASTER GDEM v.2</td>
<td>Murphy et al., 2010</td>
</tr>
<tr>
<td>Distance to rivers*</td>
<td>dtr</td>
<td>Meters</td>
<td>Euclidean distance between a cell and nearest river</td>
<td>River Shapefile</td>
<td>ArcMap 10.2.2</td>
</tr>
</tbody>
</table>

Table 1: Biophysical predictor variables evaluated for use in modeling habitat suitability for the Seringbara communities. After performing a correlation analysis, this initial set of 17 variables was reduced to 12 for use in the final model (marked with *).
3.4 Modeling Technique

To map suitable chimpanzee habitat and analyze biophysical variables contributing to suitability, I used Maxent 3.3.3 software based on the maximum entropy framework (Phillips et al., 2004). Maxent estimates relative probability of species presence given data on occurrence and user selected predictor variables (Franklin, 2010; Phillips et al., 2006) (Figure 3). Maxent has been shown to perform well with presence-only data and frequently outperforms other SDM methods (Elith et al., 2006; Elith et al., 2011; Wilson et al., 2013). The result is a best-fit model classifying locations in the study area according to probability of presence (0 to 1, with 1 indicating highest probability of presence). The model’s predictive performance is evaluated using the area under the receiver operating characteristic curve (AUC). AUC was chosen over other evaluation measures because it does not require an arbitrary selection of a threshold (Phillips et al., 2006). For presence only data, AUC describes the probability that the model scores a presence site higher than a background site (Phillips et al., 2009). An AUC of 1 indicates perfect predictive power and an AUC of 0.5 indicates random prediction. A model with a high AUC, such as 0.70, indicates that there is a greater than random chance that a randomly selected presence site will be given a higher value than a randomly selected background site (Elith et al. 2006). In other words, a model with a high AUC, has more discriminative power. A k-fold cross validation procedure was replicated 10 times to obtain an average AUC value for the final model (Dormann et al., 2013; Kumar et al., 2014; Wich et al., 2012). Additionally, Maxent was used to generate response curves showing the relationship between each predictor variables and predicted
probability of chimpanzee presence and the permutation importance was report for each variable. Permutation importance is a measure of how AUC changes when a variable is removed from the model and it is not sensitive to the order variables are put into the model (Songer et al., 2012; Wilson et al., 2013).

Figure 3 Logic model representing the model inputs used to create a habitat suitability model for the Seringbara communities.

The model was projected beyond the study area to better assess chimpanzee habitat suitability within the larger landscape. The extent, referred to as the Great Nimba Landscape for this thesis, includes the majority of the Nimba Mountain range in Guinea, Liberia and Côte d’Ivoire, as well as the regions surrounding the a few of the closest villages to the study site and an iron ore mining site (Figure 4). The total area of the
Greater Nimba Landscape is 992 km$^2$. By including these villages, namely Bossou, Seringbara, Nyon, and Zuoguepo, and their near surroundings, the model is better able to capture the landscape heterogeneity of the region and its influence on habitat suitability beyond the protected area. It is important to note a few limitations of projecting, or transferring, a model into a geographic region where data were not collected (Warren and Seifert, 2011). One issue in model transferability is the difference in predictor variable ranges between the sampled area (i.e., study area in this study) and the area into which the model is projected (i.e., Greater Nimba Landscape). If the ranges in the sampled region are narrower, it can cause the response curves to be truncated (Randin et al., 2006). In addition, transferring a model can reduce the model’s predictive ability in the new region (Eger et al., 2016). For this reason, the results from the study should be interpreted carefully while keeping these limitations in mind.
Since absence data were not available, a maximum of 10,000 background points were randomly generated to represent the availability and range of environmental conditions within the study area (Wilson et al., 2013). A minimum-convex polygon around the occurrence points was created to restrict background point generation to only the area covered while collecting data in the field. This ensures that sampling of background points is restricted to the same region from which occurrence points were collected and helps account for sampling bias (Phillips et al., 2009).
As mentioned above, the final Maxent output is a gradient model classifying each pixel according to probability of presence or habitat suitability. In many cases, SDM are converted to binary models, delineating suitable versus unsuitable habitat, which are used by conservationists and land managers (Fourcade et al., 2014; Escalante et al., 2013). Reclassification to create a binary model requires the identification of a threshold, above which a location is considered suitable for a species (Liu et al., 2005). There is not a single method for threshold selection that is better than all others regardless of the species or study objective (Liu et al., 2005). For this study, I reclassified the final model output to create binary maps of habitat suitability for the Seringbara chimpanzees based on three commonly used threshold selection approaches: minimum training presence, 10 percentile training presence, and equal training sensitivity and specificity (Escalante et al., 2013; Fourcade et al., 2014; Norris, 2014; Pearson et al., 2007). The purpose of these binary maps was to visually and quantitatively assess the amount of suitable and unsuitable habitat for the Seringbara chimpanzees in the Greater Nimba Landscape, while also emphasizing the importance of carefully choosing a threshold approach.
4. RESULTS

In evaluating correlation between variables, the following pair of variables were highly correlated ($|r| > 0.7$): TPI and curvature ($r = 1$), slope and roughness ($r = 0.85$), NDVI and greenness ($r = 0.91$), NDVI and wetness ($r = 0.74$), wetness and greenness ($r = 0.74$), and LCC and wetness ($r = -0.72$) (Appendix D). For each highly correlated pair, the variable retained in the test models was chosen because it had the higher permutation importance when an initial model was run using all variables. Thus, the final model was created using only 12 of the original 17 biophysical variables: NDVI, elevation, HSP, brightness, dtr, aspect, HLI, CTI, IMI, roughness, curvature, and relief (Table 1).

The fit of the final chimpanzee habitat suitability model for the Greater Nimba Landscape, was 0.721 with a standard deviation of 0.023. Models with AUC values greater than 0.70 are considered to have fair discriminative abilities and are ecologically useful (Araujo et al., 2005; Pearce and Ferrier, 2000; Swets, 1988). The resulting map from the final model (Figure 5) highlights areas of highest predicted suitability for chimpanzee habitat. The biophysical variables contributing most to the model, as measured by permutation importance, were NDVI (37.8%), elevation (27.3%), HSP (11.5%), brightness (6.6%), and dtr (5.4%) (Table 2).
Figure 5 The final chimpanzee habitat suitability model showing the distribution of suitable chimpanzee habitat throughout the Greater Nimba Landscape. This is a gradient model displaying habitat suitability on a scale from 0 (low suitability) to 1 (high suitability).

Table 2 Permutation importance of each biophysical predictor variable used in creating the final habitat suitability model.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Permutation importance</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDVI</td>
<td>37.8</td>
</tr>
<tr>
<td>elevation</td>
<td>27.3</td>
</tr>
<tr>
<td>HSP</td>
<td>11.5</td>
</tr>
<tr>
<td>brightness</td>
<td>6.6</td>
</tr>
<tr>
<td>dtr</td>
<td>5.4</td>
</tr>
<tr>
<td>aspect</td>
<td>2.8</td>
</tr>
<tr>
<td>HLI</td>
<td>1.9</td>
</tr>
<tr>
<td>CTI</td>
<td>1.8</td>
</tr>
<tr>
<td>IMI</td>
<td>1.7</td>
</tr>
<tr>
<td>roughness</td>
<td>1.6</td>
</tr>
<tr>
<td>curvature</td>
<td>1.1</td>
</tr>
<tr>
<td>relief</td>
<td>0.5</td>
</tr>
</tbody>
</table>
The Maxent model output includes response curves showing the relationship between the individual biophysical variables of highest permutation importance and probability of chimpanzee presence (i.e., predicted habitat suitability). The spatial distributions for the biophysical variables of highest importance were mapped and displayed above the corresponding response curves (Figure 6). The response curve for NDVI shows a positive relationship between probability of presence and NDVI, as healthy, photosynthetically active vegetation increases, so does the probability of chimpanzee presence (Figure 6A). The response curve for elevation shows that probability of presence is highest between 800m and 1200m (Figure 6B). The response curve for hierarchical slope position indicates that probability of presence fluctuates in mildly exposed areas (hsp values between 0.3 and 0.65), whereas probability of presence is relatively low in valley bottoms and toe slopes (low hsp values) and is lowest in topographically exposed areas, such as cliff faces (high hsp values) (Figure 6C). For brightness, probability of chimpanzee presence peaks at an index value of 0.35 before declining sharply at higher brightness values (Figure 6D). There is a negative relationship between dtr and probability of presence, with a sharp decline in probability of presence for areas farther than 500m from a river (Figure 6E). Response curves and maps for all other biophysical variables used in the final model, can be found in Appendix E.
Figure 6 Plots of the response curves showing the dependence of probability of presence on a given biophysical variable. Each plot represents a Maxent model using only the corresponding variable. The plots are given for the five biophysical variables with highest permutation importance (percent shown on plot). The plots show the average response (red line) and the standard deviation (blue interval around the average). X-axes show the units of the corresponding variable. Y-axes indicate the logistic output. The maps above each response curve illustrate the spatial distribution of the biophysical variable in the Greater Nimba Landscape.
C. Hierarchical Slope Position

![Hierarchical Slope Position](image)

D. Brightness

![Brightness](image)

**Figure 6 Continued**
E. Distance to Rivers

Figure 6 Continued
The final model was reclassified to create three binary models based on different threshold levels: minimum training presence (0.08), 10 percentile training presence (0.33), and equal training sensitivity and specificity (0.46) (Figure 7A-C, respectively). Using a threshold allowed the amount of suitable versus unsuitable habitat to be delineated and quantified within the Greater Nimba Landscape (992 km$^2$) (Table 3). For the minimum training presence threshold (0.08), 42 % of the landscape was classified as suitable and 58 % was classified as unsuitable for the Seringbara chimpanzees. The equal training sensitivity and specificity threshold (0.46) painted a much different picture of the Greater Nimba Landscape, as only 3 % was classified as suitable habitat and 97 % was unsuitable. Similarly, the 10 percentile training presence threshold (0.33) delineated 7 % of the Greater Nimba Landscape as suitable and 93 % as unsuitable. Although binary models can be arbitrary and over simplify the landscape for behaviorally flexible and dynamic species that may not perceive the landscape in binary terms, the ability to identify suitable versus unsuitable habitat can be useful for conservation practitioners (Escalante et al., 2013; Ferrer-Sánchez and Rodríguez-Estrella, 2016; Liu et al., 2005).
Figure 7 The final model output showing the distribution of suitable chimpanzee habitat throughout the Greater Nimba Landscape as a series of binary models of three different threshold values: (A) minimum training presence, (B) 10 percentile training presence, and (C) equal training sensitivity and specificity.

Table 3 The amount of area (km²) within the Greater Nimba Landscape that was delineated as not suitable and suitable based on the assigned threshold value.

<table>
<thead>
<tr>
<th></th>
<th>Minimum training presence: 0.08</th>
<th>10 percentile training presence: 0.33</th>
<th>Equal training sensitivity and specificity: 0.46</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not Suitable</td>
<td>580.38 (58 %)</td>
<td>925.24 (93 %)</td>
<td>957.62 (97 %)</td>
</tr>
<tr>
<td>Suitable</td>
<td>411.87 (42 %)</td>
<td>67.01 (7 %)</td>
<td>34.63 (3 %)</td>
</tr>
</tbody>
</table>
5. DISCUSSION

Data on habitat requirements of chimpanzees are needed for effective management and conservation. Constant advancements in technologies, such as remote sensing and GIS, combined with modeling techniques, such as Maxent, allow researchers to assess the variables influencing habitat suitability for many different species. In this study, I modeled the habitat suitability for the Seringbara chimpanzees in the Greater Nimba Landscape and identified the most important biophysical variables contributing to habitat suitability. The results indicate that elevation, wetness, hierarchical slope position, distance to rivers, and greenness contributed most to predicted habitat suitability.

The most important variable in predicting chimpanzee habitat suitability was NDVI. This index indicates the presence of photosynthetically active vegetation (Campbell and Wynne, 2011). The positive relationship between NDVI and probability of presence suggests that chimpanzees prefer forested areas with dense, healthy vegetation. Studies by Koops et al. (2012) showed that the Seringbara chimpanzees select larger trees with dense leaf cover in primary forests to build nests. In addition, many of the tree species, utilized by the chimpanzees for feeding, are found predominantly in primary forests (e.g., Parkia bicolor, Antiaris africana, and Aningeria altissima). This indicates that the habitat suitability model is in fact modeling the Seringbara chimpanzees’ use of the landscape.
Elevation was the second most important biophysical variable in predicting habitat suitability for the Seringbara chimpanzees. Within the Greater Nimba Landscape, elevation serves as a good proxy for climate and vegetation, as well as anthropogenic disturbance. The villages and cultivated fields surrounding the study site are all located below 700 m. Thus, as elevation increases, so does the distance from anthropogenic disturbance, especially given the protected status of the Nimba Mountains. Moreover, as elevation reaches beyond 1200 m, the landscape is dominated by high altitude grasslands, which may not provide ample resources for chimpanzees (Koops, 2011). The role of anthropogenic disturbance and vegetation in predicting chimpanzee habitat suitability will be discussed further as each of the most important biophysical variables is addressed individually.

HSP was the next most important variable in predicting chimpanzee presence. HSP is a measure of topographic exposure. Exposure can serve as a proxy for temperature and vegetation similar to the other important biophysical features, but it might also relate to the ease of movement through an area. Non-human primates have been found to distinguish between topographic features when traveling. For example, Gregory et al. (2014) found that bearded saki monkeys use ridge tops and slopes near ridges, because it may reduce the energetic cost of travel and/or serve a function in route-based mental mapping. This is yet to be explored for chimpanzees in the Greater Nimba Landscape, but future studies examining the role of topography in chimpanzee movement would contribute greatly to our understanding of their perception and utilization of the landscape.
Another important variable in predicting chimpanzee habitat suitability was the tasseled cap brightness index. As brightness values increase it indicates an increase in open canopy and an increase in bare ground (Campbell and Wynee, 2011; Cohen and Goward, 2004; Cohen et al., 1995). Cohen et al. (1995) showed that closed forest stands tend to have moderate brightness values. Previous studies from other chimpanzee research sites indicate that mature, closed forests are preferred by chimpanzees (Torres et al., 2010). Thus, the results from this study, showing highest probability of presence at moderate brightness values support previous findings. Nevertheless, caution must be taken when interpreting brightness values, because this index is responsive to topographic variation in addition to forest condition (Cohen and Goward, 2004). For example, in our study site, some of the high savannah areas have very low brightness values despite very minimal canopy cover (Figure 6D). Other very similarly vegetated savannah regions have much higher brightness value. Thus the low brightness value in some high savannah areas might be explained by the steepness of the terrain and the incidence angle of the radar from the satellite collecting the image (Cohen et al., 1995).

Habitat suitability is also affected by the proximity of an area to the nearest river. As distance increases, the probability of chimpanzee presence decreases. This biophysical variable may serve as a proxy for vegetation (Hickey et al., 2013; Koops, 2011). In evaluating the distribution of dtr throughout the Greater Nimba Landscape (Figure 6D), many of the areas that are more than 500 m from rivers are in the high savannah areas of the Nimba Mountains or in areas outside of the Mt. Nimba SNR, where the terrain is a bit flatter and rivers are more dispersed. Riverine areas may also
provide food resources not available elsewhere in the landscape (Koops, personal communication).

The behavioral plasticity and ecological flexibility of chimpanzees has been recorded at numerous sites across Africa and it has even been shown that chimpanzees sometimes thrive in anthropogenically disturbed areas (Bryson-Morrison et al., 2016; Hockings and McLennan, 2012; McCarthy et al., 2017). The limit to chimpanzees’ behavioral flexibility is not known, but the problems arising from human-chimpanzee conflict have been well studied. As chimpanzees and humans become increasingly reliant on the same land for resources, the conflict between the two will also increase and the rate of disease transmission is likely to rise (Humle, 2011; Köndgen et al., 2008; Leendertz et al., 2016; Pusey et al., 2008). At other sites, effective measures have been put in place to mitigate human-great ape conflict. In Uganda and Rwanda, buffer zones planted with tea seem to effectively discourage chimpanzees from crossing into cultivated areas (Hockings and Humle, 2009). Nevertheless, what is effective at one site may be neither effective nor feasible at other locations. Solutions to human-chimpanzee conflict must be specific to the landscape, the culture and customs of local residents, and to each chimpanzee community (Hockings and Humle, 2009).

The final model illustrates the isolation of high suitability areas within the Greater Nimba Landscape. The areas of highest predicted habitat suitability for the Seringbara chimpanzees are located almost entirely within the Nimba mountain range. This is highlighted in the binary classification of the habitat suitability map into areas of suitable and not suitable habitat based on a threshold (Figure 7). Additionally, within the
Nimba mountain range itself these high suitability areas are fragmented by terrain features such as high ridgelines, and anthropogenic disturbance such as the iron-ore mining concession in the NE region of the Nimba mountain range. Thus, not only are the Seringbara chimpanzees isolated from other chimpanzee communities outside of the Mt. Nimba SNR, they are at risk of becoming isolated from other communities within the Mt. Nimba SNR. Isolation and fragmentation of suitable habitat does not facilitate gene flow between groups and can lead to further decline in chimpanzee populations in the region.

Because maintaining viable, healthy chimpanzee populations requires chimpanzees to move between communities, the creation of corridors is one solution to restoring connectivity. One of the current efforts in the Greater Nimba Landscape is the Green Corridor Project. This project was established in 1997 with the aim of connecting chimpanzee populations in Bossou with those in the Nimba Mountains by planting trees (species consumed by chimps) in the savannah between them (Matsuzawa et al., 2011). Despite difficulties with fires, the Green Corridor Project has made and continues to make progress. One sign of this progress was the video recording of two male chimpanzees travelling into the corridor and the use of the corridor by monkeys (“The Green Corridor Project”, 2017). The project is ongoing and technologies such as remote sensing and modeling may prove very useful for monitoring and expanding the corridor.

Another key aspect to the Green Corridor Project is the involvement of the local communities and government agencies. Since the establishment of long term chimpanzee research in the region, KUPRI has performed local outreach initiatives,
employed community members as field assistants, worked with government agencies, and tried to inspire the local communities to engage in conservation issues. For conservation to succeed, continued efforts must be made to not only identify and protect key habitat but also to protect and benefit the livelihoods of the people living in the region. Future research must keep this in mind while seeking new ways to maintain, restore, and connect areas of suitable chimpanzee habitat.
6. CONCLUSIONS

In conclusion, this study demonstrates that species distribution modeling is a useful tool for identifying suitable chimpanzee habitat within montane rainforests. More specifically, the results indicate that (1) biophysical variables quantifying the landscape structure within the Greater Nimba Landscape were useful predictors of chimpanzee presence, (2) elevation, wetness, hierarchical slope position, distance to rivers, and greenness had the greatest influence on habitat suitability for the Seringbara chimpanzees in the region, (3) suitable chimpanzee habitat within the Greater Nimba Landscape is fairly isolated and does not make up a large portion of the landscape, and (4) enforcing the protection of the Mt. Nimba SNR and adjacent areas is vital to supporting chimpanzee populations.

Conservation efforts can use the methods and results from this study and expert knowledge of the region to more effectively and efficiently promote the long-term viability of chimpanzees in the region. These efforts should also keep in mind the limitations of this study. For instance, because the model was projected into a novel geographic area where data on chimpanzee occurrences were not collected, the response curves may not encompass the full range of variables. In other words, interpretation of how the probability of chimpanzee presence will respond to a predictor variable beyond the range of the collected data is unknown. This is a limitation for many predictive SDM studies, yet there are few generally applicable solutions (Eger et al., 2016; Elith et al., 2010; Peterson et al., 2007; Zurrell et al., 2012). Future research might be able to mitigate
this by surveying more areas within the greater landscape so the sampling effort is more representative of the range in predictor variables. Moreover, given that vegetation and proxies for vegetation greatly influence chimpanzee habitat suitability, this model might be improved with data that is better able to capture vegetation characteristics at a higher spatial resolution.
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Wilson, J.W., Sexton, J.O., Todd Jobe, R., Haddad, N.M., 2013. The relative
contribution of terrain, land cover, and vegetation structure indices to species
APPENDIX A

R SCRIPT – SPATIAL FILTERING

Script used to systematically sample the occurrence points for use in the final model. The first portion of the script simply identifies points with the same coordinates (spatial duplicates) and retains only one occurrence point at any given location. This resulted in N=1346 occurrence points that were used to generate a model that was compared to models generated using other techniques for reducing sampling bias. Once duplicates were removed, the script proceeds to minimize sampling bias through systematic sampling by placing a grid (30 m resolution) over the study area and randomly selects one occurrence point from each grid cell. The systematic sampling technique resulted in N=947 occurrence points that were used to generate a model that was compared to models generated using other techniques for reducing sampling bias. After comparing models generated from different bias reduction techniques, the systematic sampling techniques was used to generate the final model.

```r
library(dismo)
library(rgdal)
library(rJava)
library(raster)
library(maptools)

occur <- read.csv(“Maxent_occurrence_all.csv”, header = T)
View(occur)
dim(occur)

### Remove records with NAs ###
is.na(occur)
occur <- na.omit(occur)
write.csv(occur, “occur_all.csv”)
```
### Remove duplicate records – i.e. points recorded at same location ###
dups <- duplicated(occur)
sum(dups)
occur_dups <- occur[!dups, ]
summary(occur_dups)
View(occur_dups)
write.csv(occur_dups, “occur_dups.csv”)

### Sampling Bias ###
proj <- “+proj=utm +zone=29 +ellps=WGS84 +datum=WGS84 +units=m +no_defs”
dup_pts <- SpatialPointsDataFrame(coords = occur_dups[, 2:3], proj4string =
CRS(“+proj=utm +zone=29 +ellps=WGS84 +datum=WGS84 +units=m +no_defs”),
data = occur_dups)
r <- raster(dup_pts)
extentI <- dup_pts
resI <- 0.00027202972
r <- extend(r, extentI+1)

dupPoly <- rasterToPolygons(r, na.rm = FALSE)
plot(dupPoly)
plot(dup_pts, add = T)

dup_filter1 <- gridSample(dup_pts, r, n=1)
dup_filter1
plot(dupPoly)
points(dup_pts, col = “blue”)
points(dup_filter1, col = “red”, add = T)

write.csv(dup_filter1, “dup_filter1.csv”)
writeOGR(dupPoly, “.”, “dupPoly”, driver = “ESRI Shapefile”)

The following script was used to minimize sampling bias by spatially filtering
occurrence points using a proximity/critical distance at three different levels: 30 m, 40
m, and 50 m. This technique minimizes bias by retaining occurrence points that are not
closer than the specified critical distance. If two points are within the critical distance,
then only a single point is retained. This filtering technique, referred to as proximity
filtering, resulted in N=733 occurrence points at 30 m, N=645 at 40 m, and N=577 at 50
m that were used to generate three separate models. These three models were compared to models generated using other techniques for reducing sampling bias.

```r
SpatialFilter <- function(xy, dist, mapUnits = F) {
  ## NOTE: Probably should always work with data in geographic projection with WGS84 datum for this function
  #mapUnits=T
  #xy=monrst.spdf
  #dist=1
  ## Code by Pascal Title, Univ. Michigan, Ecology and Evol. Biology
  ## From: http://stackoverflow.com/questions/22051141/spatial-filtering-by-proximity-in-r
  #xy can be either a SpatialPoints or SPDF object, or a matrix
  # calculate desired buffer distance around presence points
  #dist is in km if mapUnits=F, in mapUnits otherwise
  if (!mapUnits) {
    d <- spDists(xy,longlat=T)
  }
  if (mapUnits) {
    d <- spDists(xy,longlat=F)
  }
  diag(d) <- NA
  close <- (d <= dist)
  diag(close) <- NA
  closePts <- which(close,arr.ind=T)
  discard <- matrix(nrow=2,ncol=2)
  if (nrow(closePts) > 0) {
    while (nrow(closePts) > 0) {
      if (!(paste(closePts[1,1],closePts[1,2],sep='_') %in% paste(discard[,1],discard[,2],sep='_'')) & !(paste(closePts[1,2],closePts[1,1],sep='_') %in% paste(discard[,1],discard[,2],sep='_'))) {
        discard <- rbind(discard, closePts[1,])
        closePts <- closePts[-union(which(closePts[,1] == closePts[1,1]), which(closePts[,2] == closePts[1,1])),]
      }
    }
    discard <- discard[complete.cases(discard),]
    return(xy[-discard[,1],])
  }
  if (nrow(closePts) == 0) {
    return(xy)
  }
```
library(dismo)
library(maptools)

# Read in User Defined Functions
source("SpatialFilter_Function.R")

# Load needed packages of raster, rgdal, dismo, rjava, and maptools (printouts not shown)
library(dismo)
library(maptools)

### Set projection ###
CRS.WGS84 <- CRS("+init=epsg:4326")

occur_dups.df <- data.frame(read.csv("occur_dups.csv", header = T))
View(occur_dups.df)

### Convert point data.frame to SpatialPointsDataFrame ###
### First, specify xy coordinates ###
xy <- occur_dups.df[,c("Longitude", "Latitude")]
### Create spatial points data fraame ###
occur_dups.spdf <- SpatialPointsDataFrame(ords=xy, data=occur_dups.df, proj4string=CRS.WGS84)

### Specify buffers for spatial thinning for presence points – in km ###
SpatFiltBuff30 <- 0.03
SpatFiltBuff40 <- 0.04
SpatFiltBuff50 <- 0.05

### 30m – Spatially filter presence points using a proximity/critical distance of 30 m ###
occur_prox30.spdf <- SpatialFilter(occur_dups.spdf, dist=SpatFiltBuff30, mapUnits=F)
View(occur_prox30.spdf)
plot(occur_prox30.spdf, col='blue')

### Project the filtered data points into WGS1984 UTM Zone 29N ###
occur_prox30_utm <- spTransform(occur_prox30.spdf, CRS("+init=epsg:32629"))
summary(occur_prox30_utm)

### Write to csv and ESRI Shapefile ###
write.csv(occur_prox30.spdf, "occur_prox30.csv")
write.csv(occur_prox30_utm, "occur_prox30_utm.csv")
writeOGR(occur_prox30_utm, ".", "occur_prox30_utm", driver = "ESRI Shapefile")

### 40m – Spatially filter presence points using a proximity/critical distance of 40 m ###

occur_prox40.spdf <- SpatialFilter(occur_dups.spdf, dist=SpatFiltBuff40, mapUnits=F)
View(occur_prox40.spdf)
plot(occur_prox40.spdf, col='blue')

### Project the filtered data points into WGS1984 UTM Zone 29N ###

occur_prox40_utm <- spTransform(occur_prox40.spdf, CRS("+init=epsg:32629"))
summary(occur_prox40_utm)

### Write to csv and ESRI Shapefile ###

write.csv(occur_prox40.spdf, "occur_prox40.csv")
write.csv(occur_prox40_utm, "occur_prox40_utm.csv")
writeOGR(occur_prox40_utm, ".", "occur_prox40_utm", driver = "ESRI Shapefile")

### 50m – Spatially filter presence points using a proximity/critical distance of 50 m ###

occur_prox50.spdf <- SpatialFilter(occur_dups.spdf, dist=SpatFiltBuff50, mapUnits=F)
View(occur_prox50.spdf)
plot(occur_prox50.spdf, col='blue')

### Project the filtered data points into WGS1984 UTM Zone 29N ###

occur_prox50_utm <- spTransform(occur_prox50.spdf, CRS("+init=epsg:32629"))
summary(occur_prox50_utm)

### Write to csv and ESRI Shapefile ###

write.csv(occur_prox50.spdf, "occur_prox50.csv")
write.csv(occur_prox50_utm, "occur_prox50_utm.csv")
writeOGR(occur_prox50_utm, ".", "occur_prox50_utm", driver = "ESRI Shapefile")

**SPATIAL FILTERING RESULTS**

Five different spatial filtering techniques to account for sampling bias within the data collection process were compared to ascertain which method retained a high model AUC while also maintaining a high number of occurrence points. I used R version 3.2.2
to apply the spatial filtering techniques. Code for each technique is located below. The results from the different methods are displayed in Table A.1. The set of occurrence points from systematic spatial filtering (dup_filter1_proj), which overlays a 30m resolution grid over the study area and randomly retains one point per grid cell, was used in the final model discussed in the main text.

<table>
<thead>
<tr>
<th>Name</th>
<th>Source</th>
<th>Function</th>
<th>Count</th>
<th>Maxent AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>occur_dups</td>
<td>R</td>
<td><code>!duplicated()</code></td>
<td>1386</td>
<td>0.753</td>
</tr>
<tr>
<td>dup_filter1_proj</td>
<td>R (csv) GIS (display xy)</td>
<td>gridSample()</td>
<td>947</td>
<td>0.721</td>
</tr>
<tr>
<td>occur_prox30</td>
<td>R</td>
<td>spatialFilter()</td>
<td>733</td>
<td>0.735</td>
</tr>
<tr>
<td>occur_prox40</td>
<td>R</td>
<td>spatialFilter()</td>
<td>645</td>
<td>0.73</td>
</tr>
<tr>
<td>occur_prox50</td>
<td>R</td>
<td>spatialFilter()</td>
<td>577</td>
<td>0.717</td>
</tr>
</tbody>
</table>

Table A.1 Comparison of model results for different spatial filtering methods
APPENDIX B

This appendix contains the methods and results for the land cover classification used in the habitat suitability model.

**Methods**

Landsat 8 satellite imagery data was obtained from December 26, 2013 (Figure B.1). Landsat 8 imagery is acquired with an Operational Land Imager sensor (OLI) and Thermal Infrared Sensor (TIRS). Bands 2 through 7 were stacked from the OLI sensor with a 30 m resolution. A shapefile of the study area was created in ArcMap 10.2.2 and subsequently used to subset the stacked image in ENVI 5.0.2 before performing a series of land cover classifications. The first classification performed on the original stacked image was an unsupervised ISODATA classification. The minimum and maximum classes were 5 and 25, respectively, the maximum number of iterations was 10, and all other parameters were left at the defaults. Secondly, a series of supervised classifications were performed including: maximum likelihood, minimum distance, mahalanobis, and parallelepiped. Regions of interest (ROIs) were identified based on field data collected from 2012 to 2014 and visual inspection of Landsat imagery. The ROIs were assessed for normality and separability. Five land cover classes were identified: dense forest, mixed forest, bare ground, village, and savannah. Dense forests consist of mostly primary, undisturbed forest. Mixed forests are mostly secondary, disturbed forests with less dense vegetation and less canopy cover. Bare ground includes areas cleared
(illegally), sparsely vegetated grasslands, and bare rock. Savannah consists of very dense, tall grass areas lacking trees. The village class includes buildings, huts, and other anthropogenic structures interspersed with bare ground. Accuracy assessments were run in ENVI 5.0.2 to determine how well each classification method distinguished between land cover classes. The methods are illustrated as a flowchart in Figure B.2.

Results

The unsupervised classification was unsuccessful and did not distinguish the spectral differences between all land cover classes, namely village and savanna (Figures B.3 and B.4). The accuracy of multiple supervised classification methods was assessed to find the most appropriate method to use for producing an accurate map of land cover classes in the region. The maximum likelihood and minimum distance had the highest overall accuracies, 90.88% and 90.78% respectively, and highest kappa coefficients, 0.8653 and 0.8658 respectively (Tables B.1-B.2). Because the difference between the overall accuracy and kappa coefficient for the maximum likelihood and minimum distance were only slightly different, the user’s accuracy for different land cover classes was taken into consideration before selecting a method to create the map for the final habitat suitability model. Other studies have shown that primate behavior is affected by human disturbance, such as distance to villages, so accuracy for this class was deemed important (Hickey et al., 2013). Although the user’s accuracy for most of the land cover classes was high for both classification methods, the village class had a much lower
user’s accuracy for the maximum likelihood classification (Table B.3). Thus, the minimum distance classification method was chosen for use in the final model.

Figure B.1. Landsat 8 image of the Greater Nimba Landscape from December 26, 2013.
Chimpanzee occurrence data was collected in the Mt. Nimba SNR from 2012 to 2014. Occurrence data includes records of the habitat type where the data was found.

**IMAGE ACQUISITION**
Download Landsat 8 image of the Greater Nimba Landscape

**IMAGE SUBSETTING**
Create a shapefile of the study area.
Use the shapefile to subset the Landsat 8 image.

**UNSUPERVISED & SUPERVISED CLASSIFICATION**
Perform ISODATA unsupervised classification on the original Landsat 8 stacked image.
Perform various supervised classification methods by creating ROI’s using chimpanzee occurrence data and habitat associations

**CLASSIFICATION ACCURACY ANALYSIS**
Assess the thematic accuracy of the classification for each image.

**CLASSIFICATION MAP CREATION**
Create a clear, usable map showing the habitat/vegetation classifications for the Greater Nimba Landscape

**Figure B.2.** Flowchart of methods for performing land cover classifications.
Figure B.3. The ISODATA unsupervised classification of the Greater Nimba Landscape.

Figure B.4. The ISODATA unsupervised classification, conversion from spectral classes to five land cover classes for the Greater Nimba Landscape.
Figure B.5. Minimum distance supervised classification from the Greater Nimba Landscape.

Table B.1. The confusion matrix for the accuracy assessment from the minimum distance supervised classification in the Greater Nimba Landscape. Highlighted tiles represent the ability of the supervised classification to accurately depict the land cover type from the spectral classes. Overall accuracy was 90.78% and kappa coefficient was 0.8653.

<table>
<thead>
<tr>
<th>Class</th>
<th>Bare Ground</th>
<th>Savannah</th>
<th>Village</th>
<th>Dense Forest</th>
<th>Mixed Forest</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare Ground</td>
<td>96.79</td>
<td>0.96</td>
<td>3.4</td>
<td>0</td>
<td>0.76</td>
<td>19.68</td>
</tr>
<tr>
<td>Savannah</td>
<td>1.81</td>
<td>96.4</td>
<td>3.4</td>
<td>0</td>
<td>4.16</td>
<td>9.5</td>
</tr>
<tr>
<td>Village</td>
<td>1.31</td>
<td>2.16</td>
<td>93.2</td>
<td>0</td>
<td>0</td>
<td>3.19</td>
</tr>
<tr>
<td>Dense Forest</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>97.82</td>
<td>25.11</td>
<td>50.06</td>
</tr>
<tr>
<td>Mixed Forest</td>
<td>0.1</td>
<td>0.48</td>
<td>0</td>
<td>2.18</td>
<td>69.97</td>
<td>17.58</td>
</tr>
<tr>
<td>Total</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>
Table B.2. The confusion matrix for the accuracy assessment from the maximum likelihood supervised classification in the Greater Nimba Landscape. Highlighted tiles represent the ability of the supervised classification to accurately depict the type of habitat from the spectral classes. Overall accuracy was 90.88% and kappa coefficient was 0.8658.

<table>
<thead>
<tr>
<th>Class</th>
<th>Bare Ground</th>
<th>Savannah</th>
<th>Village</th>
<th>Dense Forest</th>
<th>Mixed Forest</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare Ground</td>
<td>93.78</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>18.72</td>
</tr>
<tr>
<td>Savannah</td>
<td>0</td>
<td>97.84</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>8.18</td>
</tr>
<tr>
<td>Village</td>
<td>6.12</td>
<td>2.16</td>
<td>100</td>
<td>0.04</td>
<td>0.17</td>
<td>4.41</td>
</tr>
<tr>
<td>Dense Forest</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>99.6</td>
<td>31.64</td>
<td>52.4</td>
</tr>
<tr>
<td>Mixed Forest</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0.36</td>
<td>68.19</td>
<td>16.29</td>
</tr>
<tr>
<td>Total</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

Table B.3. Producer’s and User’s accuracy for the supervised minimum distance and maximum likelihood classifications for the Greater Nimba Landscape.

<table>
<thead>
<tr>
<th>Class</th>
<th>Producer (Min. Dist)</th>
<th>Producer (Max. Likeli.)</th>
<th>User (Min. Dist)</th>
<th>User (Max. Likeli.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare Ground</td>
<td>96.79</td>
<td>93.78</td>
<td>98.17</td>
<td>100</td>
</tr>
<tr>
<td>Savannah</td>
<td>96.4</td>
<td>97.84</td>
<td>84.81</td>
<td>100</td>
</tr>
<tr>
<td>Village</td>
<td>93.2</td>
<td>100</td>
<td>86.16</td>
<td>66.82</td>
</tr>
<tr>
<td>Dense Forest</td>
<td>97.82</td>
<td>99.6</td>
<td>88.15</td>
<td>85.74</td>
</tr>
<tr>
<td>Medium Forest</td>
<td>69.97</td>
<td>68.19</td>
<td>94.07</td>
<td>98.89</td>
</tr>
</tbody>
</table>

Table B.4. Commission and omission errors for the supervised minimum distance and maximum likelihood classifications for the Greater Nimba Landscape.

<table>
<thead>
<tr>
<th>Class</th>
<th>Commission (Min. Dist)</th>
<th>Commission (Max. Likeli.)</th>
<th>Omission (Min. Dist)</th>
<th>Omission (Max. Likeli.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare Ground</td>
<td>1.83</td>
<td>0</td>
<td>3.21</td>
<td>6.22</td>
</tr>
<tr>
<td>Savannah</td>
<td>15.19</td>
<td>0</td>
<td>3.6</td>
<td>2.16</td>
</tr>
<tr>
<td>Village</td>
<td>13.84</td>
<td>33.18</td>
<td>6.8</td>
<td>0</td>
</tr>
<tr>
<td>Dense Forest</td>
<td>11.85</td>
<td>14.26</td>
<td>2.18</td>
<td>0.4</td>
</tr>
<tr>
<td>Medium Forest</td>
<td>5.93</td>
<td>1.11</td>
<td>30.03</td>
<td>31.81</td>
</tr>
</tbody>
</table>
APPENDIX C

R SCRIPT – HSP

The following is the script used to derive the raster quantifying hierarchical slope position (HSP) within the Greater Nimba Landscape.

```r
### Hierarchical Slope Position
# description Calculates a hierarchical scale decomposition of topographic position index
#
# param x Object of class raster (requires integer raster)
# param min.scale Minimum scale (window size)
# param max.scale Maximum scale (window size)
# param inc Increment to increase scales
# param win Window type, options are "rectangle" or "circle"
# param normalize Normalize results to 0-1 scale (FALSE | TRUE)
#
# return raster class object
#
# note
# if win = "circle" units are distance, if win = "rectangle" units are number of cells
#
# references
#
# author Jeffrey S. Evans <jeffrey_evans@@tnc.org>
#
# examples
# library(raster)
# setwd("D:/TMP")
# r <- raster("elev.img")
# hsp27 <- hsp(r, 3, 27, 4, scale = TRUE)
# hsp1000 <- hsp(r, 90, 1000, inc=120, win="circle")
# plot(hsp27)
#
# export
hsp <- function(x, min.scale = 3, max.scale = 27, inc = 4, win = "rectangle",
normalize = FALSE) {
  scales = rev(seq(from=min.scale, to=max.scale, by=inc))
  for(s in scales) {
```

72
if( win == "circle") {
    if( min.scale < res(x)[1] * 2)
        stop("Minimum resolution is too small for a circular window")
    m <- focalWeight(x, s, type=c('circle'))
    m[m > 0] <- 1
} else {
    m <- matrix(1, nrow=s, ncol=s)
}

cat("Calculating scale:", s, "\n")
scale.r <- x - focal(x, w=m, fun=mean)
if( s == max(scales) ) {
    scale.r.norm <- 100 * ( (scale.r - cellStats(scale.r, stat="mean") /
        cellStats(scale.r, stat="sd") ) )
} else {
    scale.r.norm <- scale.r.norm + 100 * ( (scale.r - cellStats(scale.r, stat="mean")
        / cellStats(scale.r, stat="sd") )
}

if(normalize == TRUE) {
    scale.r.norm <- (scale.r.norm - cellStats(scale.r.norm, stat="min")) /
        (cellStats(scale.r.norm, stat="max") -
        cellStats(scale.r.norm, stat="min"))
}
return(scale.r.norm)

### Run HSP function on the GDEM of the study area ###
library(raster)
r <- raster("astgdem.tif")
hsp27 <- hsp(r, normalize = T)
plot(hsp27)
writeRaster(hsp27, filename = "hsp27_2.tif")
APPENDIX D

This appendix contains the correlation matrix for the 17 biophysical variables used in Maxent to create a chimpanzee habitat suitability model. Correlations were calculated in ArcMap 10.2.2. Red highlights indicate correlations greater than 0.7 or less than -0.7. The table is symmetric and the correlation between a variables and itself is always 1. Thus, the upper part of the table and the diagonal are blank for easier reading.
Table D.1 Correlation matrix for the suite of 17 biophysical variables originally considered for use in the habitat suitability model for the Seringbara Chimpanzees within the Greater Nimba Landscape.

<table>
<thead>
<tr>
<th>Variable</th>
<th>dtr</th>
<th>NDVI</th>
<th>brightness</th>
<th>TPI</th>
<th>slope</th>
<th>relief</th>
<th>IMI</th>
<th>HLI</th>
<th>curve</th>
<th>CTI</th>
<th>aspect</th>
<th>wetness</th>
<th>greenness</th>
<th>HSP</th>
<th>elevation</th>
</tr>
</thead>
<tbody>
<tr>
<td>dtr</td>
<td></td>
<td>-0.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NDVI</td>
<td>-0.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>brightness</td>
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<td>-0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TPI</td>
<td>0.05</td>
<td>-0.02</td>
<td>-0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>slope</td>
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<td>0.07</td>
<td>-0.09</td>
<td>0.01</td>
<td></td>
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APPENDIX E

RESPONSE CURVES AND MAPS OF BIOPHYSICAL VARIABLES

The response curves and maps for the biophysical variables not discussed in detail in the main text are displayed below (Figure E.1). Each response curve shows the dependence of probability of presence on a given biophysical variable and represents a Maxent model using only the corresponding variable. Permutation importance (percent) is displayed on each plot. The plots show the average response (red line) and the standard deviation (blue interval around the average). X-axes show the units of the corresponding variable. Y-axes indicate the logistic output for probability of presence. The maps above each response curve illustrate the spatial distribution of the biophysical variable in the Greater Nimba Landscape.
Figure E.1 Response curves and maps of the biophysical variables.
Figure E.1 Continued
Figure E.1 Continued
G. Relief

**Figure E.1 Continued**